Timothy D. Paine · François Lieutier
Editors

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Chapter 1
Introduction

Timothy D. Paine and François Lieutier

Abstract Mediterranean climates are characterized by mild wet winters and warm dry summer conditions. They can be found around the Mediterranean Sea and on portions of the southwest coasts of North America, South America, Australia, and Africa. All of the Mediterranean climate zones have been recognized as centers of endemism and members of the specialized communities may be at significant risk of extinction. The plant communities in regions have converged on similar dense evergreen sclerophyllous vegetation types. The insect and disease issues are often specific to the Mediterranean forest systems rather than shared with the temperate forests. In addition to the specific native insects and diseases, the forests are also subject to the invasion of exotic species. The forests are also at risk from high degrees of human activity, including changing patterns of forest fires, land management activities, intensive plantation forestry using introduced timber species from other Mediterranean climate zones, and atmospheric deposition. Combined with elements of global climate change that may disproportionately affect Mediterranean climate systems, this creates a number of significant management issues that are unique to the Mediterranean forests. This volume is an effort to compile the experiences of leaders of the research communities within the Mediterranean climate zones around the world. The research findings from one part of the world can be applied to new areas or can be used as a foundation for research to address related problems in those areas. It is our goal that the information contained in this volume will contribute to understanding the unique aspects of Mediterranean forest systems and to protecting these critical resources.

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1.1 Mediterranean Climate and Plant Community Characteristics

The Mediterranean climate conditions are unique and are generated by a specific set of geographic features. The climate is characterized by hot dry summers and mild wet winters. Precipitation is concentrated in the 6 month period of the year that includes the winter and may be completely lacking or rare during the summer months. Precipitation averages 25–100 cm annually, occurring primarily as rain with snow in higher elevations (Dallman 1998). This stands in contrast to many temperate or continental climates with that may have either mild or cold subfreezing conditions in the winter and warm summers, but have rainfall throughout the year. The Mediterranean climate zones are all located along the western or southwestern continental edges between 30° and 45° north and south latitude and, with the exception of the Mediterranean Sea, are influenced by cold offshore currents.

There are five regions of the world that can be characterized by Mediterranean climate conditions and these represent approximately 2 % of the land mass of the earth (World Conservation Monitoring Center 1992). Approximately 60 % of the total area with Mediterranean climates occurs around the Mediterranean Sea (DiCastri 1991). The southwestern part of Western Australia and the southern part of South Australia make up 22 % of the total, followed in size by California in the United States and a portion of Baja California Norte in Mexico along the west coast of North America (10 % the total), central Chile along the west coast of South America (5 %) of the total, and the Western Cape of South Africa along the southwest tip of the continent of Africa (3 %) (DiCastri 1991).

The rim of the Mediterranean Sea touches three continents and there are significant differences between the north and south rims. Unlike the other regions, there is no moderating cold ocean current along the Mediterranean basin. North Africa is warmer and drier than the European side, although the Atlantic Ocean does have a moderating effect on temperature west of the Straits of Gibraltar. The plant communities are characterized by sclerophyllous evergreen shrubs and trees. For example, the Maquis plant community is characterized by tall dense evergreen shrubs. The Maquis has ecological equivalents with similar communities in the other Mediterranean regions of the world but the species compositions in all of those communities are very different. Depending on precipitation and temperature patterns, the Mediterranean basin plant communities can vary from low growing and sparse aromatic vegetation on the drier and hotter sites to sclerophyll woodland dominated by oaks to sclerophyll forests that include denser stands of oaks and pines (Dallman 1998). In addition to native pines and oaks, plantations of exotic pines and eucalypts have been established at sites within the climate zone for the production of wood fiber for cellulose and for structural timber.

California has a complex topography that greatly influences the plant communities in the Mediterranean climate regions. As in the Mediterranean basin, many of the low elevation plant communities are characterized by sclerophyllous vegetation

(Munz 1968). Chaparral vegetation, the ecological analog to the Maquis, is composed of dense woody evergreen shrubs that grow up to 2 m tall. Foothills are covered with savannah oak woodlands that include both deciduous and evergreen oak species, many of which are locally endemic. Forest communities range from dense coastal redwood and closed cone pine forests that grow in cool moist conditions to the mixed yellow pine and fir conifer forests that grow on the western slope of the Sierra Nevada Mountains. Although there are significant efforts at replanting native forest trees following harvest or wildfires, there has been very little emphasis of establishing plantations of exotic hardwood or conifer species.

The Mediterranean region of Central Chile is bounded by the Atacama Desert in the north, the Pacific Ocean to the west, the Andes Mountains to the east, and the Drake Passage to the south. The Matorral plant community shares many common characteristics with the sclerophyll California chaparral and the Mediterranean Maquis (Dallman 1998). The sclerophyll woodland and moister forest communities are dominated by deciduous *Nothophagus* species (southern beech), evergreen *Araucaria*, and alerce or Fitzroy cypress. Dallman (1998) notes that the alerce can grow to 50 m tall, 3 m in diameter, and reach 4000 years of age. In addition to the native forests, there have been extensive plantations of exotic trees, including eucalypts and Monterey pine that have been established in this climate zone.

Mediterranean climates are found in the southwestern part of Western Australia and the southern part of South Australia. Kwongan and mallee shrublands are found along the Indian and Southern Oceans within 100 km of the coast (Dallman 1998). The Kwongan is similar to the Mediterranean Maquis, the Chilean Matorral, or the Californian Chaparral communities in structure and includes many representatives of the Proteaceae. The mallee vegetation is dominated by multi-stem *Eucalyptus*. These shrubland communities grade to *Eucalyptus* woodlands under moister conditions. Dense *Eucalyptus* forests, including Jarrah that can grow up to 30 m in height and Karri that can grow to 75 m in height, can be found in the highest rainfall areas south of Perth. In recent years, there has been some effort in establishing plantations of eucalypts from other parts of Australia on abandoned farm land for timber and cellulose production.

The Western Cape of South Africa is dominated by the fynbos plant community. The community grows on nutrient poor soils and is composed of shrublands that vary greatly in height (Dallman 1998). The Proteaceae are common components of this community. The native forest communities include yellowwood (*Podocarpus latifolius*), stinkwood (*Ocotea bullata*), and ironwood (*Olea capensis*). Like central Chile, extensive plantations of exotic trees have been established in the Western Cape. These include Monterey pine from California, Maritime pine and Aleppo pine from the Mediterranean basin, and eucalypts and *Acacia* from Australia.

Although these areas of the world comprise only a very small proportion of the area of the total land mass of the planet, they are ecologically highly significant. Myers et al. (2000) identified 25 biodiversity hotspots in the world that contain 44 % of all species of vascular plants and 35 % of all species of four groups of terrestrial vertebrates (mammals, birds, reptiles, and amphibians). Many of these species are endemic to these regions of the world, occurring only in these hotspots

(Kier et al. 2009). For example, the Mediterranean basin has 13,000 endemic plant species (Myers et al. 2000). All five of the areas of the world with Mediterranean climates are included on the list of biodiversity hotspots. Consequently, there is a great concern over conservation of the biological resources in the Mediterranean ecosystems.

1.2 Threats to the Mediterranean Forest Systems

The extraordinary high levels of endemism of the plant and animal species associated with Mediterranean ecosystems may increase the risk of extinction of those species. Although there is some range in vulnerability across the five different continental regions, that risk is very high. Malcolm et al. (2006) modeled the risk of extinction across the range of biodiversity hot spots and suggested that all of the regions of the world with Mediterranean climates, with the exception of Central Chile, were exceptionally vulnerable to species extinctions driven by climate change. Global climate change can include both changes in temperature, total precipitation, and annual patterns in precipitation. In addition to the threats posed by global climate change, these areas are also vulnerable to habitat loss due to development associated with human activities. In particular, the Mediterranean basin and Californian regions are subject to very high human population pressures.

Human activities can have direct effects such as land conversion and habitat loss, but there are also less direct effects. Air pollution, including excessive nitrogen loading, can change the interactions between species and local environmental conditions or the competitive interactions among species (Ochoa-Hueso et al. 2011). The air pollution can also affect the susceptibility of plants to herbivory (Eatough Jones et al. 2008; Eatough Jones and Paine 2006). Although most Mediterranean plant communities are adapted to natural wildfires (Dallman 1998), the human activities that increase both fire frequency and fire intensity can have dramatic effects on the plant communities (Goforth and Minnich 2008). These risks increase with increased population size.

Both the native forest systems and the plantation forest systems that are common in many of the Mediterranean climate zones are subject to the threats of environmental change and human activities. They are also subject to the introduction of exotic insects and pathogens (Paine et al. 2011). Many of the plantation forests are established using exotic conifer and angiosperm tree species. The exotic species may have an advantage in the adventive environment because they do not have the community of adapted herbivores they would have in the native range. For example, eucalypts and Monterey pine (*Pinus radiata*) are good examples of trees that have flourished in plantations in adventive environments. However, with the increasing international movement of goods and people, there has been a globalization/ homogenization of communities of key insect pests and diseases on plantation species. Unfortunately, some of these exotic pests and diseases have shifted on to closely related native forest trees which can cause significant problems in natural forest communities. Consequently, the pest communities in the native forests have expanded to include both native and introduced herbivores that must be managed.

The insect and disease issues are often specific to the Mediterranean forest systems rather than shared with the temperate forests. As noted above, the plant communities are different between the temperate and Mediterranean forest communities. The insect and disease communities are either host specific or have different environmental tolerances that limit their distributions to specific habitats. This may be particularly important in the length of time that insects are active throughout the year as well as whether they are active during the cool winter months and aestivate in the summer to avoid the high summer temperatures. *Thaumetopoea pityocampa*, the pine processionary moth feeds in the winter months and undergoes a summer diapause with pupae spending the hot dry period underground (Huchon and Demolin 1970). Similarly, *Tomicus destruens* attacks trees in the fall and the larvae feed under the bark in the winter (Horn et al. 2012).

1.3 Goal of the Volume

This volume is the outcome of the interactions within the International Union of Forestry Research Organizations working party 7.03.14 Entomological Research in Mediterranean Forest Ecosystems. It was clear from the meetings and presentations that there were very common issues that were being addressed across five continents. It was also clear that there were significant benefits derived from sharing information and experiences among the research and production communities in many parts of the world. These benefits included coordination of research, implementation of joint research efforts across different regions of the world, application or adaption of tactics for insect management, and facilitation of biological control efforts among different regions. That is, foreign explorations could be facilitated for new insect pests and successful introductions and establishment of natural enemies in one region could be implemented in different parts of the world as geographic distribution of the pest species continued to expand.

This volume is an effort to compile the experiences of leaders of the research communities within the Mediterranean climate zones around the world. The research findings from one part of the world can be applied to new areas or can be used as a foundation for research to address related problems in those areas. This will enable the research to advance much faster than if it was conducted without the benefit of experience. The chapters that make up the volume address three issues that face all Mediterranean forest systems: native insect pests and diseases of native and plantation forest systems in the different Mediterranean regions, introduced pests and diseases in those same forest systems, and potential impacts of environmental conditions on the interactions of insects and diseases with the Mediterranean forests. Comparisons of the same pest and host are insightful. The same insects or diseases may colonize the same host species, but the context may be very different if the host tree is native to the locale or if it is an introduced species. Consequently, the interactions between the pests and hosts may be different. It is critical to understand what biological or environmental factors contribute to those differences. In addition, species from the native insect or pathogen communities have the potential to be introduced into other parts of the world. An understanding of the interactions that occur in the native range will be very useful for assessing risk and developing effective management approaches in the potential adventive range. It is our goal that the information contained in this volume will contribute to understanding the unique aspects of Mediterranean forest systems and to protecting these critical resources.

References

Dallman PR (1998) Plant life in the world's Mediterranean climates. University of California Press, Berkeley

DiCastri F (1991) An ecological overview of the five regions with a Mediterranean climate. In: Groves RH, DiCastri F (eds) Biogeography of Mediterranean invasions. Cambridge University Press, Cambridge, pp 3–16

Eatough Jones M, Paine TD (2006) Detecting changes in insect herbivore communities along a pollution gradient. Environ Pollut 143:377–387

Eatough Jones M, Paine TD, Fenn ME (2008) The effect of nitrogen additions on oak foliage and herbivore communities at sites with high and low atmospheric pollution. Environ Pollut 151:434–442

Goforth BR, Minnich RA (2008) Densification, stand-replacement wildfire, and extirpation of mixed conifer forest in Cuyamaca Rancho State Park, southern California. For Ecol Manage 256:36–45

Horn A, Kerdelhué C, Lieutier F et al (2012) Predicting the distribution of the two bark beetles *Tomicus piniperda* and *T. destruens* in Europe and the Mediterranean region. Agric For Entomol 14:358–366

Huchon H, Demolin G (1970) La bioécologie de la processionnaire du Pin. Dispersion potentielle - Dispersion actuelle. Rev For Fr 22:220–234

Kier G, Kreft H, Lee TM, Jetz W, Ibisch PL, Nowicki C, Mutke J, Barthlott W (2009) A global assessment of endemism and species richness across island and mainland regions. Proc Natl Acad Sci 106:9322–9327

Malcolm JR, Liu C, Neilson RP, Hansen L, Hannah L (2006) Global warming and extinctions of endemic species from biodiversity hotspots. Conserv Biol 20:538–548

Munz PA (1968) A California flora and supplement. University of California Press, Berkeley

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Ochoa-Hueso R, Allen EB, Branquinho C, Cruz C, Dias T, Fenn ME, Manrique E, Perez-Corona ME, Sheppard LJ, Stock WD (2011) Nitrogen deposition effects on Mediterranean-type ecosystems: an ecological assessment. Environ Pollut 159:2265–2279

Paine TD, Steinbauer MJ, Lawson SA (2011) Native and exotic pests of *Eucalyptus*: a worldwide perspective. Annu Rev Entomol 56:181–201

World Conservation Monitoring Center (1992) Global biodiversity: status of the Earth's living resources. Chapman and Hall, London

Chapter 2
Introduction to Mediterranean Forest Systems: Mediterranean Basin

François Lefèvre and Bruno Fady

Abstract All around the Mediterranean, forest systems have been shaped by long-term anthropogenic impacts. Today, they provide multiple goods and services. We show how the social-ecological system approach offers a good framework to understand their biodiversity, functioning and dynamics. Mediterranean forests have a huge biodiversity, not only in terms of the number of species but also in terms of within-species genetic diversity (at least tree species). We present a tentative typology of Mediterranean forests regarding this biodiversity. Then, we explain how the dynamics of Mediterranean forests is driven in particular by a combination of three characteristics: specific environmental constraints (mainly summer water deficit), a marked spatial heterogeneity of the environment at all scales, disturbance regime (e.g. fire, droughts, pest attacks, human pressure) of variable intensity and frequency. The future challenges for the Mediterranean forests will be to respond simultaneously to: (i) increased threats related to climate change and human pressure, (ii) new demand for multiple ecosystem services locally, (iii) emerging interest for Mediterranean resources to support adaptive strategies in other regions.

2.1 General Overview

The Mediterranean biome is usually defined by its original climate, i.e. its dry and hot summer period of variable length, which imprints a strong water stress on the vegetation during its growing season. This Mediterranean climate is transitional between temperate and dry tropical climates. It is found around the world at latitudes between 25° and 45° in five different regions: the Mediterranean Basin, California, the South African Cape Province, South and South-Western Australia, and parts of Central Chile. Although the Mediterranean regions make up for only 2 % of the world's surface, they account for nearly 20 % of the earth's total plant diversity. Because of its plant diversity and endemism and because most of it under

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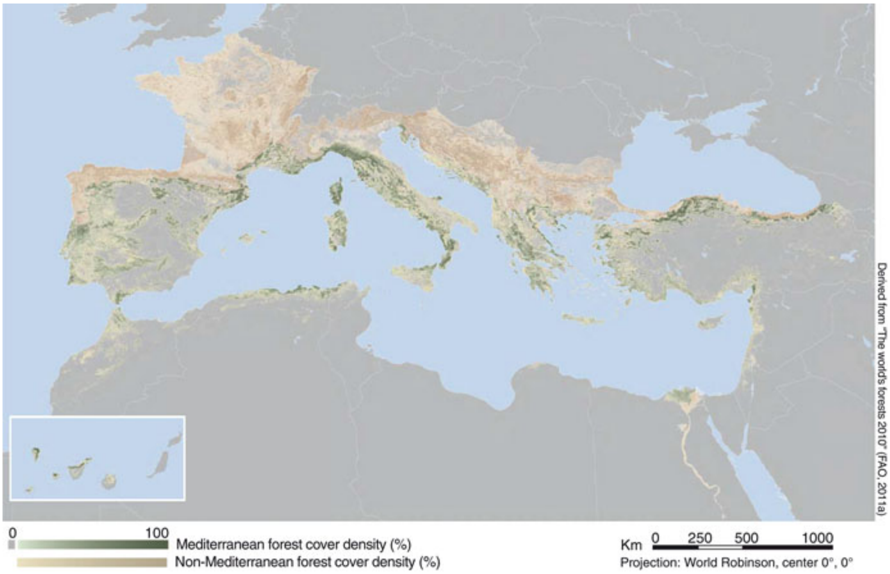
threat from current human activities, the Mediterranean biome is considered one of most significant global biodiversity hotspots (Myers et al. 2000).

The Mediterranean Basin is the largest of the five Mediterranean regions of the world with a surface of approx. 2.3 million km^2 (i.e. more than 75 % of the biome's global distribution). It contains over 30,000 different plant species, i.e. more than half that of the entire Mediterranean biome. It also contains most of the forests found in the biome which account for approx. 0.6 % of world forest area. Forests cover is estimated to be over 25.5 Mha by FAO (2013), plus approx. 50 Mha of other woodlands, globally stable since 1990 but slightly increasing in the North due to abandoned agricultural land and decreasing in the South and East due to over-exploitation. The most typical characteristics of Mediterranean forests, compared to temperate or boreal forests, are their spatial and temporal complexity and heterogeneity at multiple geographic scales, not only in terms of the physical factors which prevail where they grow (bedrock, geomorphology, soil, bioclimate), but also in terms of their biological components and attributes: functional dynamics at local and landscape levels, floristic and faunistic composition, richness and biogeographic origins. In the Mediterranean Basin itself, this complexity has no doubt been durably imprinted by millennia-long human activities (Blondel and Aronson 1999), whether it is viewed as detrimental or beneficial (Blondel 2006). In the Mediterranean Basin, geological history at least from the Tertiary, the palaeogeographical episodes of the Pleistocene, long-term human influence during the Holocene and current geographical and climatic contrasts have converged to create forests with high species and ecosystemic diversity and heterogeneity (Figs. 2.1 and 2.2).



Derived from 'The world's forests 2010' (FAO, 2011a)

Fig. 2.1 Distribution of Mediterranean forests (FAO 2013) (Credit FAO, with permission)

Fig. 2.2 Mediterranean forests and man: a long history of interactions, services and impacts (Oak forest in Morocco) (Photo F. Lefèvre, Inra)

There is an abundant literature on Mediterranean ecosystems, and in particular forests. Here we focus on four characteristics that make the forests of the Mediterranean Basin so peculiar. First, we briefly review the long-term history and current links between forests and man in this area. Then, we characterize the huge biodiversity and plurality of forest types. We then describe how these forests should be considered in a dynamic perspective and focus on three specific drivers of their dynamics. Finally, we show how the future of the Mediterranean forests combines threats and opportunities, not only for the local area but also as a global stake.

2.2 Forests in the Mediterranean Basin Are Typical Social-Ecological Systems

2.2.1 Long-Term Human Impacts

Palaeobotanical, archaeological, and historical records clearly demonstrate the consequences of human action on forest ecosystems of the Mediterranean from the Neolithic onward, that of forest destruction (Blondel 2006). Over the course of history, Mediterranean forest ecosystems were over-used for their multiple resources such as timber for construction, carpentry and ship building, wood for fuel, cork, seeds, forage for farm animals, resin, etc. Forest land was converted to agricultural and grazing land over vast expanses during the Neolithic and throughout historical times, particularly when moist and warm climates facilitated the expansion of cereal culture needed for expanding human populations. An estimated 85 % of original post glacial forests have been destroyed by man (Quézel and Médail 2003), which are now made of agricultural land, urban areas or more or less degraded pre-forest types (see Sect. 3.1). In the words of Blondel (2006): "*Apart from some remote mountainous areas, there is hardly a square meter of the Mediterranean Basin that has not been repeatedly manipulated or 'redesigned' by man over the last 300-plus generations of human occupation*".

It is only recently that the trend of forest destruction has abated, particularly in the northern Mediterranean. In France, a law was passed in the 1850s for the restoration of degraded mountain lands to prevent erosion and curb the catastrophic floods that regularly damaged mountain towns. Thousands of hectares were seeded and planted with forest species, one of the greatest such organized effort to date. Together with the sharp decrease of traditional agriculture and grazing in low elevation mountains since the early twentieth century, these non-native, often pine dominated forests are currently recolonized by local mountain species such as *Abies alba* or *Fagus sylvatica*. In North Africa, the trend is still of loss of forest area, although some initiatives are slowing it down. In Algeria, for example, the green dam initiative of the 1970s which covers hundreds of kms, aimed at protecting arid areas from sand encroachment and curbing deforestation and erosion. Climate change is placing a new threat of unpredictable magnitude on these recovering forests.

Whether destroying forests or planning and orchestrating its reintroduction, man has had a profound impact on biodiversity, from species extinction or changes in their distribution to the advent of new landscapes with potentially new adaptations within species and populations at diverse spatial scales.

2.2.2 From the Provision of Multiple Goods and Services to the Social-Ecological System Approach

Mediterranean forests are typical illustrations of the multipurpose forest management, prescribed by foresters in the mid twentieth century (production – protection – recreation), which we can now formulate more comprehensively using the concept of ecosystem-services. The social dimension of multipurpose forest management has been recognized in Europe as a support to forest sustainability in the 1990s, but it interesting to note that the multiple roles of the forests were already mentioned in Mesopotamia three millennia b.c. and that protection of the forest was already considered in laws in the ancient Greece five centuries b.c. (Farrell et al. 2000): the concepts to describe multi-purpose management are recent but practices are ancient, particularly in the Mediterranean Basin.

Today, the forests around the Mediterranean produce not only timber, but also fuel wood and a large diversity of non-wood forest products such as cork (2.2 Mha, FAO 2013), pine nuts (6000–9000 tons per year, FAO 2013), resin, mushrooms and berries, game, fodder, etc. These different products combine various socio-economic chains, at local, regional or global scale. In some areas, the demand for fuel-wood exceeds the forest biomass production causing significant deforestation (FAO 2013). Illustrating the interplay between ecology and economy, the cork oak forests are currently at stake because of the reduction of the global market for natural cork stoppers and other cork products: new valorization of the products combined with new management systems that can sustain cork production, fuel wood provision and fodder in the context of climate change are required.

Beyond the production of goods, many Mediterranean forests have a primary role to protect against desertification in the most arid zones, and more generally again soil erosion, landslide, avalanche and rock-slide. Furthermore, in the Mediterranean region where water resources are scarce, forests play a major role on the water budget at landscape scale and they contribute to the maintenance of water resources, in quantity and quality, for multiple usages (Birot et al. 2011). Southern and eastern Mediterranean countries generally consider soil and water protection as the priority objective for more than 40 % of their forest area (FAO 2013).

The Mediterranean forests have high cultural and patrimonial value due to historical heritage: stereotypes of Mediterranean forest landscapes are often associated with anthropogenic signature such as terraces, agroforestry systems, reforestation, etc. The human population is expected to continue increasing by 20 % in the Mediterranean Basin from 2010 to 2050, before stagnation or decrease, but it will decrease in the rural areas (PLAN BLEU 2009). In such a perspective of increased urban development, the recreational role of forests will become more important. Simultaneously, urban and peri-urban forests are expected to increase.

Finally, a new service is demanded to the Mediterranean forests in the context of climate change, i.e. to play a role on climate change mitigation both through carbon sequestration (in the ecosystem and in the wood products) and substitution to fossile energy. An economic valuation of the carbon stored by the forests in 2050 (Ding et al. 2011), for various climate change scenarios, assessed a sequestration value for the Mediterranean forests (37–66 billion US$) lower than for Central-Northern Europe (117–190) but higher than for Northern and Scandinavian Europe (11–46). Adaptation and mitigation are tightly linked: only healthy forests will play a role in carbon sequestration.

From what precedes, it is clear that the ecological structures and processes in the Mediterranean forests cannot be understood independently of the socio-economic structures and processes. Thus, the Mediterranean forests typically correspond to the definition of integrated social-ecological systems as proposed by Ostrom (2009). In Mediterranean forest systems, the biological potential and the ecological trajectories orientate forest management and policy, which in turn have a major impact on the ecological structures and processes in the forest. Complex systems science applied in the context of social-ecological system provides an appropriate transdisciplinary framework to study the dynamics and resilience of forest systems, particularly in the Mediterranean (Filotas et al. 2014). Illustrating the interdependency between ecological and socio-economic processes at different scale, Barbeito et al. (2009) showed that current forest management practices in the Mediterranean, even-aged as well as uneven-aged stands, favor natural regeneration of *Pinus sylvestris*; while Martin-Queller et al. (2011) showed that landscape models of woody plant species richness in Central Spain were more informative when they accounted for effects of land use and management practices.

Within this common global framework, Mediterranean forests differ greatly from site to site in terms of biodiversity composition (e.g. tree species, genetic diversity), environmental constraints (e.g. fire regime or altitudinal climatic gradients), social organization (e.g. public vs private forests), human pressure (e.g. contrasting demography between North and South or East of the Mediterranean), socio-economic context (e.g. contrasting economy between North and South or East of the Mediterranean).

2.3 The Mediterranean Hotspot of Biodiversity in Forest Ecosystems

2.3.1 A Huge Diversity of Mediterranean Forest Types: Tentative Typology

Forests here are defined as ecosystems covering over 0.5 ha, where tree crown density is more than 10 % and tree height can reach over 5 m, following the definition of the Food and Agriculture Organization (FAO) of the United Nations (UN) (FAO 2001). Forest types in the Mediterranean Basin are characterized by their dominant tree species and their structure. Dominant tree species vary according to geography (and thus geological movements that have led to contrasted floristic historical movements) and their different ecological requirements. Both climate variables and major geographic discontinuities can be used to describe forest types, while climate variables and human influence are needed to understand forest structure.

Mean minimum temperatures of the coldest month (*m*) are correlated to elevation and to a lesser extent to increased latitude and continentality. They have conveniently been used to define the geographic and altitudinal zonation of forest types in the Mediterranean (Table 2.1). The *m* of most Mediterranean forests is between 0 °C and +3 °C: extremes reach +8 to +9 °C in desert margins and −8 to −10 °C on the highest mountains. Irregular and extreme climatic events such as late spring frost also shape Mediterranean forest species distribution. For example, the extremely cold winters of 1956 and 1985 strongly affected the distribution of the olive tree (*Olea europaea*), Aleppo pine (*Pinus halepensis*) and holm oak (*Quercus ilex*) in the northern Mediterranean, which species are sometimes used to define the bioclimatic envelope of the Mediterranean Basin.

Table 2.1 Vegetation levels showing the correspondence between temperature variants and dominant (and potentially frequent) woody species of the Mediterranean Basin, according to Quézel and Médail (2003)

Vegetation level	Temperature variant	m (°C)	T (°C)	Dominant woody species
Infra-Mediterranean	Very hot	> +7 °C	> +17 °C	*Argania spinosa*, *Acacia gummifera*
Thermo-Mediterranean	Hot	+3 to +7 °C	> +17 °C	*Olea sp.*, *Ceratonia siliqua*, *Pinus halepensis and P. brutia*, *Tetraclinis articulata*, (*Quercus sp.*)
Meso-Mediterranean	Temperate	0 to +3 °C	+13 to +17 °C	*Sclerophyllous Quercus sp.*, *Pinus halepensis and P. brutia*
Supra-Mediterranean	Cool	−3 to 0 °C	+8 to +13 °C	*Deciduous Quercus sp.*, *Ostrya carpinifolia*, *Carpinus orientalis*, (*Pinus brutia*)
Mountain-Mediterranean	Cold	−7 to −3 °C	+4 to +8 °C	*Pinus nigra*, *Cedrus sp.*, *Abies sp.*, *Fagus sp.*, *Juniperus sp.*
Oro-Mediterranean	Very cold	< −7 °C	< +4 °C	*Juniperus sp.*, *spiny xerophytes*

m mean minimum temperatures of the coldest month, *T* mean annual temperature

Rainfall is also extremely variable in the Mediterranean Basin. By definition, it cannot be less than 100 mm per year, the upper boundary of the desert climate. Rainfalls higher than 1500 mm and up to 2000 mm are mostly found on coastal mountain ranges. Rainfall also plays an essential role in the organization of Mediterranean forests and can be used to define six different bioclimatic types (Table 2.2).

These large scale temperature and rainfall gradients interact to determine the potential presence of dominant woody species. They are strong drivers of species diversity because the topography of the Mediterranean Basin is highly contrasted, repeatedly changing from 0 to over 3000 m above sea level over very short distances. Their patterns are also very variable annually, increasing diversity. Locally, forest types are modified by soil type and human impact. Combined, temperature and rainfall patterns and geographically determined geological influences contribute to the diversity of forest types and forest communities found in the Mediterranean Basin (Table 2.3).

Mediterranean forests can be organized into three major structural types based on bioclimatic and/or human impact criteria:

True Forest Types are made of vegetation structures at relatively stable equilibrium. Shade tolerant plant species growing on evolved soils are dominant. These true forests can be considered as the potential structures reached at the end of a dynamic ecological cycle (previously known as climax forests). They are currently present where soil and climate conditions are favorable and where human impact is not too strong.

Table 2.2 Types of bioclimates and their theoretical correspondence with the main vegetation types of the Mediterranean Basin, according to Quézel and Médail (2003)

Bioclimate	Mean annual rainfall (for m = 0 °C)	Number of months without rainfall	Main vegetation type
Per-Arid	<100 mm	11–12	Saharan
Arid	100–400 mm	7–10	Steppe and pre-steppe (*Juniperus turbinata*, *Pinus halepensis*, *Pistacia atlantica*)
Semi-Arid	400–600 mm	5–7	Pre-forest (*Pinus halepensis*, *P. brutia*, *Juniperus spp. Quercus*)
Sub-Humid	600–800 mm	3–5	Forest (mostly sclerophyll *Quercus*, *Pinus halepensis*, *P. brutia*, *P. pinaster*, *P. pinea*, *P. nigra*, *Cedrus*)
Humid	800–1000 mm	1–3	Forest (mostly deciduous *Quercus*, *Pinus brutia*, *P. pinaster*, *P. nigra*, *Cedrus*, *Abies*, *Fagus*)
Per-Humid	>1000 mm	Less than 1	Forest (deciduous *Quercus*, *Cedrus*, *Abies*, *Fagus*)

m mean minimum temperatures of the coldest month

Pre-forest Types can be divided into two categories. Under per-humid, humid and sub-humid bioclimates, they consist of vegetation structures that have undergone severe human impact, although their soil is still relatively well preserved. They are transitory structures between true forests and open, shrub dominated systems. Under semi-arid bioclimatic conditions, or under particularly stressful conditions in any bioclimatic condition (e.g. ultramafic substrates), pre-forests are shrub-dominated vegetation structures with scattered trees or interspaced with low density forests, known as matorral, that appear close to equilibrium at the human-time scale. Conifers play an important role in pre-forest types.

Pre-steppic Forest Types are made of open-vegetation structures dominated by non-forest plant species under scattered trees. Non-forest species are steppe-type perennial species that can eventually be replaced by ruderal annual species when grazing occurs. Soils are usually poor and top soil is frequently missing. Pre-steppic forests are most frequent under warm and hot temperature variants of arid (and sometimes semi-arid) bioclimates, very frequent in the southern and eastern Mediterranean. They gradually become steppes under hotter and drier conditions. On mountains, pre-steppic forests are a transitional vegetation structure from forests (or pre-forests) to high elevation steppes dominated by low and scattered cushion-like spiny xerophytes.

Table 2.3 Main forest communities with dominant woody species of the four major geographical subdivisions of the Mediterranean Basin, arranged according to vegetation level (see Table 2.1)

Vegetation level	North-western Mediterranean communities	South-western Mediterranean communities	North-eastern Mediterranean communities	South-eastern Mediterranean communities
Infra-Mediterranean		*Argania spinosa* *Acacia gummifera*, *A. raddiana*		
Thermo-Mediterranean	*Olea europaea*, *Ceratonia siliqua* *Chamaerops humilis* *Quercus ilex*, *Q. suber*, *Q. coccifera* *Pinus halepensis*, *P. pinaster*, *P. pinea* *Juniperus turbinata*, *J. phoenicea*	*Olea europaea* *Ceratonia siliqua* *Chamaerops humilis* *Q. ilex ssp. rotundifolia*, *Q. suber*, *Q. fruticosa* *Pinus halepensis*, *P. pinaster* *Juniperus turbinata*, *J. phoenicea* *Pistacia atlantica* *Tetraclinis articulata* *Cupressus atlantica*	*Olea europaea* *Ceratonia siliqua* *Quercus ilex*, *Q. ithaburensis*, *Q. pubescens*, *Q. coccifera ssp calliprinos* *Pinus halepensis*, *P. brutia*, *P. pinea* *Cupressus sempervirens*	*Olea europaea* *Ceratonia siliqua* *Quercus ilex*, *Q. infectoria*, *Q. coccifera ssp calliprinos*, *Q. pubescens*, *Q. ithaburensis* *Pinus halepensis*, *P. brutia* *Cupressus sempervirens*
Meso-Mediterranean	*Quercus ilex*, *Q. suber*, *Q. pubescens*, *Q. coccifera*, *Q. petraea ssp. Broteroi*, *Q. canariensis*, *Q. pyrenaica* *Pinus halepensis*	*Olea europaea* *Ceratonia siliqua* *Chamaerops humilis* *Quercus ilex ssp. rotundifolia*, *Q. suber*, *Q. canariensis* *Pistacia atlantica* *Tetraclinis articulata*	*Quercus ilex*, *Q. coccifera ssp. Calliprinos*, *Q. ithaburensis*, *Q. brachyphylla*, *Q. pubescens* *Pinus halepensis*, *P. brutia*, *Cupressus sempervirens*	*Quercus ilex*, *Q. coccifera ssp. Calliprinos*, *Q. ithaburensis*, *Q. infectoria*, *Q. cerris ssp. Pseudocerris*, *Q. alnifolia*, *Pinus brutia*, *P. halepensis*, *P. pinea*, *Cupressus sempervirens*, *Cedrus brevifolia*

(continued)

Table 2.3 (continued)

Vegetation level	North-western Mediterranean communities	South-western Mediterranean communities	North-eastern Mediterranean communities	South-eastern Mediterranean communities
Supra-Mediterranean	*Quercus pubescens*, *Q. cerris*, *Q.petraea*, *Q. faginea*, *Q. robur*, *Q. petraea*, *Q. pyrenaica* *Abies alba*, *A. pinsapo* *Ostrya carpinifolia* *Carpinus betulus* *Pinus sylvestris* *Castanea sativa*	*Quercus canariensis*, *Q. faginea*, *Q. afares*, *Q. ilex ssp. rotundifolia*, *Q. suber* *Cedrus atlantica* *Abies marocana*	*Quercus frainetto*, *Q. cerris*, *Q. pubescens*, *Q. ithaburensis Q. petraea*, *Q. pubescens ssp. anatolica* *Abies cephalonica* *Cupressus sempervirens* *Ostrya carpinifolia* *Carpinus orientalis* *Castanea sativa*	*Quercus frainetto*, *Q. cerris*, *Q. infectoria*, *Q. macranthera ssp. syspirensis* *Pinus brutia*, *P. nigra ssp. Pallasiana* *Carpinus orientalis* *Ostrya carpinifolia* *Cupressus sempervirens*
Mountain-Mediterranean	*Pinus sylvestris*, *P. nigra* (*ssp. salzmanii or laricio*), *P. uncinata*, *P. mugo* *Abies alba*, *A. pinsapo* *Juniperus thurifera ssp. thurifera* *Fagus sylvatica ssp. sylvatica*	*Pinus nigra ssp. Mauretanica* *Cedrus atlantica* *Abies marocana*, *A. numidica* *Juniperus thurifera ssp. Africana* *Quercus ilex ssp. rotundifolia*	*Pinus nigra ssp. pallasiana*, *P. heldreichii* *Abies cephalonica*, *A. borisii-regis*, *A. nordmanianna*, *A. equi trojani*, *A. bornmuelleriana* *Juniperus excelsa* *Fagus sylvatica sensu lato* *Quercus petraea*	*Pinus nigra ssp. pallasiana* *Cedrus libani* *Abies cilicica* *Juniperus foetidissima*, *J. excelsa* *Fagus sylvatica ssp. orientalis* *Quercus petraea*, *Q. brantii*, *Q. ithaburensis*
Oro-Mediterranean	*Juniperus thurifera ssp. thurifera*	*Juniperus thurifera ssp. africana* *Quercus ilex ssp. rotundifolia*	*Juniperus excelsa*	*Juniperus excelsa*

Source: After Fady and Médail (2004)

2.3.2 Species Richness and Endemism: Hotspots and Refugia

Species richness and diversity, which are the most frequently used parameters to describe and assess biodiversity, are scale-dependent. At the local scale (less than 0.1 ha), mean local within habitat ("alpha") plant diversity of Mediterranean Basin forests is the richest within the Mediterranean biome, with between 10 species per m^2 and 25–110 species per 1000 m^2. Whereas the Mediterranean Basin harbors the highest tree species richness within the Mediterranean biome (290 indigenous trees including 201 endemics), differentiation among habitats ("beta") and regional ("epsilon") scale diversities can be considered as average both within the Mediterranean biome and in comparison to plant biodiversity in tropical regions. One of the most striking characteristic of the Mediterranean flora is its high rate of regional endemism: close to 60 % of all native taxa are Mediterranean endemics, half of which being narrow endemics restricted to few localities (Thompson 2005).

Plant diversity is not distributed evenly over the entire Mediterranean Basin. Médail and Quézel (1997) have defined ten regional hotspots corresponding centers of exceptional plant diversity and endemism. The endemic vascular plant richness in these hotspots is over 2000 species per 15,000 km^2 with at least 10 % narrow endemics. Forest trees are no exceptions to these patterns: woody plant species richness is congruent with overall plant species richness (Fady and Conord 2010), making it a good surrogate of overall species richness in biodiversity assessments.

Species richness and endemism in the Mediterranean Basin can be best explained as the result of the interplay between complex historical processes and heterogeneous environmental (Médail and Quézel 1997; Thompson 2005). The onset of the Mediterranean climate late in the Tertiary, the Messinian Salinity Crisis (5.77–5.33 Ma) and the Milankovitch climate oscillations that began before the Pleistocene explain the rich and heterogeneous evolutionary heritage of Mediterranean plants (Thompson 2005). Late Tertiary global cooling and the appearance of moist climates during the Plio-Pleistocene resulted in the extinction of numerous cool- and warm-temperate plants, among them many tree species (e.g. Suc et al. 1999; Svenning 2003). During the cold periods of the Pleistocene climatic cycles, glacial refugia provided suitable habitats during adverse climate periods. Médail and Diadema (2009) define refugia as areas with buffering environmental characteristics where distinct genetic lineages have persisted through a series of unfavorable climate fluctuations.

Refugia imply long-term persistence (e.g. one or more glacial–interglacial cycles) of one or more populations per species within a well-defined geographical area (e.g. mountain range, cliff or canyon). Glacial refugia during the Pleistocene thus limited species extinction (Taberlet et al. 1998; Weiss and Ferrand 2007) and potentially favor the emergence of new taxa (e.g. Hungerer and Kadereit 1998), although this is debatable for long lived organisms with little reproductive barriers such as trees (Futuyma 2010). Following this line of reasoning, the Mediterranean Basin as a whole is a refugium from where species recolonized (by migration and secondary contacts) their temperate range during the Holocene. It is also made of several regional and local refugia from where Mediterranean taxa emerged and recolonized their Mediterranean distribution range and in where they also remained. The existence of 11 major regional biodiversity hotpots in the Mediterranean Basin (Médail and Diadema 2009; Médail and Quézel 1997) is significantly explained by the location of these refugia. Médail and Diadema (2009) found that genetically defined refugia, particularly nearly all southern and insular refugia, were significantly over-represented within the 11 regional hotspots. Therefore, regional biodiversity hotspots often coincide with areas that have enjoyed relative climate stability over long periods of time. This explains their overall higher genetic diversity and identifies them as priority for conservation.

2.3.3 Genetic Diversity in Trees

Just like species diversity, genetic diversity is high in the Mediterranean Basin, making it a hotspot of genetic diversity worldwide (Fady 2005). In conifers, both within population genetic diversity and among population genetic diversity are higher than in tropical and temperate conifers. Just as for species richness, environmental variability, geological history and climate contrasts may explain this diversity within species. Interestingly, human impact in the form of deforestation is visible in only a few populations within species, presumably when very small sized populations are left (e.g. *Cedrus libani* populations in Lebanon, Fady et al. 2008). *Pinus pinea* is a remarkable exception, although its almost non-existent genetic diversity seems to be due as much as its ecological requirements as to the fact that its edible and highly sought after seeds have been extensively traded by Mediterranean people for centuries (Vendramin et al. 2008).

Forest tree species diversity and genetic diversity follow partially different spatial patterns in the Mediterranean Basin. The mosaic-like, regional hotspot structure found for species diversity which is congruent with the genetic distinctiveness of glacial refugia (Médail and Diadema 2009) does not appear when genetic diversity is measured within populations (Fady and Conord 2010). Instead, within-population genetic diversity follows an East–West pattern, where genetic diversity is higher in the eastern Mediterranean than in the western Mediterranean. Also, low elevation thermophilic species display a lower genetic diversity within populations than more mesophilic or cold tolerant species (Conord et al. 2012). These genetic patterns have been attributed to evolutionary history and past climate. Although species could have inherited their idiosyncratic population genetic diversity from their ancestral lineages during the Tertiary, past climate (which also affected species diversity patterns) remains a very convincing factor for explaining longitudinal and altitudinal genetic gradients. Past climate was the harshest during the last glacial maximum (LGM) in the western part of the Mediterranean Basin. During the LGM, also, thermophilous species are likely to have had more restricted distributions than more cold-tolerant species. Both these habitat conditions affect population size and demographic processes, thus genetic diversity. In the Mediterranean, species diversity and genetic diversity may have been shaped by different past processes, leading to different patterns. Genetic diversity may display an imprint of recent past (Pleistocene) climatic events, whereas species diversity may indicate events that have occurred both during the Pleistocene and earlier during the Tertiary or Plio-Pleistocene (Médail and Diadema 2009; Svenning et al. 2009).

2.4 Dynamics of the Mediterranean Forest Systems: Three Main Characteristics

2.4.1 Diversity of Adaptations to Summer Water Deficit

Mediterranean ecosystems have in common to experience more or less pronounced water deficit in summer, and most species have developed specific adaptations to this constraint. Adaptation of the forest ecosystem is not a fixed and stable state but it is a continuous dynamic process resulting from: (i) evolutionary forces that shape the genetic diversity between and within species, (ii) environmental fluctuations, with possible acclimation effects when an ecosystem experiencing regular moderate drought is prepared to more severe drought or, reversely, cumulative effects when successive dry years have an increased impact on long-lived species, and (iii) biotic interactions, which are complex and hardly predictable. Under Mediterranean environmental constraints, Carnicer et al. (2008) showed that random processes alone are not enough to explain the observed variation in species richness or species' distribution range, and adaptive processes play a major role there. We focus here on trees as keystone species in the forest, but the same forces act on the other organisms as well, depending on life cycle and life history traits of each species.

As regards multitrait syndromes of response to summer water deficit in forest trees, natural selection does not select for a unique adaptive strategy but for several, even-though convergent selection may be suspected for some traits under high developmental constraints (Choat et al. 2012). It can be first noticed that non-deciduous tree species, conifers and broadleaves, dominate at lower elevation, while deciduous and non-deciduous species are generally mixed at mid and high elevation. Depending on the Mediterranean tree species, adaptation to summer drought is reached through various combinations of traits that include: resistance to cavitation (Chave et al. 2009), leaf morphology (Wright et al. 2004), budburst and budset phenology (Davi et al. 2006), growth rhythm (Lo Gullo and Salleo 1988), water use efficiency (Aranda et al. 2010) and other specific traits. Mixed Mediterranean forests, e.g. pine-oak forests, benefit from this diversity of strategies in the sense that complementarity of species' niches contributes to a globally efficient use of limiting resource like water by the ecosystem. Within each species, the genetic variation for adaptive traits is also huge, not only among populations but also within each population (see Aranda et al. 2010 for an illustration on Mediterranean pines).

Biotic interactions are particularly important in such a constrained environment. Indeed, the diversity of morphological and functional adaptations to abiotic stresses interferes with biotic associations. In the Mediterranean forests, insects find a huge diversity of host trees in terms of functional traits that also impact the biotic interaction itself (e.g. phenology, leaf traits, etc.). Furthermore the ultimate response to abiotic stress depends on the biotic interactions in a very complex way so that it is generally difficult to decipher the primary causes from secondary agents when forest dieback occurs (Durand-Gillmann et al. 2013). A severe climatic event will not only affect the trees and their associated species individually, but it will also alter the modes of their interactions, for instance increasing or decreasing the resistance of trees to insects (Rouault et al. 2006).

2.4.2 Spatial Heterogeneity of the Environment

Around the Mediterranean Basin where the Mediterranean climate prevails globally, the environmental conditions are characterized by their spatial heterogeneity at all scales. The impact of this heterogeneity is all the more important than it occurs in a context of limiting resource (summer water deficit): indeed, small local variations may have detrimental effects in these conditions.

At large scale, it is noticeable that the center of the Mediterranean climate zone in this region is occupied by the sea. Thus, Mediterranean forests are distributed not in the center but at the edges of the Mediterranean climate, showing transitions with atlantic climate in the West, temperate climate in the North and arid climate in the South. Even the species that are largely distributed around the Basin have a fragmented distribution range, because of the sea, as if they mainly consisted of marginal populations (although, as previously mentioned, human induced seed movements have partially balanced this intrinsic fragmentation). Related to this context, the Mediterranean forests include not only eu-Mediterranean tree species, but also populations of temperate or atlantic species that have developed specific adaptations to this particular climate (Table 2.3). This large scale environmental

Fig. 2.3 The huge diversity of environmental conditions in the Mediterranean forests is an important driver of their biodiversity (altitudinal cline in Mont Ventoux, France) (Photo F. Lefèvre, Inra)

heterogeneity explains the genetic differentiation for adaptive traits among populations: e.g. in *Pinus halepensis* and *Pinus pinaster* Chambel et al. (2007) detected a variation of plasticity in the response to drought stress at seedling stage between provenances related to the fertility of the site of origin (provenances from poor sites were less responsive). As previously mentioned, at this scale, variation in environmental conditions combines with variation in historical and socio-economic contexts, which can indirectly strengthen the environmental pressure on the forests, or compensate.

At regional scale, another characteristic of the region is its topography, which induces important local climatic gradients depending on elevation and aspect (Fig. 2.3). Illustrating the importance of spatial heterogeneity in the Mediterranean, Loarie et al. 2009 introduced the concept of climate change velocity defined as the ratio between predicted climatic changes in time divided by local climatic change in space, which roughly represents the speed at which species should move locally to follow the displacement of their climatic envelop. Although climate change predictions are particularly severe in the Mediterranean, the velocity remains low compared with other biomes because topography can compensate locally. In the context of Mediterranean climate, the impact of altitudinal gradients on biodiversity is particularly pronounced. This can be seen at species level:

e.g. altitudinal distribution of pine species in Spain from *P. halepensis*, *P. pinea* at the bottom to *P. pinaster*, *P. nigra* and, towards the top, *P. sylvestris*, partially overlapping. Altitudinal climatic gradients contribute to genetic differentiation between low elevation and high elevation populations of the same species at short distance (i.e. despite important gene flow) (Jump et al. 2006a). While experiencing summer water deficit, populations at high elevation also experience spring frost, which induces selection for a combined adaptive strategy (Oddou-Muratorio and Davi 2014).

Furthermore, many Mediterranean forests develop on karstic soils, which are characterized by important heterogeneity at very local scale, metric scale, in particular as regards soil depth and soil texture that determine water availability for each tree. This micro-local heterogeneity of water availability is of utmost importance in the Mediterranean climate. In a high elevation Mediterranean population of *Abies alba*, South East France, Nourtier et al. (2014) analyzed the spatial heterogeneity of mortality after the 2003 heat wave and subsequent dry years: unexpectedly, they found that mortality occurred preferably in areas where soil water availability was higher, which can be interpreted as a lower acclimation to drought, and therefore higher vulnerability, in those areas. Heterogeneity of selection pressure at this micro-local scale might be of the same magnitude as the variation found at higher scale, and could explain part of the adaptive genetic variation that remains within each population: this question has still received little attention.

2.4.3 Role of Disturbance and Disturbance Regime on Biodiversity

A third characteristic of the dynamics of Mediterranean forests is the intensity and frequency of disturbance, which reshapes the biodiversity both in terms of composition and structure (e.g. more juvenile stages in areas of frequent fires), and impacts the trophic web (Fig. 2.4). Disturbance is defined as a temporary change in the environmental conditions having an impact on the ecosystem. The disturbance regime is highly variable in space, at large scale and local scale. Actually, extreme climatic events, such as severe drought or frost, are disturbances. Wildfire is another major disturbance in the Mediterranean: 2 Mha have burnt in the area between 2006 and 2010 (FAO 2013). In case of wildfire, frequency and intensity of the disturbance are not independent: frequent small fires reduce fuel and thus reduce the probability of occurrence of large scale big fires. Although wildfire is a natural factor in the dynamics of Mediterranean ecosystems, it is necessary to adopt the integrated social-ecological approach rather than stick to the ecosystem approach to analyze the adaptation of Mediterranean forests to wildfire because: (i) due to the high population density in the area, human lives and belongings are given priority, (ii) most wildfires in the region always had and still have an anthropogenic origin, voluntary or not, (iii) Mediterranean countries have developed long term experience on fire prevention and firefighting, and practices have a significant impact on fire regime.

Fig. 2.4 Disturbance and post-disturbance management drive the dynamics of Mediterranean forest systems (Corsica, France) (Photo F. Lefèvre, Inra)

Prescribed burning is an example of controlled disturbance used as a management tool to limit fuel development and prevent wildfire.

Tree species have developed various types of adaption to fire, either based on survival (*Quercus suber*, *Pinus pinea*) and resprouting (*Quercus ilex*, *Pinus canariensis*), or sexual reproduction (*Pinus halepensis*). Each strategy of adaptation to fire involves coordinated sets of traits: in *P. pinea* survival is increased by thick bark and protection of apical buds by terminal needles, in *P. halepensis* the reproductive capacity results from the combination of serotiny, seedling vigor, early reproduction, and predominant resource allocation to female reproduction in the juvenile stage (Ne'eman et al. 2004). Genetic variation for adaptation to fire does not only exist between tree species, but also within species: populations grown in areas of frequent fires appear more adapted than others (e.g. in *Pinus pinaster*, Tapias et al. 2004).

Disturbance is a complex multifactorial process where biotic and abiotic factors interact. For instance, parasite attacks may produce dead biomass in tree crowns that favor inflammability and increase the vertical continuity of fuel, inducing higher fire risk. Reciprocally, fire and post-fire management both have an impact on the biodiversity and functional response of the ecosystem (Castro et al. 2010), in particular on insect communities (Mateos et al. 2011). Disturbance can also result from the social context: Plieninger et al. (2014) showed that land abandonment in the Mediterranean Basin has a global impact on biodiversity, but highly variable in space and depending on landforms (agroforests and not strictly forests are considered in this study).

2.5 Current and Future Challenges in the Context of Global Change

2.5.1 Mediterranean Forests Under Pressure: Climate and Land-Use Change Increase the Demand for Multiple Ecosystem Services

In the next decades, Mediterranean forests will be under pressure of climate change and increased demand on ecosystem services related to human expansion in the area. The frequency and intensity of climate-related disturbance (i.e. extreme climatic events like drought, storms, floods, frosts, and their induced disturbance such as wildfire or pests outbreak) will have more impact on Mediterranean forest health than the mean elevation of temperature. Future scenarios of climate-related disturbance are even more uncertain than global climate change scenarios but the last IPCC (2014) report concludes that "*the frequency and intensity of drought has likely increased in the Mediterranean*" and clearly predicts a future decrease of precipitations in the area, while the growing period of the vegetation will extend (Gracia et al. 2002).

According to IUCN red list, 124 plant species from the Mediterranean forests are threatened to extinction, including five endemic *Quercus* species, probably related to land-use and over-exploitation (FAO 2013). Directly or indirectly related to climate, severe forest diebacks are already observed locally as for instance in the southernmost *Cedrus atlantica* forests of Belezma in Algeria (Kherchouche et al. 2012) and some Middle Atlas forests in Morocco (Linares et al. 2013). These extensive mortalities have multifactorial, abiotic, biotic and human causes and may result in the global degradation of the forest cover and soil erosion. In the North, the 2003 heat wave and subsequent dry years have induced abnormal decline and partial mortality in *Abies alba* (Cailleret et al. 2013). In Catalonia, the growth of *Fagus sylvatica* started to decline around mid 1970s (Jump et al. 2006b). In France, *Pinus halepensis* rather increased in productivity in the last decades, but reduced leaf lifespan has been observed and future decrease of growth is predicted by the models (Girard et al. 2012).

Climate change and increased demography in the Mediterranean Basin will further increase the pressure on water resources: less water, higher demand by the forest, higher demand for other human uses, remembering that Mediterranean countries already represent 60 % of the population poor in water resources (FAO 2013). Freshwater availability and water stress will severely increase, in particular in the South (Milano et al. 2012). Forest management in the Mediterranean has to consider its role on water resources, both in quantity and quality (Birot et al. 2011).

In the South and East of the Mediterranean, increasing demography and economic development will increase the demand of energy, which may further increase the pressure on fuel-wood and increase over-exploitation of the forests in rural areas, potentially leading to increased risk of desertification (FAO 2013). In the North, abandonment of agricultural land and extension of urban areas, combined with forest dieback due to drought events will increase wildfire risk (IPCC 2014). Beyond provisioning various types of goods, the role of Mediterranean forests for soil protection is at stake (FAO 2013).

2.5.2 *Mediterranean Forests Provide Knowledge and Resources for Other Regions, Conservation Efforts Are Needed*

Climate change scenarios predict an extension of Mediterranean climate areas, in particular at the northern periphery of the Mediterranean Basin. In these peripheral areas, climate change could result in profound ecological shifts: in the case of *Pinus sylvestris*, a widely distributed tree species, Castro showed that ecological processes driving seedling establishment in the Mediterranean are fundamentally different from those in the core range of the species. Actually, some Mediterranean species have started to migrate northwards and upwards: the most documented case is the pine processionary moth (Roques 2015). In the last decades, summer droughts have increased in the transition zone between temperate and Mediterranean climate causing damages to the forests. During the heat wave in 2003, in France, forest fires occurred at high altitudes that never experienced wildfire before. Therefore, as clearly expressed by Doblas-Miranda et al. (2015): "*Mediterranean terrestrial ecosystems serve as reference laboratories for the investigation of global change because of their transitional climate*, *the high spatiotemporal variability of their environmental conditions*, *a rich and unique biodiversity and a wide range of socio-economic conditions*". Indeed, forest managers in the Mediterranean have developed specific expertise on practices of interest for other areas such as wildfire prevention and post-fire management, planting techniques (from the nursery to plant conditioning, soil preparation, planting date and spacing), mixed forest management, multipurpose forest planning, water-oriented forestry practices, etc. Furthermore, Mediterranean forest genetic resources, whether Mediterranean populations of temperate species or Mediterranean species, represent an important reservoir of biodiversity for the adaptation of peripheral temperate forests to climate change.

Regarding climate change, the adaptive capacity of social-ecological systems has a biological and a socio-economical component. According to Lindner et al. (2010), compared to the forests in temperate or boreal regions, the adaptive capacity of the Mediterranean forests might be limited by lower intensity of management: this point of view can be discussed. Firstly, we can argue that expertise exists to face the new challenges, as previously explained. Secondly, it is true that low intensity management exists, mostly in the North and often related to small private property size, but multipurpose management is indeed generalized in the Mediterranean forests. Moreover, awareness of the policy makers and international commitments for the Mediterranean forests have raised (FAO 2013) due to the conjunction of (1) climate and land-use change related threats on the Mediterranean forests, (2) increased local demand for multiple ecosystem services following increased demography and economic development, and (3) general benefit of an extended use of knowledge and resources outside the Mediterranean area.

Facing these challenges, the high biodiversity found in the Mediterranean forests is a key element to find solutions (Hooper et al. 2005) and it should receive particular attention in forest management and planning activities. Beyond adaptive and sustainable forest management and planning, there is a global need to strengthen the effort on biodiversity conservation programs. Currently, the networks of protected areas are unevenly distributed; more than 90 % are located on the North of the Mediterranean (FAO 2013). Regarding forest trees, the Mediterranean genetic resources are still underrepresented in the conservation networks (Lefèvre et al. 2013).

In the global context of Mediterranean social-ecological forest systems, insects in particular play a crucial role in forest functions and services through their own biological activity, their primary interactions with trees and their interactions with other organisms.

References

Aranda I, Alia R, Ortega U et al (2010) Intra-specific variability in biomass partitioning and carbon isotopic discrimination under moderate drought stress in seedlings from four *Pinus pinaster* populations. Tree Genet Genomes 6:169–178

Barbeito I, Fortin M-J, Montes F, Canellas I (2009) Response of pine natural regeneration to small-scale spatial variation in a managed Mediterranean mountain forest. Appl Veg Sci 12:488–503

Birot Y, Gracia C, Palahi M (2011) Water for forests and people in the Mediterranean: a challenging balance, What science can tell us, 1. EFI, Joensuu

Blondel J (2006) The 'design' of Mediterranean landscapes: a millennial story of humans and ecological systems during the historic period. Hum Ecol 34:713–729

Blondel J, Aronson J (1999) Biology and wildlife of the Mediterranean region. Oxford University Press, Oxford/New York

Cailleret M, Nourtier M, Amm A et al (2013) Drought-induced decline and mortality of silver fir differ among three sites in Southern France. Ann For Sci 71:643–657

Carnicer J, Brotons L, Sol D et al (2008) Random sampling, abundance-extinction dynamics and niche-filtering immigration constraints explain the generation of species richness gradients. Glob Ecol Biogeogr 17:352–362

Castro J, Moreno-Rueda G, Hodar JA (2010) Experimental test of postfire management in pine forests: impact of salvage logging versus partial cutting and nonintervention on bird-species assemblages. Conserv Biol 24:810–819

Chambel MR, Climent J, Alia R (2007) Divergence among species and populations of Mediterranean pines in biomass allocation of seedlings grown under two watering regimes. Ann For Sci 64:87–97

Chave J, Coomes D, Jansen S et al (2009) Towards a worldwide wood economics spectrum. Ecol Lett 12:351–366

Choat B, Jansen S, Brodribb TJ et al (2012) Global convergence in the vulnerability of forests to drought. Nature 491:752–755

Conord C, Gurevich J, Fady B (2012) Large-scale longitudinal gradients of genetic diversity: a meta-analysis across six phyla in the Mediterranean basin. Ecol Evol 2:2595–2609

Davi H, Dufrêne E, Francois C et al (2006) Sensitivity of water and carbon fluxes to climate changes from 1960 to 2100 in European forest ecosystems. Agr Forest Meteorol 141:35–56

Ding H, Nunes P, Telucksingh S (2011) European forests and carbon sequestration services: an economic assessment of climate change impacts, Ecosystem services economics working paper series No 9. Division of Environmental Policy Implementation, UNEP, Nairobi

Doblas-Miranda E, Martinez-Vilalta J, Lloret F et al (2015) Reassessing global change research priorities in Mediterranean terrestrial ecosystems: how far have we come and where do we go from here? Glob Ecol Biogeogr 24:25–43

Durand-Gillmann M, Cailleret M, Boivin T et al (2013) Individual vulnerability factors of silver fir (*Abies alba* Mill.) to parasitism by two contrasting biotic agents: mistletoe (*Viscum album* L. ssp. *abietis*) and bark beetles (*Coleoptera*: *Curculionidae*: *Scolytinae*) during a decline process. Ann For Sci 71:659–673

Fady B (2005) Is there really more biodiversity in Mediterranean forest ecosystems? Taxon 54:905–910

Fady B, Conord C (2010) Macroecological patterns of species and genetic diversity in vascular plants of the Mediterranean basin. Divers Distrib 16:53–64

Fady B, Médail F (2004) Mediterranean forest ecosystems. In: Burley J, Evans J, Youngquist JA (eds) Encyclopedia of forest science. Elsevier, Londres, pp 1403–1414

Fady B, Lefèvre F, Vendramin GG et al (2008) Genetic consequences of past climate and human impact on eastern Mediterranean *Cedrus libani* forests. Implications for their conservation. Conserv Genet 9:85–95

FAO (2001) Global forest resources assessment 2000 – main report. FAO, Rome

FAO (2013) State of Mediterranean forests. FAO, Rome

Farrell EP, Führer E, Ryan D et al (2000) European forest ecosystems: building the future on the legacy of the past. For Ecol Manage 132:5–20

Filotas E, Parrott L, Burton PJ et al (2014) Viewing forests through the lens of complex systems science. Ecosphere 5(1):1. doi:10.1890/ES13-00182.1

Futuyma DJ (2010) Evolutionary constraint and ecological consequences. Evolution 64:1865–1884

Girard F, Vennetier M, Guibal F et al (2012) *Pinus halepensis* Mill. crown development and fruiting declined with repeated drought in Mediterranean France. Eur J For Res 131:919–931

Gracia CA, Sabaté S, Sánchez A (2002) El cambio climático y la reducción de la reserva de agua en el bosque mediterráneo. Ecosistemas 2. http://www.aeet.org/ecosistemas/022/investigacion4.htm

Hooper DU, Chapin FS, Ewel JJ et al (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecol Monogr 75:3–35

Hungerer KB, Kadereit JW (1998) The phylogeny and biogeography of *Gentiana L.* sect. *Ciminalis* (Adans.) Dumort.: a historical interpretation of distribution ranges in the European high mountains. Perspect Plant Ecol 1:121–135

IPCC (2014) Climate change 2014: synthesis report, Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri RK, Meyer LA (eds)]. IPCC, Geneva

Jump AS, Hunt JM, Martinez-Izquierdo JA et al (2006a) Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. Mol Ecol 15:3469–3480

Jump AS, Hunt JM, Peñuelas J (2006b) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. Glob Chang Biol 12:2163–2174

Kherchouche D, Kalla M, Guttiérrez EM et al (2012) Impact of droughts on *Cedrus atlantica* forests dieback in the Aurès (Algeria). J Life Sci 6:1262–1269

Lefèvre F, Koskela J, Hubert J et al (2013) Dynamic conservation of forest genetic resources in 33 European countries. Conserv Biol 27:373–384

Linares JC, Taïqui L, Sangüesa-barreda G et al (2013) Age-related drought sensitivity of Atlas cedar (*Cedrus atlantica*) in the Moroccan Middle Atlas forests. Dendrochronologia 31:88–96

Lindner M, Maroschek M, Netherer S et al (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For Ecol Manage 259:698–709

Lo Gullo MA, Salleo S (1988) Different strategies of drought resistance in three Mediterranean sclerophyllous trees growing in the same environmental conditions. New Phytol 108:267–276

Loarie SR, Duffy PB, Hamilton H et al (2009) The velocity of climate change. Nature 462:1052–1055

Martin-Queller E, Gil-Tena A, Saura S (2011) Species richness of woody plants in the landscapes of Central Spain: the role of management disturbances, environment and non-stationarity. J Veg Sci 22:238–250

Mateos E, Santos X, Pujade-Villar J (2011) Taxonomic and functional responses to fire and post-fire management of a Mediterranean Hymenoptera Community. Environ Manage 48:1000–1012

Médail F, Diadema K (2009) Glacial refugia influence plant diversity patterns in the Mediterranean basin. J Biogeogr 36:1333–1345

Médail F, Quézel P (1997) Hot-spots analysis for conservation of plant biodiversity in the Mediterranean basin. Ann Mo Bot Gard 84:112–127

Milano M, Ruelland D, Fernandez S et al (2012) Facing climatic and anthropogenic changes in the Mediterranean basin: what will be the medium-term impact on water stress? C R Geosci 344:432–440

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Ne'eman G, Goubitz S, Nathan R (2004) Reproductive traits of *Pinus halepensis* in the light of fire – a critical review. Plant Ecol 171:69–79

Nourtier M, Chanzy A, Cailleret M et al (2014) Transpiration of silver Fir (*Abies alba* Mill.) during and after drought in relation to soil properties in a Mediterranean mountain area. Ann For Sci 71:683–695

Oddou-Muratorio S, Davi H (2014) Simulating local adaptation to climate of forest trees with a Physio-Demo-Genetics model. Evol Appl 7:453–467

Ostrom E (2009) A general framework for analyzing sustainability of social-ecological systems. Science 325:419–422

Plan Bleu (2009) Etat de l'environnement et du développement en Méditerranée – 2009. Plan Bleu, Athens

Plieninger T, Hui C, Gaertner M et al (2014) The impact of land abandonment on species richness and abundance in the Mediterranean Basin: a meta-analysis. PLoS One. doi:10.1371/journal.pone.0098355

Quézel P, Médail F (2003) Ecologie et biogéographie des forêts du bassin méditerranéen. Elsevier, Paris

Roques A (ed) (2015) Processionary moths and climate change: an update. Springer, Dordrecht

Rouault G, Candau JN, Lieutier F et al (2006) Effects of drought and heat on insect populations in relation to the 2003 drought in Western Europe. Ann For Sci 63:613–624

Suc JP, Fauquette S, Bessedik M et al (1999) Neogene vegetation changes in west European and west circum-Mediterranean areas. In: Agusti J, Rook L, Andrews P (eds) Hominid evolution and climate in Europe. Cambridge University Press, Cambridge, pp 370–385

Svenning JC (2003) Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora. Ecol Lett 6:646–653

Svenning JC, Normand S, Skov F (2009) Plio-Pleistocene climate change and geographic heterogeneity in plant diversity-environment relationships. Ecography 32:13–21

Taberlet P, Fumagalli L, Wust-Saucy AG et al (1998) Comparative phylogeography and postglacial colonization routes in Europe. Mol Ecol 7:453–464

Tapias R, Climent J, Pardos JA et al (2004) Life histories of Mediterranean pines. Plant Ecol 171:53–68

Thompson JD (2005) Plant evolution in the Mediterranean. Oxford University Press, Oxford

Vendramin GG, Fady B, González-Martínez SC et al (2008) Genetically depauperate but widespread: the case of an emblematic Mediterranean pine. Evolution 62:680–688

Weiss S, Ferrand N (2007) Phylogeography of southern European refugia. Evolutionary perspectives on the origins and conservation of European biodiversity. Springer, Berlin

Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Chapter 3
Defoliators in Native Insect Systems of the Mediterranean Basin

Andrea Battisti, Manuela Branco, and Zvi Mendel

Abstract Native defoliating insects have been considered a threat to the forests since ancient time because of their periodic demographic explosions that have worried generations of forest managers and the public in general. Although trees generally recover from such defoliations in a relatively short time, both positive and negative consequences on growth and ecological functions of the forests have been documented. Damage by native defoliators is frequently inflicted whenever native tree species have been used for plantations, often outside of their natural range. Under such conditions the natural population regulation mechanisms, which are known to operate in pristine habitats, become less efficient or they simply need time before being established.

We selected three major forest types to represent the importance and the role of native defoliators in the Mediterranean forests: pines, oaks, and poplars and willows. For each type we provide information about taxonomic traits, guild traits, economic damage, ecological impact, impact on humans, insect-plant interactions, insect-enemies interactions, outbreak dynamics, climate change, and management. Additional information for a few species typical of the Mediterranean forests is appended at the end of the chapter.

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3.1 Pines

A total of 11 pine species are indigenous in the Mediterranean region but only few of them are widespread, i.e. *Pinus brutia*, *P. halepensis*, *P. pinea*, and *P. pinaster* (Barbéro et al. 1998; Lieutier and Ghaioule 2005). Pines are known to occur in the area corresponding to the present Mediterranean region since geological times, with fluctuations related to climatic changes and associated with the possibility of elevation shifts in mountain ranges (Millar 1998). As a consequence, association of defoliating insects with pines appear to be quite old, as confirmed by the split between current lineages of the pine processionary moth, which goes back to the Messinian salinity crisis and drying of the sea (5.3 million years ago) (Simonato et al. 2007; Kerdelhué et al. 2009).

Taxonomic Traits The discussed defoliator community is very heterogeneous and includes species in major insect orders, with a clear dominance of Lepidoptera and Hymenoptera (Masutti et al. 2005). Many of the most typical families of defoliating insects within these orders have taxa specialized on pines, indicating that the evolution of this trait has been convergent. Most insect species are not specific to a given species of host plant, although local preferences are known to occur and may vary from region to region.

Guild Traits Most species defoliating pines are external feeders although a few representatives of needle miners occur in Lepidoptera, especially in the young instars of tortricids (e.g. *Rhyacionia*), and a few midges (Diptera: Cecidomyiidae) may feed in the narrow space within the sheath at the needle base (e.g. *Thecodiplosis*) (Masutti et al. 2005). Both current and mature needles can be affected, depending on seasonality and feeding preferences. The larva is the predominant feeding stage, with the exception of adult beetles (e.g. *Cryptocephalus*). Development cycle is mostly univoltine although semivoltine (e.g. *Dendrolimus*) and multivoltine species (e.g. *Diprion*) occur as well. Defoliation may happen in every time of the year as the feeding time of the species are well diversified, with spring (e.g. *Neodiprion, Acantholyda, Choristoneura*), summer (*Lymantria, Panolis, Diprion, Sphynx, Bupalus*), autumn (e.g. *Cryptocephalus*), and winter (*Thaumetopoea*) or along several seasons (*Pachypasa*). Interestingly, *Thaumetopoea pityocampa* has locally shifted to a summer feeding period in Portugal, indicating that the Mediterranean climate may offer a wide range of conditions to which the insects may adapt (Santos et al. 2013). So, it is not surprising to find a large variation of the traits of individual species within their range, and a generalization of the patterns is often problematic.

Economic Damage There is little doubt that defoliating insects represent one of the major economic threats to pine forests in both the northern and the southern rims of the Mediterranean basin (Battisti 2005; Mouna 2005). This is likely due to the wide use of pines in afforestations, especially in the last 100 years, and to the natural colonization of disturbed areas by pines, such as following forest fire (Lombardero and Ayres 2011). Forests are particularly susceptible when they are young, as total defoliation can be more likely and the consequences on tree survival and growth limitation more dramatic. Pests can be associated with early stages of forest growth (e.g. *Acantholyda, Neodiprion, Rhyacionia, Thecodiplosis*), with mature stands (e.g. *Bupalus, Panolis, Lymantria, Diprion*), or with any stage of development of the trees (e.g. *Thaumetopoea, Dendrolimus, Sphynx*). Interestingly, some species were considered serious pests in the past, when the abundance of young stands was higher than nowadays, whereas other species are constantly requiring careful surveillance and management.

Ecological Impact Defoliation of pine forests have a number of ecological impacts at the ecosystem level, mainly because pine stands are simplified ecosystems with a rather early succession phase. Defoliation has thus be thought as a way to speed up the cycle of carbon and nutrients in the soil, which may depend on the intensity and seasonality of the event (Battisti 1988). Such an effect may have positive feedbacks on tree growth and on the diversity of the forest stand. Another ecological impact of the defoliation is related to the availability of prey to a number of generalist predators active in the trophic webs, which may become important regulators of the herbivore populations. Often the trophic webs are sustained by a specific structure of the forest stand (e.g. occurrence of clearings and edges, high connectivity among stands with different tree species composition), so that a number of management measures can be taken in order to increase the presence and effectiveness of natural enemies in regulating populations (Battisti 2006).

Impact on Humans Defoliations of pine forests may result in dramatic changes of the landscape value, which are generally lasting for a long time because of 2–3 years are required to reconstitute the normal set of needles. During the peak outbreak and following years the forest becomes less suitable to visitors and may change its functions to stakeholders and to the public. Consequences can be even worse when the species causing the defoliation is causing health troubles to humans, livestock, and pets, such as in the case of the pine processionary moth and lappet moth (Moneo et al. 2015). Besides measures that can be taken to reduce such an impact by acting directly on the herbivore populations, a good information network of the stakeholders has been shown to be the most effective measure to reduce the negative impacts on humans. For this reason, it is highly recommended that information about the organism involved and preventive measures to reduce impacts are provided as soon as the outbreak is developing.

Insect-Plant Interactions Pine trees responses to injury inflicted by defoliators are well documented, including a series of constitutive and induced defenses, with some of them being effective in regulating the density of the herbivores (Jacquet et al. 2014). This is especially true for those plant-herbivore systems which have coevolved for a long time in the Mediterranean region, as for example in the association between *Pinus nigra* and *T. pityocampa* (Masutti et al. 2005). Such a situation, however, has changed dramatically when foresters cultivate pine species outside of its native range, and even more when exotic pine species such as Monterey pine (*Pinus radiata*) have been introduced for timber (Lombardero and Ayres 2011). The higher susceptibility of these newly established stands has prompted outbreaks over large areas and still represents the most important challenge to the management (Jactel et al. 2015).

Insect-Enemies Interactions Although natural enemies guilds of pine defoliating insects are rather well studied in the Mediterranean, clear density-dependent regulation over a sufficient number of years has been rarely shown. This can be explained by the adoption of management measures which are confounding the potential establishment of natural mechanisms of regulation, as typically in the case of the pine processionary moth (Auger-Rozenberg et al. 2015). In general, the richness and complexity of trophic webs are unexpectedly high and deserve to be further explored, in the aim of finding management options which may maximize the effect of parasitoids, pathogens, and predators.

Outbreak Dynamics All major types of outbreaks have been observed in Mediterranean pine forests. Many species have occasional, eruptive outbreaks (e.g. *Dendrolimus, Panolis, Acantholyda*) whereas others are more frequent (e.g. *Diprion, Rhyacionia*) or even with a tendency to produce cycles (e.g. *Thaumetopoea*) (Battisti et al. 2015). Other species are generally common locally, although rarely build up large outbreaks (e.g. *Neodiprion, Crytocephalus*). Such knowledge becomes important for making predictions as soon as the insect shows up, although it is difficult to cope with, because the same species may display a different outbreak type depending on the local conditions.

Climate Change Climate change has been shown to be a major driver of the range expansion and outbreak dynamics of the herbivore populations in the last decades, and some important evidence is also coming from Mediterranean forest pests, such as *T. pityocampa* (Roques et al. 2015). In this species, range expansion has been explained by improved weather conditions across the winter, which allows higher survival of the colonies and subsequent occupation of new areas. It is not clear, however, if such a pattern applies to other species of defoliating insects, and the first outcome of the research are indicating idiosyncratic responses associated with the specific traits of each species. Predicting the effects of climate change on the population dynamics is even more difficult, as several guilds of natural regulators are involved, and the effect of climate change on most of the species is still unclear.

Management Pine forests in the Mediterranean basin are under intensive forest pest management, mainly due to the frequent outbreaks of the pine processionary moth in both the northern and the southern rims. Insecticides of various type have been used in the past and they are now largely replaced by preparations of *Bacillus thuringiensis kurstaki* (Btk) over hundred thousand hectares each year (Battisti et al. 1998). Still, in a cost-benefit analysis in a study case in South Portugal, the application of Btk was proved to be cost effective, i.e. profitable, only if a social profit was considered by minimizing health risks for humans (Gatto et al. 2009). Alternative or complementary methods are under development and consist mainly of changing the tree species composition of the stand in order to increase the ecosystem resistance, and to encourage natural enemies by providing them with both alternative hosts and shelters. Other methods such as seeding or inundating releases of natural enemies and mating disruption have been attempted but did not reach wide application so far (Martin 2015).

3.2 Oaks

Oak species naturally occur in all Mediterranean countries excluded Egypt. Most common species are the evergreen oaks such as the cork oak *Quercus suber*, the holm oak *Quercus ilex*, its sister species *Quercus rotundifolia*, the kermes oak *Quercus coccifera* in south-western Europe and North Africa. Deciduous and semideciduous oaks, such as *Quercus pubescens* and *Quercus cerris* among many others, occur in about the same area but generally in less dry conditions. Evergreen oaks are distinguished by retaining the mature leaves over the winter. Theoretically, the presence of green leaves all year round would offer defoliators the opportunity to feed throughout all seasons, as long as the climate conditions would allow it. Still most of the defoliators of oaks prefer young developing leaves, and feed mainly during spring, after bud break, while some species may extend the feeding period over summer. During autumn and winter the leaves become hard and less palatable such as due to changes on the concentration of leaf tannins (Feeny 1970).

Taxonomic Traits The assemblage of leaf herbivores feeding on oaks is highly diverse, represented by different families, mostly belonging to the orders Lepidoptera, Hymenoptera and Coleoptera. Among these orders, Lepidoptera are dominant, represented by several families. As an example, 32 species of moths, mostly from the families Noctuidae, Erebidae and Tortricidae were found feeding on holm oaks leaves in southern Spain (Pulido and Diaz 2002). Most of the species can feed on both evergreen and deciduous oaks. For example, the oak processionary moth *Thaumetopoea processionea* (Notodontidae), which is generally associated to deciduous oaks, has been recently also reported on evergreen oaks as well, especially on cork oak (Luciano and Roversi 2001). Some of the species are polyphagous and feed also on other genera of broadleaves, namely *Castanea*, *Fraxinus*, *Populus* and *Alnus*. This is the case of *Malacosoma neustria* and *Eriogaster philippsi* Bartel (Lasiocampidae), *Lymantria dispar* (Erebidae), *Tortrix viridana* (Tortricidae) and some Geometridae. In addition, some species also feed on Mediterranean sclerophyll shrubs, such as *Euproctis chrysorrhoea* (Erebidae) on *Arbutus unedo* in Spain (Frago et al. 2010). Still, genetically differentiated populations of *E. chrysorrhoea* were found associated with different host species (Marques et al. 2014). Also, *Orgyia trigotephras* (Erebidae) feeds on cork oak and kermes oak as well as on several shrub species, in particular *Pistacia lentiscus* as observed in Southern Italy and Tunisia (Ezzine et al. 2014, 2015).

Guild Traits Defoliators feeding on deciduous and evergreen oaks include leaf miners, bud moths, leaf chewers and skeletonizers. Leaf miners feed inside the leaf within which the confined larva eats the internal leaf tissues. Leaf miners feeding on oaks mostly belong to the genus *Phyllonorycter* (Lep., Gracillariidae), characterized by small, usually brightly colored and elegant moths. *Phyllonorycter* larvae mine the leaves causing blotches, giving rise to discolored areas on the leaf surface, usually in underside; for example oval areas on the leaf surface produced by *P. messaniella* on holm oaks. Other miners produce sinuous or linear galleries, such as those done by *Ectoedemia heringiella* (Nepticulidae), After the feeding phase, the larva remains inside the mine to pupate.

Among species that feeds on buds and young shoots of oaks, the leaf roller *T. viridana* is the most common and the most serious pest. The overwintering eggs hatch very early in spring coinciding with bud break. All larval development is completed within a month. Young larvae feed inside buds whereas the mature larvae feed on young leaves. Although neonate larvae of *T. viridana* may starve up to 10 days, synchronization with host plant phenology is most important for their survival (Ivashov et al. 2002). Since bud break timing differs with host tree species, it requires adaptation of the insect life cycle to host tree phenology. In effect different populations of *T. viridana* display differences on the hatching period according with host tree species (Du Merle 1999). For example, in Iberian evergreen oak forests, bud break is earlier on holm oak than on cork oak. As a result, *T. viridana* also hatches earlier on holm oak trees. Different races were proposed for this moth to explain such adaptive trait to host tree phenology (Du Merle 1999).

Several species of weevils, *Orchestes* spp. and the leaf roller weevil *Attelabus nitens* (Col. Curculionidae) may also feed on oak leaves and occasionally cause concern. Adults of *Orchestes* ssp. Also feed on leaves while the larvae are leaf miners. *A. nitens* typically produces a roll, cutting the edge of the leave, where females oviposit their eggs. Among sawflies (Hym: Tenthredinidae) special emphasis is given to *Periclista andrei* which is one of the most serious defoliator of cork oak in the western Mediterranean (Pereira et al. 2014). The easy recognizable light green larvae have the particularly of chewing elliptical holes on leaves.

Most of the defoliator species on oaks are univoltine, generally overwintering as egg, especially the Lepidoptera. Mating and egg laying usually occur during summer. Still, reproductive traits are highly variable among species, allowing its identification. *T. viridana* lays the eggs in pairs on young branches of the crown. Females of *M. neustria* lay bare eggs on typical sleeves surrounding twigs. The females of *E. chrysorrhoea* lay egg-masses, covered by brown scales, on the underneath of leaves. *L. dispar* lays similar although larger egg masses usually on tree trunk and, at high population densities, on branches or even on stones.

Spring feeders, like *M. neustria, E. philippsi* and *L. dispar*, hatch quite early during spring when new leaves are expanding. Several geometrid larvae, particularly

Operophthera brumata and *Erannis defoliaria*, may be also observed in springtime on oak trees, after hatching from the overwintering eggs. The larvae of *O. brumata* occur earlier, first feeding on the buds and then on the leaves, whereas the larvae of *E. defoliaria* develop later and feed exclusively on the leaves.

E. chrysorrhoea is an exception to the above described general life cycle, hatching occur in summer and young larvae feed until autumn, during winter usually the larvae hibernate to resume feeding in spring. Its presence can be recognized by the silky larval nests built in the tree crown in autumn and lasting all winter. Inside the nests the larvae live gregariously until the third instar. In spring, the mature larvae lose their gregarious instinct and spread through the tree crown feeding on buds and young leaves. They may also turn to feed on lower vegetation when the trees are completely defoliated.

Economic Damage Most of the species defoliating oaks are inconspicuous and cause no significant harm to the trees. Nevertheless a few defoliator species may reach noticeable population densities, these are those major recognized for their economic relevance. In some species, in particular of defoliating Lepidoptera, and some sawflies, such as with *P. andrei*, the populations undergo outbreaks at more or less regular intervals. Depending on the intensity and the period in which defoliation takes place, there can be economic losses due to acorn loss, reduced growth on both tree height and radial increment. In the case of cork oak, reduced cork growth and of the cork quality are also registered. If not severe, the early defoliation allows the oak trees compensating the loss of photosynthetic tissue by developing new leaves during late spring. Still, it may induce fluctuating asymmetry (Díaz et al. 2004), i.e. small deviations from perfect symmetry, which is an indicator of plant stress which may be also caused by abiotic factors (Cornelissen et al. 2004). In evergreen oak agro-ecosystems, acorns production is a most important non-wood forest product, particularly for feeding pigs during the winter fattening period in the Iberian evergreen oak agroforest ecosystems (Rodriguez-Estevez et al. 2009). In the case of *T. viridana*, which also feeds on floral buds, a reduction in acorn production in consequence of floral bud consumption was proposed to explain reduced pig production in years of outbreak. Also, resulting fluctuating asymmetry of leaves may per se further decrease acorn production in the following year (Díaz et al. 2004).

Among the above reported species, *L. dispar* and *T. viridana* are probably the most serious damaging defoliators all over their distribution range. *E. philippsi* is a major defoliator of *Q. calliprinos* and *Q. coccifera* in East Mediteranean (Halperin 1963). *P. andrei* is also a major defoliator in the Iberian Peninsula (Pereira et al. 2014). Other species, like *M. neustria* are of minor importance, although during outbreaks it may produce relevant damage on cork oaks (Luciano and Roversi 2001). Geometrid species are known to produce cyclic outbreaks all over Europe on deciduous oaks and other broadleaved tree species, which marginally affect Mediterranean ecosystems (Tenow et al. 2013).

Ecological Impact During outbreaks, which may last a number of years, oaks may suffer intense defoliation. Many researchers consider such attacks as one of the main biotic factors causing physiological decline of evergreen oaks, causing remarkable ecological and economic impacts, particularly in cork oak woodlands (Prota et al. 1991). Ecological damage may consist also of altering the composition of the animal and plant communities associated with the defoliated trees, whose effects can be dependent on the duration of the outbreak. Unfortunately, few data are available in this respect. Finally, aesthetic damage to the landscape can be observed when spiteful crowns are left by the attacking insects after severe population outbreaks.

Impact on Humans Apart from the damage caused to the trees, larvae of some Lepidoptera feeding on oaks, such as *E. chrysorrhoea*, also cause public health concern due to larval irritating setae present on the abdominal segments after the third instar. These setae are harmful on contact and can be blown by the wind, causing irritations to the skin, the respiratory tract and the eyes of warm-blooded animals. Primary concern is also due to the setae of the larvae of the oak processionary moth *T. processionea* for their high allergenic power (Moneo et al. 2015), still this species only very occasionally was observed on evergreen oaks (Niccoli and Tiberi 1986).

Insect-Enemies Interactions Being near the bottom of food webs, the insect defoliators in their various development stages support various organisms of higher trophic levels, among them many species of arthropods, birds, and mammals. Many insectivorous bird species are associated with predation of distinct stages of defoliating pests during the breeding season (Pereira et al. 2014; Ceia and Ramos 2014). For instance, in southwestern Iberian Peninsula 26 bird species were found potential regular predators of 20 major pests on Mediterranean oak woodlands ecosystem (Ceia and Ramos 2014). Different bird species are complementary due to divergent food niches and breeding seasons. Ground-foragers prey on overwintering pupae, tree-foragers prey on eggs, larvae and pupae and aerial-sweepers prey on moths during flight. A large community of parasitoid and predators further regulate the communities of oak defoliators. An example is *Calosoma sycophanta* (Col: Carabidae) which occurs in evergreen oak forests with high densities associated with *L. dispar* outbreaks (Serrão 2002; Justicia et al. 2007). High numbers of dipteran and hymenopteran parasitoids attacking mainly the immature stages (eggs, larvae and pupae) play a significant role in restraining the populations during the latent phase and accelerate their collapse of the outbreaks. However, their integrated role in keeping the populations at low density needs to be further explored.

Outbreak Dynamics Most defoliators experience cyclic population outbreaks, with peaks generally lasting 2 years, during which intense defoliation is observed, with several years interval, as 6–7 years observed for *L. dispar* in Sardinia (Luciano and Roversi 2001; Cocco et al. 2010). During outbreaks complete defoliations may occur. Defoliated trees normally do not die, but suffer a severe physiological decline, they may be then predisposed to attacks of secondary pathogens and xylophagous insects.

Climate Change Drought has been one of the most important factors affecting oaks in the Mediterranean, especially cork oak. The impact of drought on the two most common evergreen oaks of the Mediterranean has been shown to increase with climate change (David et al. 2007). Whereas, drought stress has a well-known predisposal effect on bark beetles and wood borers, the impact on defoliators may be not so straightforward. The guild of defoliators is generally responding positively to mild drought in a meta-analysis of Jactel et al. (2012). Drought stress may decrease allocation of nutrient resources to growth and conversely increase secondary metabolism according to the growth-differentiation balance hypothesis (Hale et al. 2005). Thus, it may be detrimental for those that feed on foliage, especially for those insects that feed during summer when drought stress is more pronounced, such as *L. dispar*. Also, leaves, under extended drought stress become harder sooner in early summer and so less palatable for defoliators. This effect may be one of the reasons why outbreaks of *L. dispar* in cork oak forest in Portugal are less frequent and spatially confined to smaller areas than used to be in the past, as before the 1960s when outbreaks were intense and frequent (Azevedo e Silva 1960). On the other hand, in Israel the outbreaks of *L. dispar diaspirina* in native forests of *Q. calliprinos* had been considered rare events, but have become more frequent in the twenty-first century.

Elevated CO_2 concentration has also been claimed to affect the performance of defoliating insects; although, the relationships are difficult to clarify because of the multi- factor interactions involved (Hunter 2001).

Management Defoliator insects in oak forests have been treated mainly with microbiological insecticides, namely with preparations of Btk by aerial spraying (Luciano et al. 1992; Serrão 2002). Diflubenzuron based insecticides have been also applied to control *L. dispar* in cork oak forests in Portugal (Serrão 2002). Pheromone traps have been used for monitoring populations; however, pheromone-based control tactics, such as mating disruption, are too costly and therefore were not practiced in the Mediterranean basin for the control of defoliators on oaks so far.

3.3 Poplars and Willows

Poplars and willows are important components of the Mediterranean forest and farming systems and they are central in the socio-economic development of the human communities associated with forests (FAO 2009). A very large number of species occur in the area, with some of them being used in afforestation and agroforestry schemes for centuries. Insect and disease impacts on these trees are notoriously high, as documented in several reviews (e.g. Delplanque 1997).

Taxonomic Traits More than 24 European native insect species feed on *Populus* and *Salix* (de Tillesse et al. 2007). This list include polyphagous moth species that feed on many other broadleaves, like *E. chrysorrhoea*, *L. dispar*, *O. brumata*, *Orgyia antiqua* and ermine moths *Yponomeuta* spp., as well as some species that feed mostly or exclusively on *Populus* and *Salix*, such as the satin moth *Leucoma salicis* (Lep. Erebidae) and two species from Notodontidae family, *Cerura vinula* and *Clostera anastomosis*. Lepidoptera species include leaf miners, like *Phyllocnistis unipunctella* (Phyllocnitidae) and *Phyllonorycter populifoliella* (Gracillariidae), leaf rollers as *Epinotia solandriana*, and several leaf-chewers as *L. salici* and *C. anastomosis*. A few leaf beetles species (Chrysomelidae) such as *Chrysomela populi*, *C. tremulae* and *Phratora* spp., and some weevils (Curculionidae), such as the leaf-roller weevil *Byctiscus populi*, *B. betulae, Phyllobius* spp., *Polydrusus impressifrons* and *Cryptorhynchus lapathi*, feed on poplars and willows. Some are specialized on poplars such as the two chrysomelids and the leaf-roller weevil *B. populi*. Some sawflies (Hym. Tenthredinidae) also feed on poplars leaves, in particular *Trichiocampus viminalis* and *Nematus* spp.

Guild Traits The large diversity of defoliator species associated with poplars and willows is mirrored by their diverse feeding types, which can take very distinctive forms. It is the case of the leaf-rollers *Byctiscus* spp., which produce typical tubes using a single leaf containing the eggs and larvae inside. The larvae of chrysomelids usually skeletonize the epidermis of the leaf in one side, generally underneath. The adult beetles chew the leaves, frequently leaving small holes in the leaf surface. The larvae of sawflies usually begin their attack from the edge of the leaf. Larvae of leaf miners form thin galleries within the leaf tissues.

Some species have gregarious larvae and form leaf tents, this is the case of *M. neustria* and *Yponomeuta* species, whose larvae spin silk tents and feed gregariously on the leaves. Such structures may further serve as shelters to other organisms. Although these tent-caterpillar species are polyphagous they may be occasionally seen on poplars.

Although some species are univoltine, like *C. vinula*, many species feedings on poplars and willows have more than one generation per year, some up to three or four generations depending on climatic conditions. This is the case of the leaf miner *P. unipunctella*, of the leaf chewer *C. anastomosis* and the two chrysomelids *C. populi* and *C. tremulae*. Spring, summer and autumnal feeding are thus observed on poplar and willow trees.

Economic Damage Attack by defoliators in poplars mature plantations is usually moderate, but in young plantations, especially in susceptible clones, damage may be impressive, and may lead to total defoliation. In consequence of intense defoliation, tree growth slows down up to 80 % in comparison with non-defoliated trees (Caldbeck et al. 1978).

Among coleopteran species, *C. populi* is the most damaging leaf-feeding beetle of poplars, causing most concern, especially in young plantations and nurseries.

Leaf chewers Lepidoptera such as *L. salici* may cause significant loss during outbreak years (Ziemnicka 2008). Other species are only of minor importance. Leaf miners can occasionally be extremely numerous and attack a large proportion of the leaves, such as observed for *P. unipunctella* in Belgium where 75 % of the leaves of susceptible clones were found mined (Nef 1988). Although the attacks by leaf miners do not cause immediately defoliation, the surface area, and thus the photosynthesis of leaves is reduced delaying tree growth as observed with leaf chewers. Further, leaf miners speed up leaf-fall as observed with *P. populifoliella* (Belova and Vorontsov 1987).

The impact of defoliation on poplar growth also depends on season. When defoliation takes place in spring, the poplars may produce new foliage and therefore the impact of defoliation will have minor consequences on tree growth. In contrast, summer defoliation may have stronger impact on tree growth. Repeated defoliation over several consecutive years can sometimes kill the trees.

Ecological Impact Severe defoliation may favor several indirect negative impacts, for example it can reduce the shelter function of windbreaks. If poplars are used as windbreaks, when attacked by polyphagous pests, they can be also a source of undesirable pests into adjacent agricultural crops (Tertyshnyi 1991) but also as a refuge of natural enemies. Defoliation and leaf-drop induced by leaf miners further diminish the aesthetic value of poplars in rural an urban environments (Belova and Vorontsov 1987).

Impact on Humans Occasional defoliations by *E. chrysorrhoea* may represent a threat to human health, especially in towns (Battisti et al. 2011).

Insect-Plant Interactions The main chemical defenses of Salicaceae are phenolic glycosides (salicinoids) and condensed tannins. These secondary compounds reduce feeding, growth and survival of insect herbivores (Lindroth and Clair 2013). Still, the production of these chemical defense compounds is costly and its expression depends on the interaction of genotype with environmental factors. Therefore, the impact of defoliators depends on the tree physiological status and site conditions. For example, comparative experiments showed that the leaf miner moth *P. unipunctella* was less abundant on sandy soils than on muddy and wet ones (Nef 1982).

The effect of soils in the chemical composition of the leaves would justify the observed differences on the leaf miner mortality. Conversely, trees growing on rich soils were found to be more susceptible to attack by *C. lapathi* (Attard 1978). A negative correlation between growth and total phenolic glycoside concentration, in line with an exchange between primary and secondary metabolism, could explain this pattern.

Following attacks by defoliators and leaf miners, the expression of defense mechanism is also induced in plants; secondary metabolites of leaves, such as polyphenols and mineral contents are then modified, which consequently reduces the development and fecundity of the survivors and slows down the insect population growth (Nef 1986). Following defoliation, trees undergo compensatory mechanisms, well-known as tree tolerance, which may balance foliar loss via new foliage production or raising photosynthesis efficiency allowing increase tree growth. In poplars, tolerance seems to increase with tree age (Hale et al. 2005).

Insect-Enemies Interactions Similarly to other taxonomic groups of Mediterranean native trees, large communities of natural enemies, namely arthropod predators and parasitoids, insectivorous birds and mammals, and entomopathogens (virus, fungi and bacteria), all contribute to reduce and regulate the populations of insect defoliators on poplars and willows. As an example, in an extensive study done in Serbia and Montenegro of Braconidae fauna related with *Populus* spp., 52 braconid species from 29 genera were found associated with insect pests on poplar trees (Žikić et al. 2013). Among these, many braconid parasitoids were found parasitizing defoliator insects, namely the leaf-roller weevil *B. populi*, two species of sawflies, *Fenusella hortulana* and *Nematus bipartite* and 24 Lepidoptera defoliators from several families.

Outbreak Dynamics Some polyphagous moth species that feed on various tree species undergoing outbreak cycles, such as *M. neustria*, may also cause damage to poplars during exceptional outbreak years. Also, some Lepidoptera specialist on poplars, such as *L. salicis*, undergoes outbreaks, which only occasionally bear some importance (Ziemnicka 2008).

Climate Change There are no specific studies addressing the impact of climate changes on poplars defoliators in the Mediterranean. Drought might be a stressor factor for poplars on these climatic regions. In North America it was found an effect of drought stress on the susceptibility of poplar trees to defoliators, yet the effect varied with pest species (Hale et al. 2005). The authors found that in black poplar *P. nigra* drought stress decreased larval growth on *L. dispar* whereas it had no effect on the North American species *Orgyia leucostigma*.

Management Site preparation, soils with good ventilation, water and pH conditions, and forest management practices providing trees optimal conditions, reduce plant physiological stress, and are thus essential to maintain the resistance and tolerance of trees in general and poplars in particular.

Low plant diversity is also a factor favoring insect pest's outbreaks. For example in poplar plantations with an abundant and varied understorey, *L. salicis* outbreaks are observed to be rare (de Tillesse et al. 2007). This can in part be explained by the concentration of resources. As the larvae migrate regularly from tree to tree, when poplars become sparse, the odds of finding a suitable host tree and survive diminishes. Trees in the center of plantations are those usually more prone to attack by *C. lapathi* (Attard 1978), which may be also explained by resource concentration hypothesis and low diversity usually found in inner stands.

Microbiological control using products based on Btk, fungi such as *Beauveria bassiana*, viruses and entomopathogenic nematodes are efficient against many species of defoliators. For example, trials using Btk against *L. salicis* suggest a positive benefit-cost ratio as the economic losses due to defoliation in non-treated trees is further prevented (Schotveld and Wigbels 1975).

Genetic resistance is a strategy to deal with poplars insect pests. Different genetic materials and their hybrids highly differ on their susceptibility to insect defoliator. For example, resistance to *P. unipunctella* was found to differ greatly among different poplar hybrids (Nef 1986). It has been suggested that monoclonal plantations of poplars, which started hundred years ago in Europe, and have become very widespread thereafter, may be responsible for the high susceptibility to insect pest populations and the severe damage (de Tillesse et al. 2007)

3.4 Other Species of Interest

3.4.1 Cypress False Silk Moth

Pachypasa otus (Drury) (Lep. Lasiocampidae) is mainly occur in East Mediterranean, although may found in large area between Italy, Armenia and Iran. This is a rather big moth; the wingspan is 36–45 mm. In Israel, the flight and egg laying occur in late summer (September). The larval development takes about 10 months. The larvae spin grey cocoons measuring about 9.0 × 7.5 cm. In ancient times, the silk was taken to make the crimson-dyed silk cloths. In East Mediterranean the host tree list includes *Cypress*, mainly *Cupressus sempervirens*, different pine species, and several species of *Eucalyptus*, mainly, *E. camaldulensis* and *E. occidentalis. C. sempervirens* and *E. camaldulensis* are the main hosts in Israel (Halperin 1976). In its northern range, the moth may feed on *Juniperus* spp., *Quercus* spp. and *Thuja occidentalis*. The damage inflicts on infested trees is usually limited and the defoliation seldom observed. The larvae may cause some public concern when descend from infested trees in great numbers during pupation phase and due sensitivity of some people to urticating hairs occurring on the first abdominal segment of the last instars.

3.4.2 Ash Sawflies

Tomostethus nigritus (Fabricius 1804) (Hym. Tenthredinidae) and other *Tomostethus* species are pests of *Fraxinus* spp. They damage entire mixed and pure ash forests and also urban plants, with outbreaks observed more frequently in the Mediterranean in the last three decades. *T. nigritus* is a univoltine sawfly, with adults flying in early spring and voracious larvae that feed on ash leaves in a few weeks, and then burrow in the soil to overwinter as a prepupa in a cocoon. Part of them pupate at the beginning of the next spring and will originate new adults, the rest stay in diapause in the soil. Monitoring is essential to predict the damage and it consists of cocoon census in soil samples and adult capture by suspension of yellow sticky traps. As natural enemies are not efficient enough to restrain *T. nigritus* populations, application of insect growth regulator products (IGRs) are applied to prevent of lower the outbreaks. IGR application should be well timed at the beginning of the larval feeding, since advanced larval stages are not sufficiently sensitive to these products.

3.4.3 Moroccan Locust

The Moroccan locust *Dociostaurus maroccanus* (Orthoptera, Acrididae) occurs in all Mediterranean countries. It may develop high densities in the more dry areas of Northern Africa and Eastern Mediterranean. It is usually a solitary grasshopper but occasionally after rainy winters the population steeply increases; and then, in early summer when the vegetation dry out the grasshoppers become gregarious and fly to nearby forest stands. In Israel, the damage is usually inflicted on eucalyptus trees planted as small forests for recreation and shade for cattle. Young plantations may be destroyed by these attacks.

3.4.4 Bush-Crickets (Contributed by L. Mazzon, University of Padua)

The bush-cricket *Barbitistes vicetinus* Galvagni and Fontana 1993 (Orthoptera, Tettigoniidae) is an endemic species of the Veneto Region of Italy, and it has been considered rare in the past and confined to small wooded areas. The genus *Barbitistes* is common in the Mediterranean area and the species seem to share similar ecological traits. Since 2008 the species causes outbreaks that, during the subsequent years, affects gradually larger forest areas. The triggering mechanism of these outbreaks is still unknown. Although this species feeds on a very wide spectrum of plants, it shows a marked preference to *Fraxinus ornus*, *Ostrya carpinifolia*, *Quercus pubescens* and *Castanea sativa. B. vicetinus* may cause intense defoliations that could also affect the neighboring vineyards or olive groves adjacent to the wooded areas. At the end of March, immediately after hatching, young nymphs climb up into shrubs and tree crowns where they feed on foliage and complete their development until the adult stage. The females lay eggs in the ground from the end of June to the beginning of July. A large amount of the eggs hatch during the next March (annual life cycle) while a variable portion of eggs remain in the soil for another year (biennial life cycle).

References

Attard G (1978) Extension des dégâts du charançon du peuplier sur les peupleraies d'Aquitaine. Phytoma 30:298

Auger-Rozenberg MA, Barbaro L, Battisti A et al (2015) Ecological responses of parasitoids, predators and associated insect communities to the climate-driven expansion of pine processionary moth. In: Roques A (ed) Processionary moths and climate change: an update. Springer-Quae, Dordrecht/Versailles, pp 311–358

Barbéro M, Loisel R, Quézel P et al (1998) Pines of the Mediterranean basin. In: Richardson DM (ed) Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, MA, pp 153–170

Battisti A (1988) Phytophagous insects in the energy flow of an artificial stand of *Pinus nigra* Arnold in Northern Italy. Redia 71:139–159

Battisti A (2005) Overview on the entomological research in the forest ecosystems of the northern rim of the Mediterranean Sea. In: Ghaioule D, Lieutier F (eds) Entomological research in Mediterranean forest ecosystems. INRA, Paris, pp 15–22

Battisti A (2006) Insect populations in relation to environmental change in forests of temperate Europe. In: Paine TD (ed) Invasive forest insects, introduced forest trees, and altered ecosystems. Springer, Dordrecht, pp 127–140

Battisti A, Longo S, Tiberi R, Triggiani O (1998) Results and perspectives in the use of *Bacillus thuringiensis* Berl. var. *kurstaki* and other pathogens against *Thaumetopoea pityocampa* (Den. et Schiff.) in Italy (Lep., Thaumetopoeidae). Anz Schädlingsk Pflanz Umweltschutz 71:72–76

Battisti A, Holm G, Fagrell B et al (2011) Urticating hairs in arthropods – their nature and medical significance. Annu Rev Entomol 56:203–220

Battisti A, Avcı M, Avtzis DN et al (2015) Natural history of the processionary moths (*Thaumetopoea* spp.): new insights in relation to climate change. In: Roques A (ed) Processionary moths and climate change: an update. Springer-Quae, Dordrecht/Versailles, pp 15–80

Belova NK, Vorontsov AI (1987) The poplar moth. Zashchita Rastenii (Moskva) 4:32–35

Caldbeck ES, McNabb HS, Hart ER (1978) Poplar clonal preferences of the cottonwood leaf beetle. J Econ Entomol 71:518–520

Ceia RS, Ramos JA (2014) Birds as predators of cork and holm oak pests. Agrofor Syst:1–18. Published online 30 September 2014

Cocco A, Cossu AQ, Erre P et al (2010) Spatial analysis of gypsy moth populations in Sardinia using geostatistical and climate models. Agric For Entomol 12:417–426

Cornelissen T, Stiling P, Drake B (2004) Elevated CO2 decreases leaf fluctuating asymmetry and herbivory by leaf miners on two oak species. Glob Chang Biol 10:27–36

David TS, Henriques MO, Kurz-Besson C et al (2007) Water-use strategies in two co-occurring Mediterranean evergreen oaks: surviving the summer drought. Tree Physiol 27:793–803

de Azevedo e Silva F (1960) Pragas do sobreiro em Portugal. Bolm Jta Nac Cortiça 265:3p

De Tillesse V, Nef L, Charles J et al (2007) Damaging poplar insects. FAO, Rome

Delplanque A (ed) (1997) Les insectes du peuplier. INRA, Paris

Díaz M, Pulido FJ, Møller AP (2004) Herbivore effects on developmental instability and fecundity of holm oaks. Oecologia 139:224–234

Du Merle P (1999) Egg development and diapause: ecophysiological and genetic basis of phenological polymorphism and adaptation to varied hosts in the green oak tortrix, Tortrix viridana L. (Lepidoptera: Tortricidae). J Insect Physiol 45:599–611

Ezzine O, Hausmann A, Branco M et al (2014) Genetic patterns, host use and larval morphology in Tunisian populations of *Orgyia trigotephras*. Bull Insectol 67:73–79

Ezzine O, Branco M, Villemant C et al (2015) Host use in *Orgyia trigotephras* (Erebidae, Lymantriinae) during outbreak: effects on larval performance and egg predation. Ann For Sci. doi:10.1007/s13595-015-0484-7

FAO (2009) Improve the contribution of Poplars and Willows in meeting sustainable livelihoods and land-use in selected Mediterranean and Central Asian countries. FAO project GCP/INT/059/ITA, Izmit, 27–31 July 2009. Available at http://www.fao.org/docrep/012/k6000e/k6000e00.htm

Feeny P (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565–581

Frago E, Guara M, Pujade-Villar J et al (2010) Winter feeding leads to a shifted phenology in the browntail moth *Euproctis chrysorrhoea* on the evergreen strawberry tree *Arbutus unedo*. Agric For Entomol 12:381–388

Gatto P, Zocca A, Battisti A et al (2009) Economic assessment of managing processionary moth in pine forests: a case-study in Portugal. J Environ Manage 90:683–691

Hale BK, Herms DA, Hansen RC et al (2005) Effects of drought stress and nutrient availability on dry matter allocation, phenolic glycosides, and rapid induced resistance of poplar to two lymantriid defoliators. J Chem Ecol 31:2601–2620

Halperin J (1963) Some insects affecting oak. Hora'at Hateva 13–14:43–48 (Hebr.)

Halperin J (1976) Insect pests of forest trees. Encycl Agric (Tel Aviv) 3:623–640. (Hebr.)

Hunter MD (2001) Effects of elevated carbon dioxide on insect plant interactions. Agric For Entomol 3:153–159

Ivashov AV, Boyko GE, Simchuk AP (2002) The role of host plant phenology in the development of the oak leafroller moth, Tortrix viridana L. (Lepidoptera: Tortricidae). For Ecol Manage 157:7–14

Jacquet JS, Bosc A, O'Grady A et al (2014) Combined effects of defoliation and water stress on pine growth and non-structural carbohydrates. Tree Physiol 34:367–376

Jactel H, Petit J, Desprez-Loustau M-L et al (2012) Drought effects on damage by forest insects and pathogens: a meta-analysis. Glob Chang Biol 18:267–276

Jactel H, Barbaro L, Battisti A et al (2015) Insect – tree interactions in *Thaumetopoea pityocampa*. In: Roques A (ed) Processionary moths and climate change: an update. Springer-Quae, Dordrecht/Versailles, pp 265–310

Justicia AI, Sánchez AS, Gonzalvo MM et al (2007) Distribución y abundancia de *Lymantria dispar* (Linnaeus, 1758) (Lepidoptera: Lymantriidae) en las principales masas de carrasca *Quercus ilex* (L.) subsp. *rotundifolia* (Lam.) y alcornoque *Quercus suber* (L.) de la Comunitat Valenciana. Bol San Veg Plag 33:491–502

Kerdelhue C, Zane L, Simonato M et al (2009) Quaternary history and contemporary patterns in a currently expanding species. BMC Evol Biol 9:220. doi:10.1186/1471-2148-9-220

Lieutier F, Ghaioule D (2005) Preface to entomological research in Mediterranean forest ecosystems. INRA, Paris, pp 5–6

Lindroth RL, Clair SBS (2013) Adaptations of quaking aspen (*Populus tremuloides* Michx.) for defense against herbivores. For Ecol Manage 299:14–21

Lombardero MJ, Ayres MP (2011) Factors influencing bark beetle outbreaks after forest fires on the Iberian Peninsula. Environ Entomol 40:1007–1018

Luciano P, Roversi PF (2001) Fillofagi delle querce in Italia. Ed Poddighe, Sassari

Luciano P, Floris I, Lentini A et al (1992) Utilization of *Bacillus thuringiensis* Berl. to control *Lymantria disp*ar in Sardinian cork oak forests. II Results of tests carried out in 1991. Redia 75:549–563

Marques JF, Wang HL, Svensson GP et al (2014) Genetic divergence and evidence for sympatric host-races in the highly polyphagous brown tail moth, *Euproctis chrysorrhoea* (Lepidoptera: Erebidae). Evol Ecol 28:829–848

Martin JC (2015) Development of environment-friendly strategies in the management of the processionary moths. In: Roques A (ed) Processionary moths and climate change: an update. Springer-Quae, Dordrecht/Versailles, pp 411–427

Masutti L, Battisti A, Faccoli M (2005) Insect fauna of the *Pinus nigra* group in Italy. In: Ghaioule D, Lieutier F (eds) Entomological research in Mediterranean forest ecosystems. INRA, Paris, pp 79–88

Millar CI (1998) Early evolution of pines. In: Richardson DM (ed) Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, pp 69–93

Moneo I, Battisti A, Dufour B et al (2015) Medical and veterinary impact of the urticating processionary larvae. In: Roques A (ed) Processionary moths and climate change: an update. Springer-Quae, Dordrecht/Versailles, pp 359–410

Mouna M (2005) Overview of entomological research on the forest ecosystems of the regions south of the Mediterranean Sea. In: Ghaioule D, Lieutier F (eds) Entomological research in Mediterranean forest ecosystems. INRA, Paris, pp 23–34

Nef L (1982) Relation between population density of *Phyllocnistis suffusella* and genetical and environmental characteristics of poplars. In: Visser JH, Minks AK (eds) Proceedings 5th international symposium on insect-plant relationships, Wageningen

Nef L (1986) Interactions between *Phyllocnistis suffusella* Z. and poplar leaves. In: Mattson WJ, Levieux J, Bernard-Dagan C (eds) Mechanisms of woody plant defense against insects. Springer, New-York, pp 239–251

Nef L (1988) Etude quantitative de populations de *Phyllocnistis suffusella* Z. (Lep., Lithocolletidae) en Belgique. Ann Sci For 45:255–263

Niccoli A, Tiberi R (1986) Osservazioni sulla biologia e sul comportamento delle larve di *Thaumetopoea processionea* L. (Lepidoptera, Thaumetopoeidae). Redia 69:285–297

Pereira P, Godinho C, Roque I et al (2014) Time to rethink the management intensity in a Mediterranean oak woodland: the response of insectivorous birds and leaf-chewing defoliators as key groups in the forest ecosystem. Ann For Sci 71:25–32

Prota R, Floris I, Lentini A et al (1991) Aspetti entomologici della quercia da sughero e prospettive di protezione in Sardegna. In: Aspetti fitopatologici delle Querce, Atti del Convegno «Problematiche fitopatologiche del Genere Quercus in Italia», Firenze, 19–20 Nov 1990, pp 284–304

Pulido FJ, Díaz M (2002) Dinámica de la regeneración natural del arbolado de encina y alcornoque. In: Pulido FJ, Campos P, Montero G (eds) La gestión forestal de las dehesas. IPROCOR, Mérida, pp 39–62

Rodríguez-Estévez V, García A, Peña F et al (2009) Foraging of Iberian fattening pigs grazing natural pasture in the dehesa. Livest Sci 120:135–143

Roques A, Rousselet J, Avcı M (2015) Climate warming and past and present distribution of the processionary moths (*Thaumetopoea* spp.) in Europe, Asia Minor and North Africa. In: Roques A (ed) Processionary moths and climate change: an update. Springer-Quae, Dordrecht/Versailles, pp 81–162

Santos HM, Paiva MR, Rocha S et al (2013) Phenotypic divergence in reproductive traits of a moth population experiencing a phenological shift. Ecol Evol 3:5098–5108

Schotveld A, Wigbels V (1975) Control of *Leucoma salicis* in East Flevoland. Populier 12:77–78

Serrão M (2002) Damage evolution and control of *Lymantria dispar* L. in a cork oak forest of southern Portugal. IOBC WPRS Bull 25:109–114

Simonato M, Mendel Z, Kerdelhué C et al (2007) Phylogeography of the pine processionary moth *Thaumetopoea wilkinsoni* in the Near East. Mol Ecol 16:2273–2283

Tenow O, Nilssen A, Bylund H et al (2013) Geometrid outbreak waves travel across Europe. J Anim Ecol 82:84–95

Tertyshnyi AS (1991) Are poplar windbreaks effective? Sadovodsto Vinogradarstvo 2:18

Ziemnicka J (2008) Outbreaks and natural viral epizootics of the satin moth *Leucoma salicis* L. (Lepidoptera: Lymantriidae). J Plant Prot Res 48:23–39

Žikić V, Stanković SS, Ilić M et al (2013) Braconid parasitoids (Hymenoptera: Braconidae) on poplars and aspen (*Populus* spp.) in Serbia and Montenegro. North West J Zool 9(2):264–275

Chapter 4
Native Fruit, Cone and Seed Insects in the Mediterranean Basin

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Abstract Tree reproductive structures represent both an extremely rich source of food and breeding sites for many insect species, which are considered the most important seed predators during the pre-dispersal phase of seed development. In the Mediterranean Basin, a total of 99 native species, distributed among 47 genera, 21 families and 5 orders (Coleoptera, Diptera, Hemiptera, Hymenoptera and Lepidoptera), are currently known to colonize the fruiting structures of both angiosperms and gymnosperms. Such entomofauna displays a particularly high level of endemism. Species can be included in different guilds, depending on whether they feed or develop only in the fruit (including the seeds) or if they can also feed or develop in other habitats (e.g. foliage, shoots and twigs, cone-bearing shoots, bark) when fruits are unavailable. Specialist and generalist insect species have developed diverse ecological strategies to exploit this particular kind of resource, which, unlike other parts of the plant such as leaves, can display important spatio-temporal variations in abundance. Additionally to direct consumption, insect attacks can lead to fruit abortion or facilitated introduction of microbes and pathogens. Fruiting structure insects can have important impacts on both plant demography and evolution, which make them contribute to key ecological processes in Mediterranean forest ecosystems. Economic impacts of fruiting structure insects are related to reductions in the availability of high quality seeds for reforestation and afforestation programs, or by affecting supplies of non-wood forest products. This chapter provides the first synthesis on the diversity, the evolutionary ecology and the impacts of the insect fauna associated with fruits and seeds of forest trees in the Mediterranean Basin.

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4.1 Introduction

Tree reproductive structures, or fruiting structures, include pollen, flowers, nuts, cones and seeds. These plant structures interact with diverse mutualistic and antagonistic insect species. Mutualistic insects may be essential for plant reproduction during pollination, while antagonistic insects may be damageable to plants by consuming and removing parts of their reproductive tissues and by selectively feeding on their seeds (Crawley 1989). This chapter will specifically address plant antagonistic insects that use fruiting structures as feeding and/or breeding sites, with an emphasis on their representatives in Mediterranean forest ecosystems.

Compared to other insect groups, insects that feed on fruiting structures have received little attention from both entomologists and ecologists until the 1980s because their predominantly cryptic way of life makes them difficult to detect with simple external fruit examination, and because their economic impact on seed crops was hardly quantifiable. But the multiplication of tree improvement and planting programs relying on both seed certified collections and seed orchards progressively pointed out the need of developing research on the ecology and the impact of seed insects (Roques 1983). Since then, insects exploiting fruiting structures have not only received considerable attention from ecologists for their crucial role in plant demography, spatial distribution, diversity and evolution (Hulme 1998; Maron and Crone 2006; Kolb et al. 2007), but also for the numerous attributes that distinguish them from other forms of herbivory in shaping insect-plant interactions (Janzen 1971; Turgeon et al. 1994; Hulme and Benkman 2002). Interestingly, certain insect seed feeders can be considered as parasites when seeds are used only during a part of the life cycle, while others can be considered as predators when they feed exclusively on seeds[1] (Crawley 1989; Hulme 1998). Additionally to direct consumption, insect attacks can lead to fruit abortion (Sallabanks and Courtney 1992) or to facilitated introduction of microbes and pathogens (Battisti et al. 1999; Luchi et al. 2012). Fruit and seed insects are thus likely drivers of key ecological processes in tree populations, which makes them ideal model systems to address key ecological and evolutionary issues in forest ecosystems. But many species have also important economic impacts by reducing the amount of seeds available to both afforestation and natural regeneration-based management programs (Roques 1983; Turgeon et al. 1994). Moreover, fruiting structure insects can affect forest services in non-wood product supplies such as nuts, chestnuts, pine nuts and acorns (Alford 2007). High levels of insect damages may lead to greater investment in both time and money in seed harvesting activities to compensate seed and fruit losses to insects.

A distinction is usually made between pre-dispersal consumers that feed on fruiting structures as long as fruits and seeds remain on their parent plants, and post-dispersal consumers that forage for fruits or seeds after they have been dispersed. Although numerous plants species can suffer from great levels of post-dispersal consumption from insects, e.g. ants and weevils (Crawley 1989; Hulme 1998), this

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[1] The embryo is considered as a preyed-individual.

chapter will focus exclusively on insect pre-dispersal consumers. There are three reasons. First, a greater diversity of taxa (especially invertebrates) feed on fruiting structures pre- rather post-dispersal. Second, insects are considered the most important seed predators during the pre-dispersal phase of seed development (Janzen 1971; Turgeon et al. 1994; Hulme and Benkman 2002). Finally, the economic services provided by fruiting structures that are affected by insects concern principally the pre-dispersal phase.

Numerous synthetic studies have been carried out to list the arthropod fauna feeding on tree reproductive structures in the Mediterranean Basin (e.g. Roques 1983; Roques and Battisti 1999; El Alaoui El Fels and Roques 2005; Roques and El Alaoui El Fels 2005), but these concerned exclusively seed cone pests of conifer species. Standing on the shoulders of such extensive previous works, this chapter aims at gathering current knowledge on the Mediterranean entomofauna exploiting both gymnosperms and angiosperms. As a first step, we propose an overview of the challenges posed to insects when exploiting fruiting structures (Sect. 4.2). We further describe and analyse both diversity and guild patterns of the entomofauna found in Mediterranean forest ecosystems (Sects. 4.3 and 4.4, respectively). The ecological and the evolutionary implications for insects to feed on fruiting structures are reviewed and discussed in Sect. 4.5, and the impacts that such insects may have on host populations and on the economic services that hosts provide, respectively. While many of the concepts provided in Sects. 4.5 and 4.6 arose from a wide range of biomes, i.e. temperate, tropical and Mediterranean forests worldwide, we believe that they will help to shed critical light and stimulate specific research on Mediterranean insect communities. General considerations on pest management options are given in Sect. 4.7, before providing some concluding remarks (Sect. 4.8).

4.2 Tree Reproductive Structures as Food for Insects

4.2.1 A Nutrient Rich Resource

Tree reproductive structures represent a critical source of food for many insect species as they are generally extremely aggregated in space with high local abundance. Fruits and seeds may also offer protection against desiccation and natural enemies for a short or a long period of their life-cycle (Sallabanks and Courtney 1992). Fruiting structures consist in a plant embryo and reserve storage organs surrounded by accessory tissues acting as a protective coat or as a nutritious appeal to attract dispersers. The reserve storage organs can be located within the embryo (e.g. cotyledons) or in surrounding tissues (e.g. endosperm). During seed development, most angiosperms and gymnosperms invest substantial resources to give the embryo compounds upon which it may draw during embryogenesis and germination. Seeds provide a concentrated source of carbohydrates (61 %), fat (4 %) and proteins (10 %) due to a low water content (12 %), compared to young leaves (4 %, 1 %, 5 %

and 76 %, respectively) (Jordano 2000). Such particularly high energy and nutrient contents in fruiting structures make this kind of resource highly sought after by many insect species. However, insects can also target very early developmental stages of tree reproductive structures such as male and female flowers, or seed-bearing organs such as the axis-bract ovuliferous scale complexes that constitute conifer seed cones (Beck 1988; Turgeon et al. 1994). Fruiting structure insects display two different feeding habits to acquire nutrients from their host plants. Species belonging to the Coleoptera, Lepidoptera and Hymenoptera orders burrow through and feed within flowers, seeds, or seed-bearing structures, while those belonging to the Hemiptera suck out the contents of seeds or seed-bearing structures.

4.2.2 A Well Defended Resource

The high nutritional value of fruiting structures is generally associated with a greater investment of plants in physical or chemical defense mechanisms than vegetative tissues (Janzen 1971). In many plant species, seeds are confined in dry fruits that dehisce and liberate seeds (e.g. capsules, cones, pods) or are indehiscent (e.g. nuts). These structures may have a thick and woody wall, which may also display additional protective structures such as spines, bristles or irritant hairs. In fleshy fruits, seeds are rather protected by a fibrous seed-coat (Primack 1987; Hulme and Benkman 2002). Seeds can also accumulate a broad spectrum of toxins and antifeedants such as non-protein amino acids, cyanogenic glycosides, protease and amylase inhibitors, and phytohaemaglutinins, which may represent a challenge to insects for resource acquisition (Hulme and Benkman 2002). Interestingly, plant investment in noticeable physical defense mechanisms may result in low levels of toxins in seeds, while their absence suggests that plant defense mainly relies on secondary chemicals (Agrawal 2007). All seeds are however not equally toxic to insects because levels of toxicity primarily reflect tradeoffs between the strength of selection exerted by seed feeders and the maximization of both protection and stored reserves. Chemical defenses are costly to plants, which may result in negative correlations between toxicity levels and the number of seeds produced or the amount of reserves stored in seeds (Zangerl and Berenbaum 1997). In order to counter-balance such a constraint, some plant species produce seed toxins that can be metabolized to serve as storage products, or that are effective at low dosages (Harborne 2001).

4.2.3 A Resource that Varies in Time and Space

In natural forests, seed production can be highly irregular in both space and time. Many tree species display synchronous highly variable seed production among years, a phenomenon referred to as masting, or mast seeding (Kelly 1994). Masting results in intermittent production of large seed crops (mast years) and low to null seed crops (non-mast years) occurring at the tree population scale. The evolutionary advantages of masting of forest trees are assumed to be associated with improved pollination and seed-consumers satiation (e.g. Kelly and Sork 2002; Iwasa and Satake 2004). According to the latter hypothesis, large intermittent seed crops are expected to reduce losses to seed predators by imposing alternations of satiation and starvation periods to consumer populations. In most cases of pre-dispersal seed predation, there is an inverse density-dependence of seed predation rates on seed density. This results in greater seed crop damages if the previous years' seed crop is large than when the previous seed crop is small, because large seed crops favour insect population growth (Turgeon et al. 1994). This has two major implications. First, seed predation rates by specialist seed feeders generally depend on the relative differences in seed density between successive seed crops. Second, seed predation rates are positively correlated with the size of the seed crop that the previous generation experienced. In Mediterranean ecosystems, the production of fruits by such trees as pines, oaks or cedars varies by several orders, ranging from 2 to 7 years (Tapias et al. 2004; Espelta et al. 2008; Krouchi et al. 2004; Cyprus Forestry Department 2005). Important demographic implications in Mediterranean insect populations are thus expected.

The spatial distribution of fruiting structures can be heterogeneous as it usually varies among both trees and crown levels. In the Atlas cedar *Cedrus atlantica*, inter-individual variation in fruit production is maximal in mast years but minimal in non-mast years (Gidoin 2014). Microsite-scale nutritional factors and environmental conditions influence fruit abundance at the individual tree level, and upper crowns that are more exposed to light generally produce more fruits than shaded lower ones (Turgeon et al. 1994). Similarly, the greatest level of heterogeneity in fruit production at the stand scale may occur between edges and the bulk of the population, where increased density may affect the amount of available light to individual trees.

Spatio-temporal variation in fruit abundance may also result from spatio-temporal variations in pollination success, which depends on pollen (e.g. quantity, quality), pollination factors (e.g. pollinators, wind), and tree populations and communities (e.g. density, fragmentation level) (Wilcock and Neiland 2002). In most angiosperms and some gymnosperms (e.g. Cupressaceae), pollination is required for the initiation and the normal development of both the ovule and the reserve storage organs, and ovules soon abort out of fertilization (Singh 1978; Owens and Blake 1985). Failures in pollination and/or fertilization success may thus directly affect the reproductive success of insects specialized on tree reproductive structures by limiting the availability of suitable oviposition and breeding sites (Rouault et al. 2004). Another interesting aspect of plant responses to seed predation is the production of far more fruits than eventually mature, with a large proportion of inbred seeds being aborted at relatively late developmental stage. The adaptive significance of such a strategy relies on the role that inbred seeds may play as seed predator sinks, thereby diluting the impact of seed predation and increasing the survival probabilities of outcrossed and fully viable seeds (Ghazoul and Satake 2009).

4.3 Insect Diversity in the Mediterranean Basin

4.3.1 General Patterns of Diversity

In the Mediterranean Basin, the entomofauna exploiting the reproductive structures of angiosperms and gymnosperms is characterized by a great level of diversity, including a total of 99 species distributed among 47 genera, 21 families and 5 orders (Fig. 4.1). One support of such great diversity is the substantial 20 % contribution of Mediterranean seed cone insects to the entomofauna exploiting seed cones worldwide (ca. 400 species, according to Turgeon et al. 1994). A list of these species is provided in Appendix 4.1. It is likely however, that species richness may be underestimated as sampling, research and publication efforts may be biased towards countries, host tree species and the relative economic and/or ecological importance of insect damages. Three mite species (Acarina: Nalepellidae) have been also described on cones of cypresses (*Trisectatus juniperinus* on *Cupressus atlantica* and *C. sempervirens*), pines (*T. ehmanni* on *Pinus pinaster*) and junipers (*T. quadrisetus* on *Juniperus cedrus*, *J. communis*, *J. oxycedrus*, *J. phoenicea* and *J. thurifera*) (Roques and El Alaoui El Fels 2005), but we will focus on insects hereafter.

The five insect orders exploiting fruiting structures are, ranked by order of species contribution, the Lepidoptera (31.3 %), Coleoptera (28.3 %), Hemiptera (18.2 %), Hymenoptera (11.1 %) and Diptera (11.1 %) (Fig. 4.2). Such a diversity pattern is similar to that described on the seed cone entomofauna in both Western

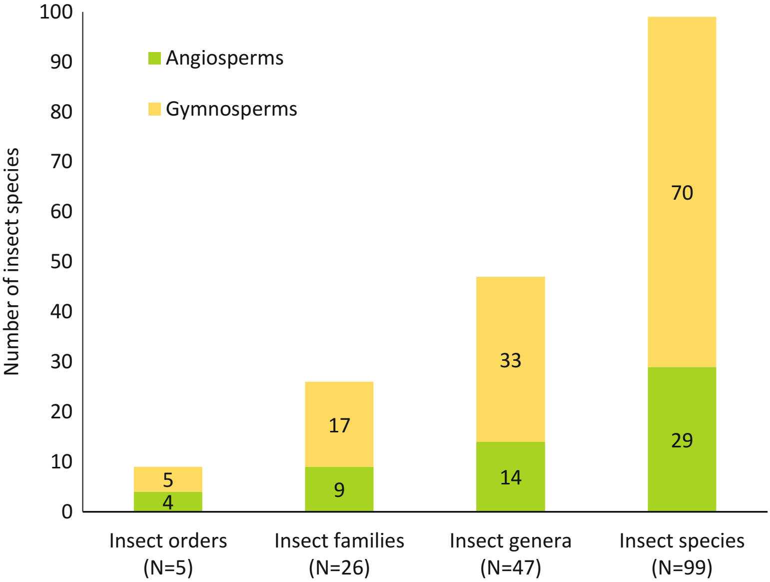

Fig. 4.1 General patterns of diversity of the entomofauna of tree reproductive structures in the Mediterranean Basin

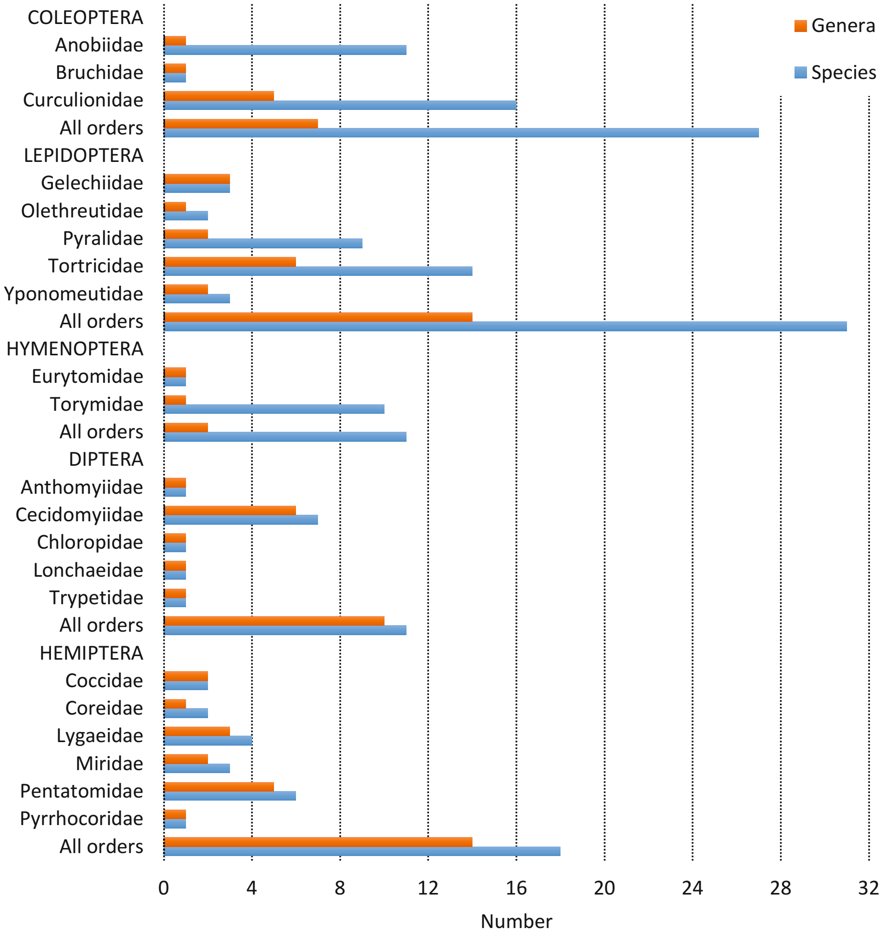

Fig. 4.2 Diversity of the entomofauna of tree reproductive structures in the Mediterranean Basin

Europe and Northern America, except for the Thysanoptera that seem to be absent in the Mediterranean Basin (Roques 1991; Turgeon 1994). The Diptera provide one of the highest numbers of families but diversity is very low at both genus and species levels, except in the Cecidomyiidae. This contrasts with the Coleoptera that are represented by one of the lowest number of families but by two of the highest species richness in two of them (the Anobiidae and the Curculionidae). The Hymenoptera comprises only two families, but also one of the highest species richness observed, which is concentrated in the Torymidae family and the sole genus *Megastigmus*. The Lepidoptera are the most diverse at both genus and species levels, and most of such diversity is provided by the Tortricidae and the Pyralidae. Interestingly, the Mediterranean Basin may be one important diversity spot of the Coleoptera and Hemiptera feeding on the fruiting structures of conifers, as species richness estimated in this area accounts for 28 % and 44 % (respectively) of the worldwide species richness estimated in these two orders by Turgeon et al. (1994).

Overall, the mean number of genera per family is estimated to 2.2, which is low and may reflect a selection for limited diversification to few insect genera that specialize on different structures of fruits and seed cones.

4.3.2 Geographic Patterns of Diversity Within the Mediterranean Basin

Geographic patterns of insect diversity may be assessed by sub-dividing published diversity data into three main geographic sub-regions: (i) the Northern Mediterranean sub-region[2] (N-MSR: France, Greece, Italy, Spain and Portugal), (ii) the Western sub-region (W-MSR: Algeria, Morocco and Tunisia, and (iii) the Eastern Mediterranean sub-region (E-MSR: Cyprus, Lebanon, Western Iran, Israel, Palestine and Turkey).

Insect diversity is not equally distributed across the Mediterranean Basin as N-MSR exhibits much higher diversity than both E-MSR and W-MSR (Table 4.1). This may reflect a lack of studies related to the latter areas, where less attention has been paid to host species with limited ranges, e.g. Eastern Mediterranean junipers (Roques and El Alaoui El Fels 2005). This may also result from both lower host diversity associated with fruiting structure insects in both W-MSR and E-MSR (8 and 8 genera, respectively) than in N-MSR (10 genera) and a greater extent of forest area in N-MSR than in W-MSR and W-MSR (FAO 2010).

Another geographic pattern of insect diversity relates to the important proportion of species that occur in only one of the three areas (68 %), i.e. in N-MSR, W-MSR or E-MSR, compared to that of species distributed across the whole Mediterranean Basin (4 %), i.e. across N-MSR, W-MSR and E-MSR (Table 4.1). Among these 'one-area' insect species, 67 % are endemic[3] to the Mediterranean, with the non-endemic ones occurring in N-MSR only where they exploit southern populations of pan-European tree species (e.g. chestnut, silver fir, beech, common juniper, oaks, poplars). This may provide strong support for a close link between the range size and patchiness of hosts and the distribution of their associated fruiting structure insects in the Mediterranean.

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[2] Listed countries refer to areas in which studies on insects of Mediterranean fruiting structure have been carried out so far.

[3] See Sect. 4.3.3 for a definition of endemism.

Table 4.1 Geographic patterns of diversity of the entomofauna of tree reproductive structures in the Mediterranean Basin

	Number of families	Number of genera	Number of species
Mediterranean sub-region			
Northern (N-MSR) (Cyprus, France, Greece, Italy, Portugal, Spain)	16	31	68
Western (W-MSR) (Algeria, Marocco, Tunisia)	12	18	28
Eastern (E-MSR) (Turkey, Lebanon, Iran, Israel, Palestine)	16	30	39
Occurrence in			
One sub-region	19	36	67
Two sub-regions	11	20	27
All sub-regions	4	4	5

4.3.3 *Endemism*

Endemism, the percentage of insect species endemic to the Mediterranean Basin among the total number of species occurring in this area, is estimated to the especially high value of 69 %, which corroborates the hotspot of plant species diversity with high endemism that characterizes the Mediterranean (Médail and Quézel 1997). Endemism is higher in species feeding on gymnosperms (76 %) than on those feeding on angiosperms (52 %). However, it greatly varies between host genera, whatever the group they belong to. Depending on host plant, endemism can be complete (*Acacia*, *Cupressus*, *Pistacia*, *Tetraclinis*: 100 %), quite complete (*Juniperus*: 91 %; *Cedrus*: 83 %), much lower (*Pinus*: 56 %; *Quercus*: 38 %; *Abies*: 29 %), or null (*Castanea*, *Fagus* and *Populus*: 0 %). Such heterogeneity may primarily result from variation in host distribution range as endemism increases significantly with the proportion of purely Mediterranean host species within the host genera targeted by insects (Fig. 4.3). An additional support of such association of endemism with host range breadth is evidence of lower endemism in the Northern Mediterranean sub-region (55 %) than in both Western (91 %) and Eastern (80 %) ones, where natural forest ecosystems concentrate mostly purely and endemic Mediterranean tree species (Médail and Quézel 1997; FAO 2013).

4.3.4 *Host-Insect Diversity Associations*

In the Mediterranean Basin, six angiosperm (*Acacia*, *Castanea*, *Fagus*, *Pistacia*, *Populus* and *Quercus*) and six gymnosperm (*Abies*, *Cedrus*, *Cupressus*, *Juniperus*, *Pinus* and *Tetraclinis*) genera have been proved to be colonized by fruiting structure insects. The distribution of insect diversity among these two plant groups is clearly

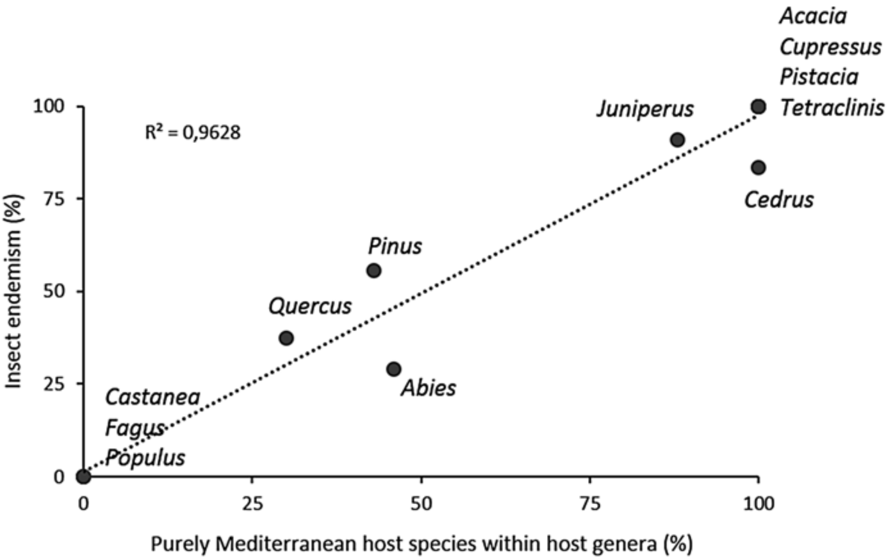

Fig. 4.3 Relationship between endemism level and host range breadth in the entomofauna of tree reproductive structures in the Mediterranean Basin

asymmetrical as gymnosperms concentrate most of insect diversity at the species (71 %), genera (70 %) and family (65 %) levels (Fig. 4.1). There may be two main explanations for this. Fruiting structures of gymnosperms, i.e. seed cones, generally consist in a complex structure with diverse characteristics (bract, dwarf-shoot, ovules, seed wing, aril, and seed), whereas fruits of flowering plants consist in a mature ovary with limited number of ovary tissues (the pericarp). Compared to fruits, seed cones and seeds thus represent microhabitats with potentially more diverse niche opportunities that may increase selection for both guild and species diversification.[4] Discrepancies in species richness between angiosperms and gymnosperms may also stress an important gap in research on Mediterranean angiosperms. There is indeed a significant imbalance between the numbers of study cases on gymnosperms and angiosperms relative to the available diversity among each of these host groups. Current literature on woody gymnosperms describes insect associations with six of the seven genera listed in the Mediterranean Basin by Quézel and Médail (2003), while that on woody angiosperms associate fruiting insect with a small proportion (10 %) of the 57 genera occurring in this area. The sole genus exception in the gymnosperms is *Taxus* (Taxaceae), e.g. the European yew *Taxus baccata* L., for which there is no evidence for insect pre-dispersal seed predation (Thomas and Polwart 2003).

Most of the studied angiosperms display poor insect diversity at both genera and species levels. *Pistacia* and *Quercus* are most intensively colonized as they host

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[4] See Sect. 4.4.

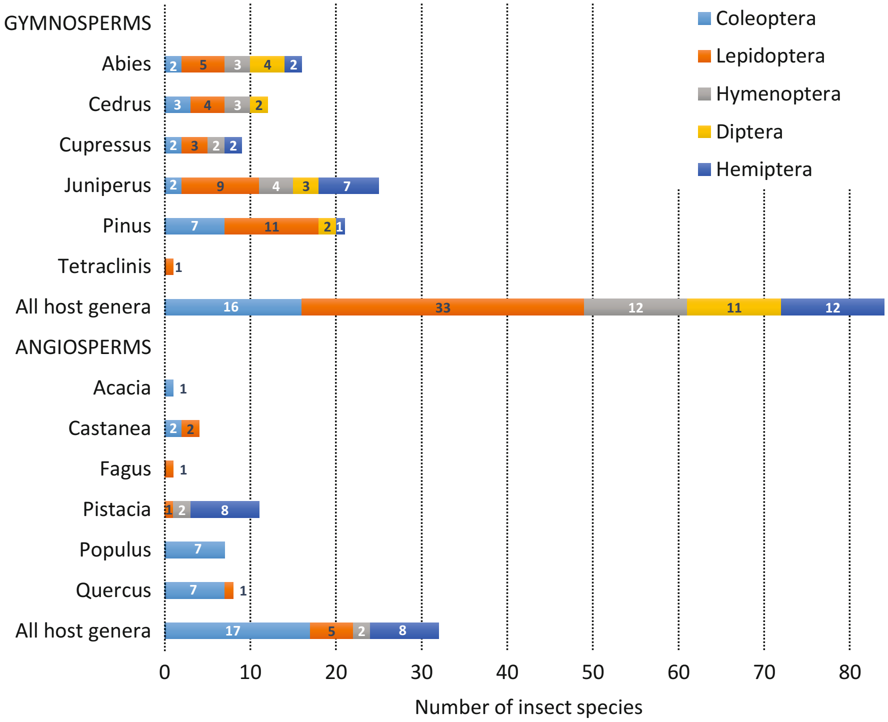

Fig. 4.4 Order level diversity according to host genera of the entomofauna of tree reproductive structures in the Mediterranean Basin

together 85 % and 70 % of both total insect genera and species richness, respectively. Among gymnosperms, *Cedrus* and *Cupressus* host low levels of insect diversity (13–17 %), while *Juniperus*, *Pinus* and *Abies* peak at 31 %, 26 % and 20 % of hosted insect diversity, respectively. These data overall suggest that species richness varies greatly between host genera, e.g. from 1 on *Acacia*, *Fagus* and *Populus* to 11 on *Pistacia* in angiosperms, and from 1 on *Tetraclinis* to 22 on *Juniperus* in gymnosperms.

In the same line, contributions of the different insect orders to diversity vary greatly among both host groups and genera (Fig. 4.4). Gymnosperms are colonized by all five insect orders, with a preponderance of the Lepidoptera that comprise almost half of total species richness (47 %) with 33 species. *Tetraclinis* is colonized by only one Lepidoptera species (*Pseudococcyx tessulatana*), while *Juniperus* cumulate the five orders with noticeable contributions of both the Lepidoptera and Hemiptera. Angiosperms lack the Diptera and they are predominantly colonized by the Coleoptera (58 %), which essentially target *Populus* and *Quercus*. *Acacia* and *Fagus* host only one species each (Coleoptera: *Bruchidius raddianae* and Lepidoptera: *Cydia fagiglanda*, respectively), which contrasts with *Pistacia* that hosts all Hemiptera species found on angiosperms and 37 % of the total species richness on this plant group. Overall, the Lepidoptera display the widest host range with evidence of 10 colonized host genera, followed by the Coleoptera (9 genera), the Hymenoptera (5 genera), the Hemiptera and the Diptera (4 genera each).

4.4 Guilds

4.4.1 Definitions

A guild structure of insects feeding on conifer seed cones has been proposed by Turgeon et al. (1994). In this chapter, we will consider two classification criteria used by these authors that are transposable to a broader range of host species, i.e. to both angiosperms and gymnosperms, despite some of them include a terminology that is specific to conifer structures.

The first classification criteria refers to the type of association between insects and fruiting structures, which will be defined here as insects' guilds. Insects that can feed or develop in other habitats (e.g. foliage, shoot, bark, pollen) when fruiting structures are not available are referred to as *heteroconophytes*, which belong to a guild of generalists regarding food resource. Insects that can feed or develop exclusively in a fruiting structure are referred to as *conophytes*, which thus belong to a guild of specialists. The life-cycles of conophytes can be considered either as *endoconophytic*, when the insect spends its entire pre-imaginal development (egg to pupa) within the fruiting structure, or *exoconophytic* when it exits the fruiting structure as a mature larvae to pupate elsewhere. Most endophytic species overwinter as diapausing larvae or pupae within the brood cone or seed.

The second classification criteria refers to the pattern of exploitation of the fruiting structure, which will be define here as insects' feeding guild. *Conophages* feed on fruit/cone tissues (e.g. flower bud, flower, bract, cone scale) but do not damage the seeds directly. *Conospermatophages* feed on both fruit/cone tissues and seeds, moving from seed to seed in a discriminate pattern. *Spermatophages* develop exclusively within seeds. All of the spermatophages have an endophytic life-cycle, while most conophages and conospermatophages are exoconophytic. Two other guilds can complement the list proposed by Turgeon et al. (1994). *External seed predators* feed directly upon the seeds from the cone surface (Roques and El Alaoui El Fels 2005). Finally, *inflorescence-feeding* insects target tree flowering structures, e.g. flower buds and developing male or female flowers.

4.4.2 Guild and Feeding Structures in the Mediterranean Basin

Congeneric species generally belong to the same guild, regardless of the host, and have similar life-cycles, regardless of the reproductive cycle of the host (Turgeon et al. 1994; Roques and El Alaoui El Fels 2005). In the Mediterranean Basin, guild

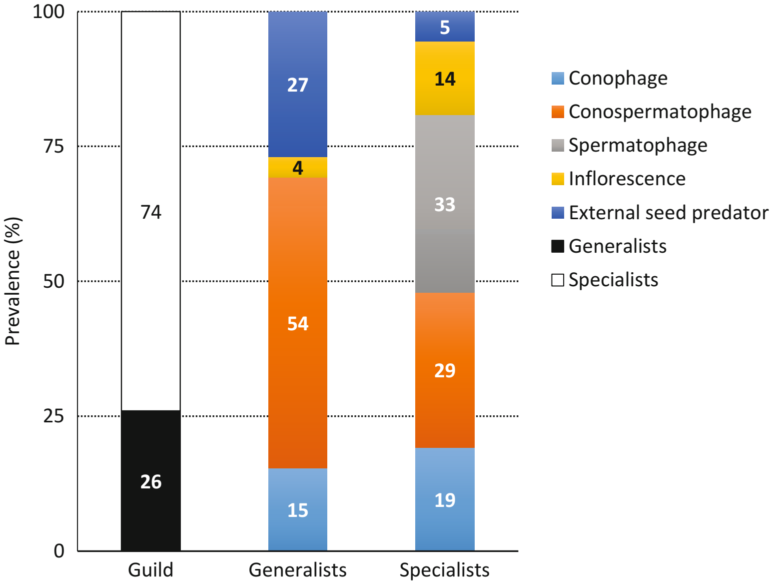

Fig. 4.5 Relative prevalences of the specialist and generalist guilds, and of the feeding guilds among guilds, in the entomofauna of tree reproductive structures in the Mediterranean Basin

structure is importantly biased towards specialists as they account for 74 % (73 species) of the entomofauna found on both angiosperms and gymnosperms. A minority of species (26 species) display generalist habits by using other tree structures (e.g. buds, shoots, twigs) when fruiting structures are not available (Fig. 4.5). On Mediterranean gymnosperms, the prevalence of specialists is slightly higher (75 %) than that on both Mediterranean angiosperms (69 %) and Western Europe indigenous conifers (70 %; Roques 1991), and it is much higher than that reported on Canadian indigenous conifers (60 %, Turgeon 1994). There are however, noticeable differences in the prevalence of specialists among host genera: 100 % on *Acacia*, *Castanea*, *Fagus*, *Quercus* and *Tetraclinis*, 75–90 % on *Abies*, *Cedrus*, *Juniperus*, *Cupressus* and *Populus*, 57 % on *Pinus*, and only 27 % on *Pistacia.*

Specialist and generalist guilds exploit differently tree reproductive structures, as suggested by the diverging feeding guild structures within these two guilds (Fig. 4.5). Generalists are predominantly conospermatophages (54 %) and external seed predators (27 %), and conophages and inflorescence feeders to a much lower extent. Conversely, specialists are predominantly spermatophages and conospermatophages (33 % and 29 %, respectively), and display higher proportions of conophages and inflorescence feeders (19 % and 14 %, respectively). A few external seed feeders are specialists (5 %).

Feeding guild structure differs significantly between insect communities feeding on gymnosperms and those feeding on angiosperms (Fig. 4.6). Gymnosperms are mainly targeted by conospermatophages and external seed predators, but there is a non-negligible contribution of spermatophages. Angiosperms are preferentially used by spermatophages, inflorescence feeders and external seed predators, but they

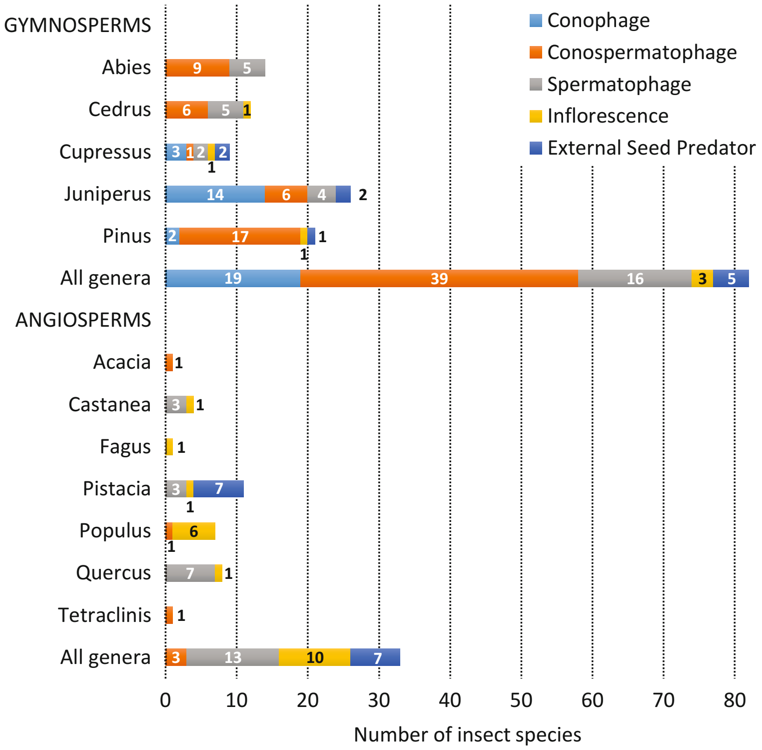

Fig. 4.6 Insect feeding guild diversity according to host genera in the Mediterranean Basin

lack conophages, which is not surprising given the structure of fruits in this plant group. However, the contribution of each feeding guild varies greatly at the host genus level as *Tetraclinis*, *Pinus*, *Abies* and *Acacia* are predominantly colonized by conospermatophages, while spermatophages are more abundant on *Quercus*, *Castanea* and *Cedrus*. *Populus* is essentially targeted during the flowering stage, and seeds are mostly the sole resource of insect feeding on *Pistacia* (spermatophages and external seed feeders). Overall, it appears that the number of feeding guilds depends greatly on host genera, which may attest for different evolutionary processes leading to niche differentiation for the use of fruiting structures as a habitat (Lewinsohn et al. 2005). These data also suggest that the proportion of insect species that affects seeds, i.e. all feeding guilds except conophages, is particularly high in Mediterranean forest ecosystems (82 %), especially when compared to that estimated in Western Europe ones (68 %, Roques and El Alaoui El Fels 2005).

4.4.3 *Diversity Within Guilds and Feeding Guilds*

Diversity is not equally distributed among guilds, as all five orders found on Mediterranean tree fruiting structures are represented within specialist insects, while only three orders (mainly Coleoptera and Hemiptera, and Lepidoptera)

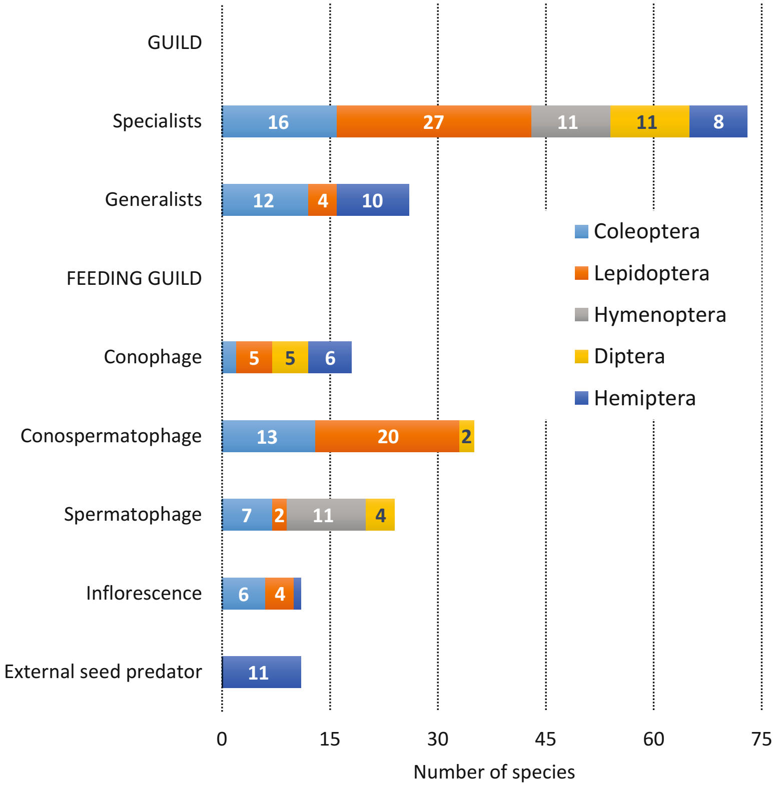

Fig. 4.7 Diversity within guilds and feeding guilds of the entomofauna of tree reproductive structures in the Mediterranean Basin

constitute the generalists (Fig. 4.7). This implies that the Hymenoptera and Diptera are exclusively specialists when exploiting tree fruiting structures in the Mediterranean Basin. Feeding guild differentiation within the different insect orders followed different patterns as follows (Fig. 4.7, Appendix 4.1):

Coleoptera They are represented in all feeding guilds, except that of external seed predators. Spermatophagous species are all weevils of the genera *Curculio* and *Onyxacalles* (Curculionidae). Coleoptera represent half of the entomofauna specialized on flowering structures with a single genus, *Dorytomus* (Curculionidae). Conospermatophages are the most diverse, including four genera: *Bruchidius* (Bruchidae), *Dorytomus* (Curculionidae), *Ernobius* (Anobiidae), and *Pissodes* (Curculionidae).

Lepidoptera They are represented in all feeding guilds, except that of external seed predators. About 65 % of Lepidoptera species are conospermatophages, including three families (Olethreutidae, Pyralidae, and Tortricidae) and eight genera (*Assara*, *Barbara*, *Cydia*, *Dioryctria*, *Gravitarmata*, *Pammene*, *Pseudococcyx*, and

Rhyacionia). Only two species are spermatophages: *Pammene fasciana* (Tortricidae) and *Palumbina guerinii* (Gelechidae).

Hymenoptera They are exclusively spermatophages, which probably makes them the most specialized insect order on fruiting structures. They are represented by only two families, the Torymidae and Eulophidae, and two genera, *Megastigmus* (10 species) and *Eurytoma* (1 species).

Hemiptera They are mostly external seed predators (61 % of Hemiptera species) and conophages (33 %). They represent the totality of external seed predators, including four families (Lygaeidae, Miridae, Pentatomidae, and Pyrrhocoridae) and 9 genera (*Acrosternum*, *Brachynema*, *Campylomma*, *Liorhyssus*, *Lygus*, *Nysius*, *Orsillus*, *Pitieda*, and *Spilostethus*).

Diptera Most Diptera species are conophages (54 %), and spermatophages and conospermatophages to a lower extent (36 % and 18 %, respectively). This order gathers 5 families (Anthomyiidae, Cecodomiidae, Lonchaeidiae, Trypetidae, and Chloropidae) and 10 genera (*Asynapta*, *Camptomyia*, *Contarinia*, *Dasineura*, *Earomyia*, *Hapleginella*, *Oligotrophus*, *Resseliela*, *Rhagoletis*, and *Strobilomyia*), but species is overall relatively low.

Altogether, these data suggest that tree fruiting structures provide important opportunities for niche differentiation and species diversification to Mediterranean insect communities.

4.5 Evolutionary Ecology

4.5.1 Host Plant Specialization

Frugivory and granivory during the pre-dispersal phase generally tend to favour host plant specialists, while excluding generalists (Janzen 1971; Crawley 2000). Host plant specialization is indeed favoured when resources are aggregated in space and display high local abundance. High investment of plants in defense mechanisms also leads to a strong selection for counter-defense abilities that contribute to the exclusion of less-specialized seed feeders. Fruiting structures often represent an ephemeral resource during the pre-dispersal phase to which consumers' life-cycles must be well synchronized. Compared to other organisms, insects are particularly well adapted to synchronize their life-cycles with such ephemeral availability in resources from one or a few closely related host plants (Hulme and Benkman 2002). The evolution of specialization is favoured when the parasite's development is dependent on a single plant organ or tissue in its life cycle (Gaston et al. 1992). This has a particular meaning for insect species in which both oviposition and larval development occur on immature fruiting structures, as there may be strong selection for synchronizing insect life history with the target stage of the host plant (McClure et al. 1998; Harman 1999). Overall, these patterns contrast with post-dispersal consumers that feed on a diverse and spatially heterogeneous resource that requires generalist feeding habits (Hulme 1998).

Evidence of strong host plant specialization in Mediterranean insect communities relies on the observation that species are predominantly associated with a single host plant family (97.9 %) and a single host plant genus (85.6 %). In the Diptera, no species is found on more than one host genus, conversely to the other insect orders, in which this can happen at least once (Appendix 4.1). In the same line, 80 % of fruiting structure specialists (conophytes) are associated with only one host genus, and about 15 % with two host genera.

Such close connection between the insects and their hosts can also be reflected by the phylogenetic relationships[5] between species belonging to the same insect genus. For most phytophagous insects, long-term association with a particular host eventually results in the loss of genetic variation for the ability to use alternative hosts. Specialists thus might become constrained irreversibly on a restricted set of host plant species. For instance, a molecular phylogeny of the *Megastigmus* seed wasps related to conifers revealed that species are clearly separated according to host families (Auger-Rozenberg et al. 2006). Species infesting Cupressaceae seem to be specialized to particular host genera or even to be species specific, whereas those associated with Pinaceae appear capable of shifting onto different congeneric species or even onto a new host genus. In the same way, the weevil *Curculio elephas* is capable to attack two different host genera, e.g. *Quercus* and *Castanea*, whereas *Curculio glandium*, another European species exploiting only *Quercus* sp. does not belong to the same genetic clade as *C. elephas* (Hughes and Vogler 2004; Bonal et al. 2011). According to the species or group species, genetic data tend to indicate that the specialization clearly refers to targeted host structure, but that phylogenetic relationships may be more or less tight, with an evolution more or less constrained by plant association.

Host plant specialization may have strong evolutionary implications for seed insects, as recently shown in *Megastigmus* wasps including several Mediterranean species (Boivin et al. 2014). In this group, asexuality (thelytoky) evolved from sexuality (arrhenotoky) through the horizontal transmission and the fixation of a bacterial reproductive manipulator, *Wolbachia*, in the favour of host plant specialization. Effective horizontal transmission of *Wolbachia* depends on: (i) intimate ecological associations which provide within-host community horizontal transmission opportunities (i.e. an encounter filter), and (ii) on the phylogenetic similarity of donor and recipient host species because internal defence mechanisms against infections are likely to be more similar between closely related hosts (i.e. a compatibility filter). In *Megastigmus*, the spread of asexuality was thus tightly linked to host plant specialization, which may favour *Wolbachia* transmission due to the narrow ecological niches shared by closely related wasp species.

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[5] When such genetic data are available.

4.5.2 Insect Adaptations to Tree Reproductive Structures

Tree reproductive structures pose numerous challenges to insects due to their physical-chemical characteristics and their important variation in abundance in both space and time and at both tree and stand scales. This section reviews the biochemical and behavioural strategies developed by insects to cope with such constraints linked to their hosts.

4.5.2.1 Biochemical Adaptations

Like many herbivores, seed insects have co-evolved biochemical adaptations to overcome the impact that seed toxins may have on growth and survival. These may include detoxification, sequestration, conjugation, target site insensitivity and excretion mechanisms. They have however not been as intensively investigated as that of other plant structures, e.g. leaves (Harborne 2001; Strauss and Zangerl 2002). The difficulties of coping with more than a few secondary compounds may however favour the evolution of specialization, and it may explain why so many seed feeders are specialists (Hulme and Benkman 2002). The evolution of counter-adaptations to chemical defenses of seeds is thought from a long time to be one key driver of the diversity of seed specialists. This hypothesis relies on an escape-and-radiate process, during which mutant plants radiate by developing new chemicals allowing them to escape seed predators, and the seed predators that evolve counter-adaptations to these novel chemicals radiate on the plant (Janzen 1969).

4.5.2.2 Host Selection

Animals are expected to develop foraging strategies that maximize fitness, e.g. many herbivore insect species have adjusted their oviposition choices with the occurrence of target host organs that maximize growth and survival of their progeny (Moegenburg 1996). Compared to other tree structures such as foliage, the heterogeneous spatial distribution of fruiting structures at both stand and tree scales requires effective host and resource recognition and selection mechanisms for insects. Tree silhouette, size and shape play a key role in initiating long-range insect orientation; the contrast between the fruit or seed cone structure and foliage colour may also act as a stimulus at the stand scale; when closer, fruit or seed cone size, structure and chemistry determine short-range detection and host suitability for mating, feeding and ovipositing (Turgeon et al. 1994). Both visual and chemical cues operate sequentially or simultaneously in host location, but insect response may vary among sexes and may depend on the reproductive and nutritional status of individuals. In *Megastigmus* seed wasps, unfed adults are attracted primarily by colour designs mimicking the non-host flowers they feed on to mature sexually (e.g. yellow), while satiated and mature adults shifted to colour designs mimicking conifer host characteristics (e.g. green) to oviposit. Similarly, while sexually immature females of seed wasps are not attracted by seed cone volatiles, mature ones respond preferentially to pentane extracts of the seed cone stage at which oviposition takes place (Roques 1987). Some foraging seed-predators can also use infrared (IR) radiation from living plants as a host-finding cue. The western conifer seed bugs, *Leptoglossus occidentalis* possess IR receptive organs and orient towards pine cones, which are warmer and emit more near-, mid- and long-range IR radiation than needles (Takács et al. 2009).[6]

The recognition and the selection of suitable feeding and breeding sites involves both the adult female and its progeny when larvae are capable to move and find resources, e.g. *Dioryctria* spp., while the female has sole responsibility of an appropriate host choice when larvae remain in the same fruit until pupation, e.g. *Megastigmus* spp. (Turgeon et al. 1994; Rouault et al. 2004). In the latter case, female host preference and host suitability for larval development are then highly positively correlated. The two major groups of seed plants, angiosperms and gymnosperms, accumulate seed storage reserves in two different ways. Most angiosperms and some gymnosperms (e.g. Cupressaceae) require pollination to trigger normal development of both reserve storage organ (megagametophyte) and ovule; storage products only begin to accumulate following fertilization (Singh 1978; Owens and Blake 1985). For *Megastigmus* species that feed on *Cupressus* and *Juniperus* species, reproductive success strongly depends on female's ability to find the fertilized ovules to lay eggs. In some other gymnosperms (e.g. cycads and conifers), storage may begin in megagametophytes prior to fertilization, sometimes even in the absence of pollination. However, unpollinated megagametophytes will eventually abort, resulting in a so-called empty seed (Owens and Blake 1985). *Megastigmus* species that feed on such gymnosperms, e.g. *Cedrus* spp., should parasitize any of the potential seeds present in a seed cone, independently from fertilization success. The reason is that the insect is able to redirect seed ontogeny to the larva's advantage. Parasitized unfertilized ovules not only fail to abort, they begin to accumulate storage reserves as if they had been fertilized. The manipulated fattening seed is consumed by the parasitic larva (von Aderkas et al. 2005).

4.5.2.3 Dispersal

Tree populations that are spatially and/or temporally heterogeneous in the production of fruiting structures represent stochastic environments with which insects have to cope. In insect species that cannot shift to alternative hosts when resource is at low abundance and when intra- or interspecific competition increases, life histories are under strong selection to offset such heterogeneity in resource availability. The two main strategies exhibited by insects are spatial dispersal and prolonged diapause, as both of them reduce the risk of local extinction.

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[6] *Leptoglossus occidentalis* is now a common pine seed predator in southern Europe, but it has been introduced from the U.S.A. See Chap. 11 for more details on this invasive species.

Short- and Long-Range Spatial Dispersal Colonization of appropriate, i.e. fruiting, habitats and host-finding within such habitats rely on long- and short-range dispersal flights that involve active or passive dispersal mechanisms, or a combination of both (Mosseler et al. 1992; Turgeon et al. 1994; Liebhold and Tobin 2008). Dispersal range between and within tree populations depends on species' active flight ability, but also on the occurrence of passive flight assisting factors, e.g. wind, that species may be able to use. In seed wasps, adults having landed on host trees use visual and olfactory cues to find oviposition sites during active flights. In the absence of cones, wasps can fly up in a slow vertical movement to the tree top to be blown away from the tree (Roques et al. 2008). Long-distance windborne passive dispersal may occur when individuals fly to higher altitudes where there are stronger winds and air turbulence (Jarry et al. 1997). Wind can be an effective agent of long-distance dispersal in insect specialist species for whom both landscape fragmentation and inability to use alternative habitats represent natural barriers to simple diffusion. In particular, mountainous regions may favour long-distance dispersal events as wind speed is typically greater at high elevation than at low elevation (Lander et al. 2014). Although the mechanisms for passive wind dispersal and location of specific hosts are not well understood, it is clear that various insects routinely travel long distances, successfully locate their hosts, and actively quit the air flow potentially in response to visual or olfactory stimuli (Bullock et al. 2002; Lucchetta et al. 2008). The demography of highly mobile generalist and specialist seed feeders is thought to depend less of the previous seed crops than that of species with low mobility (Hulme and Benkman 2002).

Prolonged Diapause If fruiting structure insects can disperse in space to cope with environmental stochasticity, they can also exhibit temporal dispersal by extending the life cycle of a part of their population over several years. Diapause is a well-known adaptive response to predictable portions of the year that are inappropriate for growth and reproduction (Danks 1987). However, when conditions are less predictable and species experience severe spatial or inter-annual fluctuations of their environment diapause may extend over more than 1 year (Hanski 1988). Such prolonged diapause can be concentrated on a single extra year of emergence, e.g. in the oak weevil *Curculio venosus*, but in most cases emergences of a cohort are spread over several years, with continuously decreasing emergence frequencies during further years, e.g. the oak weevil *Curculio elephas* (Fig. 4.8, Pélisson et al. 2013). One unique prolonged diapause strategy has been however discovered in the Mediterranean seed wasp *Megastigmus schimitscheki*, in which a bimodal pattern of adult emergence displays two consistently major emergence peaks at the second and fourth years, while only a small fraction of a cohort (less than 5 %) emerges at the third and fifth years (Suez et al. 2013). This pattern even differs from that commonly observed in other *Megastigmus* species, e.g. *M. pinsapinis*, possibly reflecting adaptation to the highly stochastic inter-annual seed production of *M. schimitscheki*'s native host, the endemic Cyprus cedar *Cedrus brevifolia* (Fig. 4.8). These different examples show that propensity to temporal dispersal is highly species specific, even

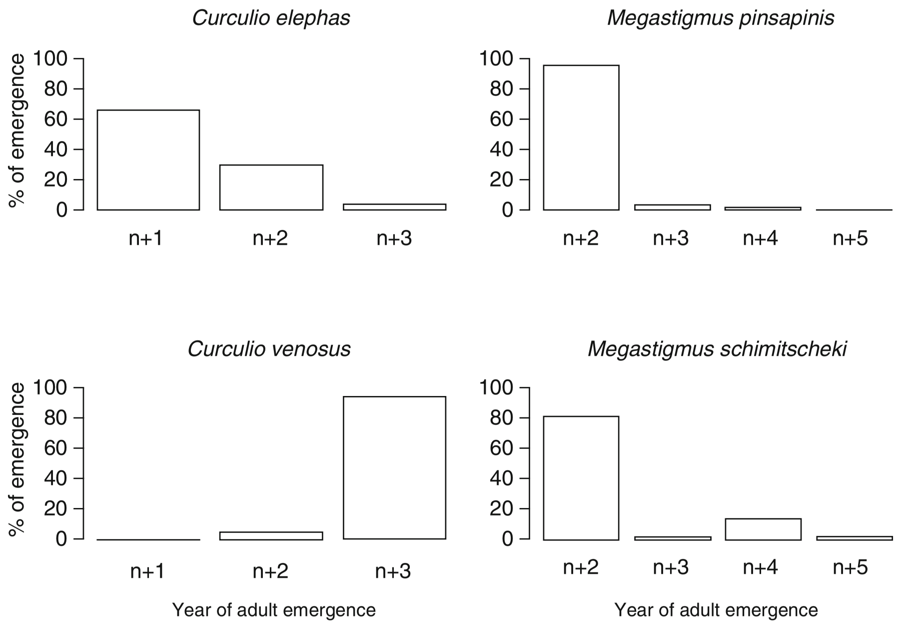

Fig. 4.8 Spreading of adult emergence over years by two oak weevil species, *Curculio elephas* and *C. venosus*, and two cedar seed wasp species, *Megastigmus pinsapinis* and *M. schimitscheki*. With regard to egg-laying followed by larval development at year n [From data of Pélisson et al. (2013) and Suez et al. (2013)]

showing great variation among species of a single genus feeding on similar host species or genus.

Prolonged diapause is expressed in at least 70 species feeding on conifer seed cones, belonging to the Diptera, Hymenoptera and Lepidoptera (Turgeon et al. 1994). All species developing this strategy are fruiting structure specialists (conophytes) as generalists (heteroconophytes) can feed on other plant structures in the absence of fruits or seed cones. Prevalence of prolonged diapause is thought to be higher in conophyte communities that use hosts with a 1-year cone development cycle than on those using host with multi-year cycles. This possibly explains why seed cone insects prolonging diapause are less frequent in the Mediterranean (14 %), where almost all conifers have a multi-year cycle for cone development, than in Western Europe (62.5 %), where hosts with a 1-year cycle are common (Roques and El Alaoui El Fels 2005). However, one cannot exclude the potential for phenotypic plasticity to climate as northwards translocation of populations of the Mediterranean cypress seed wasp, *Megastigmus wachtli*, induced prolonged diapause, while such behaviour was unknown in its southern range (Roques and Raimbault 1986). The adaptive value of prolonged diapause is well documented (Hanski 1988; Menu et al. 2000; Gourbière and Menu 2009). Variation in diapause duration has been mainly attributed to diversified bet-hedging, a risk-spreading strategy maximising the mean geometric fitness by minimising the fitness variance at the cost of lower arithmetic mean fitness (Philippi and Seger 1989). Although expanding diapause is associated with metabolic, survival and reproductive costs (Soula and Menu 2005), it is generally thought to generate a population buffer against environmental constraints acting against non-diapausing stages, e.g. sudden limitation in food resource, enhanced predation, or pathogenic risks (Menu et al. 2000). From a genetic standpoint, prolonged diapause may help promote the maintenance of genetic diversity, as late-emerging individuals may not experience demographic or selection events similar to early-emerging ones (Ellner and Hairston 1994). In the cedar seed wasp *M. schimitscheki*, there is recent empirical evidence that prolonged diapause phenotypes can substantially contribute to reproduction and impact temporal genetic structures, supporting the role of prolonged diapause as both demographic and genetic refuges for insect populations living in fluctuating environments (Suez et al. 2013).

The physiological basis and the factors governing the different stages of the prolonged diapause process (induction, duration, and termination) remain poorly documented. Diverging hypotheses have been formulated, including a simple extension of the winter diapause, or all individuals (i.e., short and long-cycle insects) restart their development after the winter diapause, and that long-cycle individuals re-enter a second diapause afterwards (Soula and Menu 2005). Some studies suggested that the larval prolonged diapause corresponds to physiological processes that are independent of those underlying short (obligatory) diapause and that may be governed by other environmental factors (Roux et al. 1997). The chemical composition of seeds during larval development, abiotic factors and genetic and/or non-genetic parental inheritance have been suspected of affecting propensity to prolonged diapause in seed wasps and in other cone and seed insects (Roques 1988; Roux et al. 1997).

Trade-Offs Between Spatial and Temporal Dispersal Interestingly, it has been suggested that spatial dispersal and prolonged dormancy may be alternative strategies for organisms living in environments that vary over time and space, as spatial dispersal may release selective pressure exerted on variable dormancy duration or vice versa (Snyder 2006). In particular, active dispersal may reduce the advantage of dormancy as a risk-spreading strategy as species actively disperse to select their reproductive locality. This may be true for fruiting structure insects. Pélisson et al. (2013) explored the dormancy and dispersal capacities of several actively dispersing sibling weevil species (*Curculio* spp.) that exploit the same, highly variable resource (oak acorns). The authors showed that *Curculio elephas* exhibited a propensity to prolonged diapause but only medium flight capacities. In contrast, *C. glandium* was able to fly over very long distances, but was hardly capable of prolonged diapause. Surprisingly, *C. pellitus* proved inefficient in both spatial dispersal and prolonged diapause, but exhibited earlier seasonal emergence and oviposition timing that *C. elephas* and *C. glandium*. One interesting conclusion is that such strong diversification of dispersal–diapause strategies might contribute to stabilizing the coexistence of these sibling species in oak populations.

4.6 Impacts of Insects Feeding on Tree Reproductive Structures

The consequences of insect feeding activity on fruiting structures are diverse, and they essentially depend on the developmental stage or the tissues that insects target (Roques 1983). Insect damages on early developmental stages, e.g. flowers or young cones, generally inhibit their growth, accelerate their lignification and dehydration processes, which leads to a premature drop of the fruiting structure (e.g. the *Gravitarmata* moths). On conifers, insect damages on latter developmental stages have a weaker influence on cone growth, but they generally lead to an intense resin flow that sticks together cone scales, which prevents the release of the unaffected and viable seeds (e.g. the pine cone weevil *Pissodes validirostris*). Spermatophages and external seed predators have no direct impact on fruiting structure development with the exception of seeds, which makes them undetectable by simple visual observation on fruits or cones (e.g. *Megastigmus* seed wasps, Hemiptera spp.). The magnitude at which insects may affect components of host reproductive success, i.e. the number or the quality of viable seeds remaining at the post-dispersal stage, is thus expected to differ between insect feeding guilds. Inflorescence feeders, conophages and conospermatophages may have a greater negative impact as they constrain the production or the release of all seeds of the targeted fruiting structure, while the specialization of both spermatophages and external seed predators on seeds allows a certain proportion of seeds to escape predation and disperse. Exceptions to such predictions however exist (see further).

Box 4.1. Conceptual framework of the ecological, evolutionary and economic impacts of insects feeding on tree reproductive structure during the pre-dispersal phase.

Seeds directly influence tree populations by: (i) the local increase in populations, (ii) the re-placement of individuals that die in a population, and (iii) the colonization of new areas. By di-rectly affecting tree reproductive success, the demographic and evolutionary consequences of the feeding activities of fruiting structure insects are thus likely to differ from most forms of herbivory which only result in partial removal of tissues from individual plants (Hulme 1998). The ecological (A), evolutionary (B) and economic (C) consequences of pre-dispersal fruit, cone and seed consumption have to be contextually defined, as they generally depend on multiscale inter-actions involving exogenous factors referring to community (e.g. competitors or predator abundance), host, landscape and climate features, and endogenous factors referring to the biology of pre-dispersal seed predators (Fig. Box 4.1).

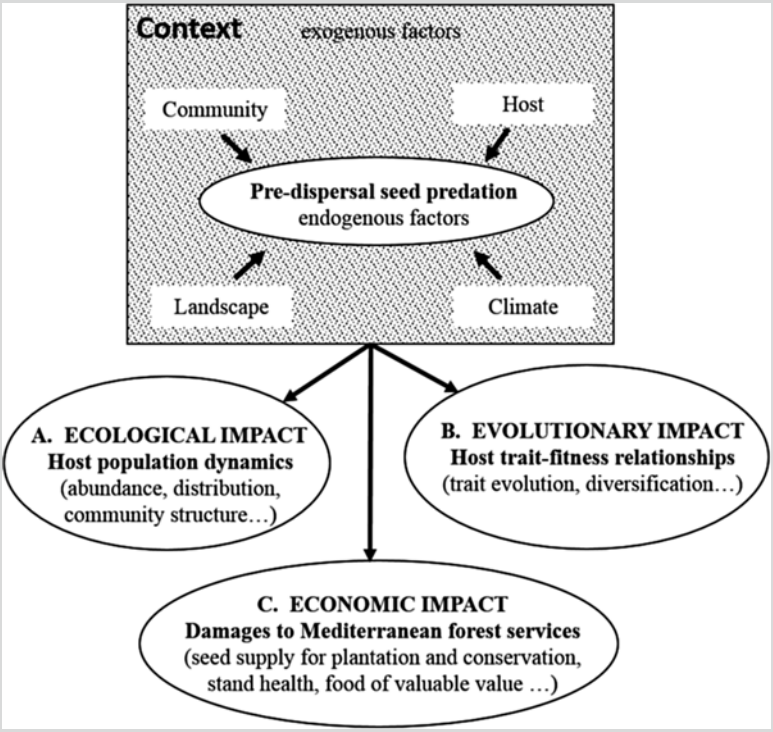

Fig. Box 4.1 The context-dependent ecological, evolutionary and economic impacts of pre-dispersal seed predation by insects (adapted from Kolb et al. 2007)

4.6.1 Ecological Impact on Host Populations

Because both seed production and seed dispersal are major components of plants' spatial dynamics, pre-dispersal seed consumers are expected to play a central role in the abundance, the distribution and the dynamics of plant populations (Box 4.1). Many tree species suffer from large seed losses due to pre-dispersal seed feeders (Janzen 1971; Crawley 2000; Hulme and Benkman 2002). One obvious outcome of these observations is that the performance of plant individuals is negatively affected by such losses, which can have negative effects on recruitment and plant population growth rate (Maron and Crone 2006; Kolb et al. 2007). This may have important consequences in endangered plant species, for which natural regeneration success is constrained by the extremely low rate of seeds escaping insect damages, e.g. *Juniperus thuriferana* in the Canary Islands (Guido and Roques 1996). On the other hand, pre-dispersal seed predation may enhance survival of seedlings that escaped predation through a reduction of intraspecific competition resulting from lower seed outputs (Halpern and Underwood 2006). The effect of seed feeders on the long term fitness of their host plant thus appears controversial, mainly due to the lack of data addressing this issue, especially on perennial plants. There is indeed dependence between the sensitivity of overall plant performance to changes in seed production and the magnitude at which seed predation influences population dynamics (Kolb et al. 2007). Such a sensitivity actually depend on plant life history, including: (i) an ability in vegetative regeneration, (ii) a large and persistent seed bank, or (iii) large seed crops that satiate seed-feeder (Hulme and Benkman 2002). If densities of seedlings are higher after mast years than non-mast years, i.e. more seeds escape predation in mast years, then one expect plant recruitment opportunities to be seed-limited. If seedling densities are not higher with seed addition than without, i.e. a release in seed predation does not increase seedling recruitment; then plant recruitment is likely to be micro-site limited. One fundamental implication is that seed-feeders may influence plant population density in seed-limited species,[7] e.g. masting tree species, but not in microsite-limited ones (Turnbull et al. 2000; Maron and Crone 2006; Kolb et al. 2007). But because of a lack of experimental studies that combine simultaneously seed addition, disturbance and seed-feeder exclusion, the extent to which plant populations are either micro-site- or seed-limited is still uncertain (Hulme and Benkman 2002). Overall, this suggests that the demographic impact of pre-dispersal seed feeders on plants should not be restricted to the amount of seed loss alone, as seed-feeder effects on components of fitness such as seed production cannot be used as surrogates for effects on total fitness or plant population dynamics (Kolb et al. 2007).

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[7] Masting species are generally seed-limited.

4.6.2 Evolutionary Impact on Host Populations

Insects feeding on plant reproductive structures potentially affect tree evolution when they differentially decrease seed production among individuals that vary in some heritable traits (Kolb et al. 2007). Any change in plant trait-fitness relationships due to seed predation may potentially result in evolutionary change in terms of trait evolution, speciation, extinction or diversification (Box 4.1). Evidences for phenotypic selection on heritable traits by pre-dispersal seed feeders relate to flowering synchrony, flowering phenology, inflorescence characteristics, flower size, flower longevity and mast seeding (Janzen 1971; Brody 1997; Fenner et al. 2002; Cariveau et al. 2004; Rose et al. 2005; Strauss and Whittall 2006). However, tradeoffs resulting from different selection pressures shaping such heritable traits may limit evolutionary change[8] (Cariveau et al. 2004). This suggests that conflicting selection pressures may shape and constrain overall evolutionary trajectories, but this does not impede plants to respond to individual selection pressures with potentially measurable strength (Kolb et al. 2007). Moreover, by eradicating individuals in a tree population, seed feeders may impact plant population dynamics with possible genetic drift effects when population size is limited. There is still a crucial need for studies examining the genetic consequences of massive seed losses within a host tree population, especially in a context in which pre-dispersal seed predation shows significant variation between trees. Indeed, seed loss due to seed-specialized chalcid wasps may vary from less than 1–100 % between trees (Roques 1981; Rappaport et al. 1993; Gidoin 2014). At the tree population level, this raises the question of how such local variation in pre-dispersal seed predation may increase or, reversely, decrease the variance of effective seed set among trees, which influences effective population size (Lefèvre et al. 2013). Theoretical developments of the impact of seed predation on the dynamics of genetic diversity within expanding host populations showed that an Allee effect resulting from seed predation at the tree expanding front may increase the genetic contribution of host individuals situated in the bulk of the population. Interestingly, this phenomenon results in a limited erosion of genetic diversity during the expansion phase of the host population (Gidoin 2014).

4.6.3 Economic Impact

In addition to their impacts on the ecology and the evolution of their hosts, fruiting structure insects can severely affect the economic services that Mediterranean forest ecosystems are expected to provide (Roques 1983; Turgeon et al. 1994). First, fruiting structure insects may decrease high quality seed supply for ornamental, reforestation, afforestation and conservation purposes when infesting established seed

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[8] Certain plant traits may attract both seed feeders and pollinators.

orchards and seed selected stands.[9] Seed wasps (*Megastigmus* spp.) generate 20–90 % seed loss to seed suppliers in selected southern French stands of *Cedrus atlantica*, and they may act as a biotic threat to natural regeneration of the currently declining native *C. atlantica* forests in Algeria (Mouna 2013). The moth *Dioryctria abietella* (Pyralidae) and the seed wasp *M. suspectus* affect up to 93 % and 79 % of cones of the highly endemic Trojan fir in Turkey, respectively (Ayberk and Cebeci 2010). The bruchid *Bruchius raddianae* (Bruchidae) can destroy 26–86 % of the seeds of *Acacia tortilis*, a socio-economically important tree species that has undergone population decline owing to seed predation in the Bou Hedma national park in Tunisia (Derbel et al. 2007). Second, seed insects can also affect tree plantations through indirect negative impacts on the survival their host by disseminating pathogens. The cypress seed bugs *Orsillus maculatus* and *O. depressus* were shown to be the main agents disseminating the spores of *Seiridium cardinale* (Battisti et al. 1999; Luchi et al. 2012), an invasive fungus responsible for the cypress canker, a serious disease that killed for instance 80 % of infected trees in Greece (Xenopoulos and Diamandis 1985). Finally, the production of valuable forest products for food can be seriously compromised by insect feeding activity. The chestnut weevil *Curculio proquinquus* (Curculionidae) has been shown to affect up to 60–70 % of chestnut crop in Italy (Paparatti and Speranza 2004), the wasp *Eurytoma plotnikovi* (Eurytomidae) has been shown to consume up to 97 % of *Pistacia vera* nut crop in Tunisia (Braham 2005), and the moth *Dioryctria mendacella* (Torticidae) has been found to attack 80 % of cones of *Pinus pinea* in Italy (Innocenti and Tiberi 2002).

For given insect and host species, severity of damages to seed crops generally exhibit important temporal and spatial variations that can be hardly predictable, as a result of complex interactions between the dynamics of both host reproduction (e.g. pollination success, masting) and insect populations (e.g. phenology, prolonged diapause, dispersal) and exogenous factors related to climate, landscape patterns or abundance of insect natural enemies (Box 4.1). Defining effective operational responses to seed losses to insects thus relies on a contextual approach integrating precise knowledge of both ecological and environmental drivers of insect abundance.

4.7 Management of Insects Feeding on Tree Reproductive Structures

Protection of tree reproductive structures from pest insects is generally a complex process, partly due to the cryptic internal feeding habits of many pest species that makes them difficult to detect and control, and to the spatial heterogeneity of fruiting structures at both tree and stand levels. Fruiting structure insects are essentially controlled within seed orchards and tree stands providing seeds or fruits as food,

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[9] See FAO (1997) for a list of the sources of Mediterranean conifer seeds.

which share some of the features of an agro-ecosystem but also those of a forest ecosystem. This adds significant complexity in establishing effective pest management programs.

Reforestation and afforestation programs require high quality seeds from selected genotypes that represent high value material, for which the establishment and maintenance of high seed outputs relies on low tolerance for cone and seed damage (Turgeon et al. 1994; Mangini et al. 2003). Seed orchard managers conduct integrated pest management (IPM) programs aiming at combining all suitable direct (e.g. insecticide treatments) and indirect (e.g. use of natural enemies) techniques to maintain populations below a desired economic threshold. There has been however an increasing concern that keeping low environmental risk levels in pesticide use is often incompatible with the rates needed for effectively controlling pest insects in seed orchards (Mangini et al. 2003). Consequently, conventional spraying of both chemical and biological insecticides (e.g. pyrethroids, organophosphates, *Bacillus thuringiensis*) on foliage and cones, and trunk injection of systemic insecticides (e.g. dimethoate) have been continuously abandoned in Northern America and Europe (Rosenberg et al. 2014). There was a similar environmental concern in chestnut orchards, e.g. in Italy, as chestnut fruit consumers demanded important production without any chemical residues and very limited environmental impacts. This revealed increasing constraints in spraying the active ingredients currently registered for chestnut crops, stimulating new research on the potential for entomopathogenic fungi, e.g. *Beauveria bassana* and *Metarizium anisopliae*, to control chestnuts weevils (Paparatti and Speranza 2004).

Crop-monitoring systems are required to aid decision in IPM programs, i.e. defining if and when insecticides should be sprayed (Turgeon et al. 1994). Egg sampling techniques may be deployed at specific stages of fruiting structure development to estimate annual potentials for seed loss to conophytes, despite such procedure is both time consuming and labour intensive, and eggs of spermatophages are impossible to detect by external examination of fruiting structures. Adult trapping techniques involving mimic visual cues used by insects or host volatiles may be used to assess emergence and flight periods, but these are rarely species specific. Sex pheromones can be useful for trapping male moths to assess their relative abundance and to predict damages by their offspring (Suckling et al. 2005), but the only European conophytes for which a pheromone is available are *Dioryctria abietella* and *Cydia strobilella* (Witzgall et al. 2010; Löfstedt et al. 2011). Mating disruption is a strategy that involves the release of large quantities of sex pheromone to prevent communication between male and female insects, which results in reduced or delayed mating, fewer fertile eggs and less damage. It has been proved to be successful against *Dioryctria* spp. and *C. strobilella* populations in Northern America (DeBarr et al. 2000; Trudel et al. 2006).

Prophylactic management practices may also affect insect densities and hinder population growth in forest orchards. The removal of all cones or fruits at harvest is an effective strategy to reduce conophyte populations living in the orchard (Roques 1983; Turgeon et al. 1994; Paparatti and Speranza 2004). Alternatively, destruction of unharvested cones or fruits left on the soil surface by tilling and discing the orchard floor may contribute to reduce overwintering populations of many pest species. Such prophylactic tactics are likely to prevent the formation of local pest inoculums, which can be particularly sustainable in species expressing the prolonged diapause syndrome, and make new stand infestations rely on immigration from surrounding areas only. When possible, combining the limitation of a local inoculum with the removal of host trees from within a substantial radius of an orchard may be thus a major obstacle to seed losses to fruiting structure insects. Finally, careful inspection of collected seed lots can prevent or limit long-range dispersal of endophytic spermatophages at the regional scale, to other countries of the Mediterranean Basin, and beyond.[10]

4.8 Conclusion

Reproductive structures are by definition essential components of a tree's fitness. They also provide important economic services with regard to reforestation, afforestation and conservation programs, as well as to highly valuable forest resources as food. Insects are considered the most important seed predators during the predispersal phase of seed development. The high nutrient content of seeds makes them targets of choice for an extremely diverse entomofauna native to the Mediterranean Basin, which a particularly high level of endemism. A majority of these species are specialized on particular tissues and developmental stages that characterize tree reproductive structures (from flower to seed). In this chapter, we emphasized a number of bias in our current knowledge of insect diversity towards host plant groups and geographic areas, which could be attributed to ecological factors (e.g. niche opportunities and host range) as well as to some imbalance in research efforts at both host and geography scales. Moreover, although most of the Mediterranean entomofauna is probably identified in the most widespread Mediterranean tree species, many taxonomic uncertainties remain and consequently impede the precise knowledge of their specific distribution, life cycles and damages. This may be confirmed by continuous development of genetic tools that suggest that separate species may still coexist under the same taxon.

The interactions between insects and tree reproductive structures prove to be key model systems for addressing important issues of plant-herbivore relationships, in particular the characteristics of the fruiting structure habitat allows stimulating approaches of the effect of spatio-temporal variation of resources on plant-animal interactions. Unknowns remain to be resolved on the determinants of prolonged diapause, one key component of insects' adaptive responses to fluctuating seed production in their obligate host. Also, both qualitative and quantitative impacts of pre-dispersal seed predation have to be more deeply investigated in order to precise both genetic and demographic consequences of seed loss to insects in tree populations. Given the fundamental role that some tree species are expected to play

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[10] See Chap. 9 for invasion issues in fruiting structure insects in the Mediterranean Basin.

in Mediterranean ecosystems facing climate change (e.g. *Pinus*, *Cedrus*), there is a crucial need for both foresters and seed suppliers for ongoing research clarifying the ecological drivers of pre-dispersal seed predation and its impacts on Mediterranean forest dynamics.

Appendix 4.1: Entomofauna of tree reproductive structures in the Mediterranean Basin, and its host plants, distribution and guilds

Species	Host family	Host genus	Distribution	Guild	Feeding guild	References
COLEOPTERA						
Anobiidae						
Ernobius anatolicus	Pinaceae	*Cedrus*	E	HC	CS	Roques (1983), Roques and El Alaoui El Fels (2005)
Ernobius angusticollis	Pinaceae	*Abies, Cedrus, Pinus*	N, E	HC	CS	Johnson (1975), Roques (1983), Roques and El Alaoui El Fels (2005)
Ernobius cupressi	Cupressaceae	*Cupressus*	N	HC	C	Roques (1983)
Ernobius fructuum	Pinaceae	*Cedrus*	W	HC	CS	Roques (1983), Roques and El Alaoui El Fels (2005), Mouna (2013)
Ernobius impressithorax	Pinaceae	*Pinus*	N	HC	CS	Roques and El Alaoui El Fels (2005), Bracalini et al. (2013)
Ernobius kaidilisi	Pinaceae	*Abies*	N	HC	CS	Roques (1983), Roques and El Alaoui El Fels (2005)
Ernobius mollis	Pinaceae	*Pinus*	N, E	HC	CS	Roques and El Alaoui El Fels (2005)
Ernobius oertzenii	Pinaceae	*Pinus*	N	HC	CS	Roques (1983), Roques and El Alaoui El Fels (2005)

(continued)

Species	Host family	Host genus	Distribution	Guild	Feeding guild	References
Ernobius oxycedri	Cupressaceae	*Juniperus*	N, W, E	HC	CS	Roques and El Alaoui El Fels (2005)
Ernobius parens	Pinaceae	*Pinus*	N, W	HC	CS	Roques and El Alaoui El Fels (2005), Bracalini et al. (2013)
Ernobius pini crassiusculum	Pinaceae	*Pinus*	E	HC	CS	Roques and El Alaoui El Fels (2005)
Bruchidae						
Bruchidius raddianae	Fabaceae	*Acacia*	W	CO	CS	Derbel et al. (2007)
Curculionidae						
Curculio elephas	Fagaceae	*Castanea, Quercus*	N, W, E	CO	S	Pélisson et al. (2013), Speranza (1999)
Curculio glandium	Fagaceae	*Quercus*	N, W, E	CO	S	Pélisson et al. (2013)
Curculio nucum	Fagaceae	*Castanea, Quercus*	N	CO	S	Martin (1949)
Curculio pellitus	Fagaceae	*Quercus*	N	CO	S	Pélisson et al. (2013)
Curculio propinquus	Fagaceae	*Quercus*	N	CO	S	Paparatti and Speranza (2004)
Curculio venosus	Fagaceae	*Quercus*	N	CO	S	Pélisson et al. (2013)
Dorytomus affinis	Salicaceae	*Populus*	N	CO	IF	Delplanque (1998)
Dorytomus dejeani	Salicaceae	*Populus*	N	CO	IF	Delplanque (1998)
Dorytomus icter	Salicaceae	*Populus*	N	CO	IF	Delplanque (1998)
Dorytomus longimanus	Salicaceae	*Populus*	N, W	HC	CS	Delplanque (1998)
Dorytomus subauratus	Salicaceae	*Populus*	N	CO	IF	Delplanque (1998)
Dorytomus taeniatus	Salicaceae	*Populus*	N	CO	IF	Delplanque (1998)
Dorytomus tortrix	Salicaceae	*Populus*	N	CO	IF	Delplanque (1998)
Nanodiscus transversus	Cupressaceae	*Cupressus, Juniperus*	N, W	CO	C	Roques (1983), El Alaoui El Fels and Roques (2005)

(continued)

Species	Host family	Host genus	Distribution	Guild	Feeding guild	References
Onyxacalles portusveneris	Fagaceae	*Quercus*	N, W	CO	S	Komeza and Germann (2005)
Pissodes validirostris	Pinaceae	*Pinus*	N, E	CO	CS	Roques (1983)
DIPTERA						
Anthomyiidae						
Strobilomyia carbonaria	Pinaceae	*Abies*	N	CO	CS	Roques (1983), Roques and El Alaoui El Fels (2005)
Cecidomyiidae						
Asynapta strobi	Pinaceae	*Pinus*	E	CO	C	Toper Kaygin et al. (2014)
Camptomyia pinicolana	Pinaceae	*Pinus*	N	CO	C	Roques (1983)
Contarinia sp1	Cupressaceae	*Juniperus*	W	CO	C	Roques and El Alaoui El Fels (2005)
Contarinia sp2	Pinaceae	*Cedrus*	W	CO	S	Roques (1983), Roques and El Alaoui El Fels (2005)
Dasineura abiesemia	Pinacea	*Abies*	E	CO	S	Ayberk and Cebeci (2010)
Oligotrophus sp	Cupressaceae	*Juniperus*	W	CO	C	Roques and El Alaoui El Fels (2005)
Resseliela picae	Pinacea	*Abies*	E	CO	S	Ayberk and Cebeci (2010)
Lonchaeidae						
Earomyia impossibile	Pinaceae	*Abies*	N	CO	CS	Roques (1983), Roques and El Alaoui El Fels (2005)
Trypetidae						
Rhagoletis flavigenualis	Cupressaceae	*Juniperus*	E	CO	C	Roques and El Alaoui El Fels (2005)
Chloropidae						
Hapleginella laevifrons	Pinaceae	*Cedrus*	W	CO	S	Mouna (2013)
HEMIPTERA						
Coccidae						
Carulaspis sp	Cupressaceae	*Juniperus*	N, E	HC	C	Ulgenturk and Canakcioglu (2004)

(continued)

Species	Host family	Host genus	Distribution	Guild	Feeding guild	References
Diaspis sp	Cupressaceae	*Juniperus*	E	HC	C	Roques and El Alaoui El Fels (2005)
Coreidae						
Gonocerus insidiator	Cupressaceae	*Juniperus*	N, W	CO	C	Moulet (1995), Roques and El Alaoui El Fels (2005)
Gonocerus juniperi	Cupressaceae	*Juniperus*	N, E	CO	C	Roques and El Alaoui El Fels (2005), Samin et al. (2011)
Lygaeidae						
Nysius sp	Cupressaceae	*Juniperus*	N, E	CO	ESP	Roques and El Alaoui El Fels (2005)
Orsillus depressus	Cupressaceae	*Cupressus*	N, W	CO	ESP	Rouault (2002)
Orsillus maculatus	Cupressaceae	*Cupressus*	N, W	CO	ESP	Rouault (2002)
Spilostethus pandurus	Anacardiaceae	*Pistacia*	E	HC	ESP	Mehrnejad et al. (2013)
Miridae						
Campylomma diversicorne	Anacardiaceae	*Pistacia*	E	HC	ESP	Mehrnejad et al. (2013)
Campylomma verbasci	Anacardiaceae	*Pistacia*	E	HC	IF	Mehrnejad et al. (2013)
Lygus gemellatus	Anacardiaceae	*Pistacia*	E	HC	ESP	Mehrnejad et al. (2013)
Pentatomidae						
Cyphostethus tristriatus	Cupressaceae	*Juniperus*	N, E	CO	C	Lodos and Onder (1979), Roques and El Alaoui El Fels (2005)
Holcogaster fibulata	Cupressaceae	*Juniperus*	E	CO	C	Dursun and Fent (2011)
Pitieda pinicolana	Pinaceae, Cupressaceae	*Pinus, Juniperus*	N, E	CO	ESP	Roques (1983)
Acrosternum arabicum	Anacardiaceae	*Pistacia*	E	HC	ESP	Mehrnejad et al. (2013)
Brachynema germari	Anacardiaceae	*Pistacia*	E	HC	ESP	Mehrnejad et al. (2013)
Acrosternum breviceps	Anacardiaceae	*Pistacia*	E	HC	ESP	Mehrnejad et al. (2013)

(continued)

Species	Host family	Host genus	Distribution	Guild	Feeding guild	References
Pyrrhocoridae						
Liorhyssus hyalinus	Anacardiaceae	*Pistacia*	E	HC	ESP	Mehrnejad et al. (2013)
HYMENOPTERA						
Eurytomidae						
Eurytoma plotnikovi	Anacardiaceae	*Pistacia*	N, W, E	CO	S	Mourikis et al. (1998), Braham (2005), Doğanlar et al. (2009)
Torymidae						
Megastigmus amicorum	Cupressaceae	*Juniperus*	N, E	CO	S	Roques and Skrzypczyńska (2003)
Megastigmus atlanticus	Cupressaceae	*Cupressus*	W	CO	S	Roques and Skrzypczyńska (2003)
Megastigmus bipunctatus	Cupressaceae	*Juniperus*	N	CO	S	Roques and Skrzypczyńska (2003)
Megastigmus juniperi	Cupressaceae	*Juniperus*	E	CO	S	Roques and Skrzypczyńska (2003)
Megastigmus pinsapinis	Pinaceae	*Abies, Cedrus*	N, W	CO	S	Fabre et al. (2004)
Megastigmus schimitscheki	Pinaceae	*Abies, Cedrus*	N, E	CO	S	Fabre et al. (2004), Auger-Rozenberg et al. (2012)
Megastigmus suspectus	Pinaceae	*Abies, Cedrus*	N, E	CO	S	Fabre et al. (1999), Stojanova et al. (2012)
Megastigmus thuriferana	Cupressaceae	*Juniperus*	N, W	CO	S	Auger-Rozenberg et al. (2006)
Megastigmus wachtli	Cupressaceae	*Cupressus*	N, W	CO	S	Roques and Raimbault (1986)
Megastigmus pistaciae	Anacardiaceae	*Pistacia*	N, W, E	CO	S	Roques and Skrzypczyńska (2003), Doğanlar et al. (2009)

(continued)

Species	Host family	Host genus	Distribution	Guild	Feeding guild	References
LEPIDOPTERA						
Gelechiidae						
Brachyacma oxycedrella	Cupressaceae	*Cupressus, Juniperus*	N	CO	C, CS	Roques (1983)
Gelechia senticetella	Cupressaceae	*Juniperus*	N	HC	C	Roques and El Alaoui El Fels (2005)
Palumbina guerinii	Anacardiaceae	*Pistacia*	N	CO	S	Mourikis et al. (1998)
Olethreutidae						
Gravitarmata margarotana	Pinaceae	*Pinus*	N, E	CO	CS	Toper Kaygin et al. (2014)
Gravitarmata retiferana	Pinaceae	*Pinus*	E	CO	CS	Toper Kaygin et al. (2014)
Pyralidae						
Assara conicolella	Pinaceae	*Pinus*	N	CO	CS	Roques (1983)
Assara praestantella	Pinaceae	*Cedrus*	W	CO	CS	Mouna (2013)
Dioryctria abietella	Pinaceae	*Abies*	N	CO	CS	Roques (1983), Roques and El Alaoui El Fels (2005)
Dioryctria resiniphila	Pinaceae	*Abies*	N	CO	CS	Roques (1983), Roques and El Alaoui El Fels (2005)
Dioryctria mendacella	Pinaceae	*Abies, Pinus*	N	CO	CS	Roques (1983), Roques and El Alaoui El Fels (2005)
Dioryctria mutatella	Pinaceae	*Abies, Pinus*	N, E	HC	CS	Roques (1983), Roques and El Alaoui El Fels (2005)
Dioryctria peltieri	Pinaceae	*Cedrus*	W	CO	CS	Mouna (2013)
Dioryctria peyerhimoffi	Cupressaceae, Pinaceae	*Cupressus, Cedrus*	W	CO	IF	Roques and El Alaoui El Fels (2005), Mouna (2013)
Dioryctria pineae	Pinaceae	*Pinus*	N, E	CO	CS	Roques (1983)

(continued)

Species	Host family	Host genus	Distribution	Guild	Feeding guild	References
Tortricidae						
Barbara herrichiana	Pinaceae	*Abies*	N	CO	CS	Roques (1983), Roques and El Alaoui El Fels (2005)
Barbara osmana	Pinaceae	*Cedrus*	E	CO	CS	Roques (1983), Roques and El Alaoui El Fels (2005)
Clavigesta sylvestrana	Pinaceae	*Pinus*	N	CO	IF	Karanikola and Markalas (2001)
Cydia conicolana	Pinaceae	*Pinus*	N, E	CO	CS	Roques (1983), Karanikola (2002)
Pammene juniperana	Cupressaceae	*Juniperus*	N	CO	CS	Roques and El Alaoui El Fels (2005)
Pammene mariana	Cupressaceae	*Juniperus*	E	CO	CS	Roques and El Alaoui El Fels (2005)
Pammene oxycedrana	Cupressaceae	*Juniperus*	N, W	CO	CS	Roques (1983), El Alaoui El Fels and Roques (2005)
Pseudococcyx tessulatana	Cupressaceae	*Cupressus, Juniperus, Tetraclinis*	N, W, E	CO	CS	Roques (1983), El Alaoui El Fels and Roques (2005)
Rhyacionia frustrana	Pinaceae	*Pinus*	N, E	HC	CS	Roques (1983), Toper Kaygin et al. (2014)
Rhyacionia buoliana	Pinaceae	*Pinus*	N	HC	CS	Roques (1983)
Cydia strobilella	Pinaceae	*Pinus*	N, E	CO	CS	Toper Kaygin et al. (2014)
Cydia fagiglanda	Fagaceae	*Fagus*	N	CO	IF	Alford (2007)
Cydia splendana	Fagaceae	*Castanea, Quercus*	N	CO	IF	Speranza (1999), Alford (2007)
Pammene fasciana	Fagaceae	*Castanea*	N	CO	S	Speranza (1999)

(continued)

Species	Host family	Host genus	Distribution	Guild	Feeding guild	References
Yponomeutidae						
Arghyrestia reticulata	Cupressaceae	*Juniperus*	N, W	CO	C	Roques and El Alaoui El Fels (2005), El Alaoui El Fels and Roques (2005)
Arghyrestia chrysidella	Cupressaceae	*Juniperus*	N	CO	C	Roques (1983)
Arghyrestia praecocella	Cupressaceae	*Juniperus*	N, E	CO	C	Roques and El Alaoui El Fels (2005)

E, N, W Eastern, Northern and Western Mediterranean sub-region, respectively; *CO, HC* conophyte (fruiting structure specialist), heteroconophyte (generalist), respectively; *C, CS, ESP, IF, S* conophage, conospermatophage, external seed predator, inflorescence feeder, spermatophage, respectively

References

Agrawal AA (2007) Macroevolution of plant defense strategies. Trends Ecol Evol 22:103–109

Alford DV (ed) (2007) Pest of fruit crops: a color handbook. Academic Press, San Diego

Auger-Rozenberg M-A, Kerdelhué C, Magnoux E et al (2006) Molecular phylogeny and evolution of host-plant use in conifer seed chalcids in the genus *Megastigmus* (Hymenoptera: Torymidae). Syst Entomol 31:47–64

Auger-Rozenberg MA, Boivin T, Magnoux E et al (2012) Inferences on population history of a seed chalcid wasp: invasion success despite a severe founder effect from an unexpected source population. Mol Ecol 21:6086–6103

Ayberk H, Cebeci H (2010) Survey of Trojan fir seed orchard in Edremit-Gurgendag region of Turkey. Afr J Biotechnol 9:6963–6965

Battisti A, Roques A, Colombari F et al (1999) Efficient transmission of an introduced pathogen via an ancient insect-fungus association. Naturwissenschaften 86:479–483

Beck CB (ed) (1988) Origin and evolution of gymnosperms. Columbia University Press, New York

Boivin T, Henri H, Vavre F et al (2014) Epidemiology of asexuality induced by the endosymbiotic *Wolbachia* across phytophagous wasp species: host plant specialization matters. Mol Ecol 23:2362–75

Bonal R, Espelta JM, Vogler AP (2011) Complex selection on life-history traits and the maintenance of variation in exaggerated rostrum length in acorn weevils. Oecologia 167:1053–1061

Bracalini M, Benedettelli S, Croci F et al (2013) Cone and seed pests of *Pinus pinea*: assessment and characterization of damage. J Econ Entomol 106:229–234

Braham M (2005) Management of the pistachio seed wasp, *Eurytoma plotnikovi* Nikolskaya (Hymenoptera, Eurytomidae), in Tunisia: integration of pesticide sprays and other means of control. Int Pest Control 47:319–324

Brody AK (1997) Effects of pollinators, herbivores, and seed predators on flowering phenology. Ecology 78:1624–1631

Bullock JM, Kenward RE, Hails RS (2002) Dispersal ecology: 42nd symposium of the British ecological society. Cambridge University Press, Cambridge

Cariveau D, Rebecca EI, Brody AK et al (2004) Direct and indirect effects of pollinators and seed predators to selection on plant and floral traits. Oikos 104:15–26

Crawley MJ (1989) Insect herbivores and plant population dynamics. Annu Rev Entomol 34:531–564

Crawley MJ (2000) Seed predators and plant population dynamics. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities. CABI Publication, Wallingford

Cyprus Forestry Department (2005) Cyprus. In: Merlo M, Croitoru L (eds) Valuing Mediterranean forests: towards total economic value. CABI Publication, Wallingford

Danks HV (ed) (1987) Insect dormancy: an ecological perspective. Biological Survey of Canada, Ottawa (Terrestrial Arthropods)

DeBarr GL, Hanula JL, Niwa CG et al (2000) Synthetic pheromones disrupt male *Dioryctria* spp. moths in a loblolly pine seed orchard. Can Entomol 132:345–351

Delplanque A (ed) (1998) Les insectes associés aux peupliers. Editions Memor, Bruxelles

Derbel S, Noumi Z, Anton KW et al (2007) Life cycle of the coleoptera *Bruchidius raddianae* and the seed predation of the *Acacia tortilis* subsp. *raddiana* in Tunisia. C R Biol 330:49–54

Doğanlar M, Karadağ S, Mendel Z (2009) Notes on pistachio seed wasps from two locations in the east Mediterranean. Phytoparasitica 37:147–151

Dursun A, Fent M (2011) Additional records on the *Halyini*, *Carpocorini*, *Aeliini* and *Eysarcorini* (Hemiptera: Pentatomidae: Pentatominae) of the Kelkit Valley, Turkey. Bihar Biol 5:151–156

El Alaoui El Fels MA, Roques A (2005) Guide d'identification des arthropodes inféodés aux graines de conifères autochtones dans le Haut Atlas occidental (Maroc). Bilingual français-arabe. Naturalia Marocana, Rabat

Ellner S, Hairston NG Jr (1994) Role of overlapping generations in maintaining genetic variation in a fluctuating environment. Am Nat 143:403–417

Espelta JM, Cortés P, Molowny-Horas R et al (2008) Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. Ecology 89:805–817

Fabre J, Mouna M, Du Merle P , Benhalima S (1999) Le point sur certains ravageurs du Cèdre de l'Atlas en Afrique du Nord, en France et en Europe. For Médit 20:203–221

Fabre JP, Auger-Rozenberg MA, Chalon A et al (2004) Competition between exotic and native insects for seed resources in trees of a Mediterranean forest ecosystem. Biol Invasions 6:11–22

FAO (1997) Directory of seed sources of the Mediterranean Conifers. www.fao.org/docrep/006/ad112e/AD112E00.htm

FAO (2010) Global forest resources assessment. Main report. FAO Forestry Paper No. 163, Rome

FAO (2013) State of Mediterranean Forests, Rome

Fenner M, Cresswell JE, Hurley RA et al (2002) Relationship between capitulum size and predispersal seed predation by insect larvae in common Asteraceae. Oecologia 130:72–77

Gaston KJ, Reavy D, Valladares GR (1992) Intimacy and fidelity: internal and external feeding by the British microlepidoptera. Ecol Entomol 17:86–88

Ghazoul J, Satake A (2009) Nonviable seed set enhances plant fitness: the sacrificial sibling hypothesis. Ecology 90:369–377

Gidoin C (2014) The ecological impacts of an invasive seed-predator (Hymenoptera: Torymidae) in a Mediterranean forest ecosystem. PhD thesis, University of Montpellier, France (In French)

Gourbière S, Menu F (2009) Adaptive dynamics of dormancy duration variability: evolutionary trade-off and priority effect lead to suboptimal adaptation. Evolution 63:1879–1892

Guido M, Roques A (1996) Impact of the phytophagous insect and mite complex associated with cones of Junipers (*Juniperus phoenicea* L. and J. *cedrus* Webb and Berth.) in the Canary Islands. Ecol Mediterr 22:1–10

Halpern SL, Underwood N (2006) Approaches for testing herbivore effects on plant population dynamics. J Appl Ecol 43:922–929

Hanski I (1988) Four kinds of extra long diapause in insects: a review of theory and observations. Ann Zool Fenn 25:37–53

Harborne JB (2001) Twenty-five years of chemical ecology. Nat Prod Rep 18:361–379

Harman HM (1999) The effect of variability in the phenology of the reproductive stages of Scotch broom (*Cytisus scoparius*) on the synchronization of the life stages of broom seed beetle (*Bruchidius villosus*) in New Zealand. Biol Control 15:228–234

Hughes J, Vogler AP (2004) The phylogeny of acorn weevils (genus *Curculio*) from mitochondrial and nuclear DNA sequences: the problem of incomplete data. Mol Phylogenet Evol 32:601–615

Hulme PE (1998) Post-dispersal seed predation: consequences for plant demography and evolution. Perspec Plant Ecol Evol Syst 1:32–46

Hulme PE, Benkman CW (2002) Granivory. In: Herrera CM, Pellmyr O (eds) Plant–animal interactions: an evolutionary approach. Blackwell, Oxford

Innocenti M, Tiberi R (2002) Cone and seed pests of *Pinus pinea* L. in Central Italy. Redia 85:21–28

Iwasa Y, Satake A (2004) Mechanisms inducing spatially extended synchrony in mast seeding: the role of pollen coupling and environmental fluctuation. Ecol Res 19:13–20

Janzen DH (1969) Seed-eaters versus seed size, number, toxicity and dispersal. Evolution 23:1–27

Janzen DH (1971) Seed predation by animals. Annu Rev Ecol Syst 2:465–492

Jarry M, Candau JN, Roques A, Ycart B (1997) Impact of emigrating seed chalcid, *Megastigmus spermotrophus* Wachtl (Hymenoptera: Torymidae), on seed production in a Douglas-fir seed orchard in France and modelling of orchard invasion. Can Entomol 129:7–19

Johnson C (1975) Review of the palearctic species of the genus *Ernobius* Thomson. Entomol Bl 71:65–93

Jordano P (2000) Fruits and frugivory. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities, 2nd edn. CABI Publication, Wallingford

Karanikola P (2002) *Cydia* (*Laspeyresia*, *Enarmonia*) *conicolana* Heyl. (Lepidoptera, Torticidae) an important seedworm infesting cones in plantations of *Pinus brutia* Ten. in North Greece. Ereuna 15:71–80

Karanikola P, Markalas S (2001) Insects attacking the cones of *Pinus brutia* Ten. in Northern Greece. In: Proceedings of international conference forest research: a challenge for an integrated European approach, Thessaloniki, 27 August–1 September

Kelly D (1994) The evolutionary ecology of mast seeding. Trends Ecol Evol 9:465–470

Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? Annu Rev Ecol Syst 33:427–447

Kolb A, Ehrlén J, Eriksson O (2007) Ecological and evolutionary consequences of spatial and temporal variation in pre-dispersal seed predation. Perspect Plant Ecol 9:79–100

Komeza N, Germann C (2005) New conclusions on the distribution of *Onyxacalles portusveneris* (Mayet, 1903) in France (Coleoptera: Curculionidae, Cryptorhynchinae). - Weevil News: http://www.curci.de/Inhalt.html. CURCULIO-Institute, Mönchengladbach (27)

Krouchi F, Derridj A, Lefevre F (2004) Year and tree effect on reproductive organisation of *Cedrus atlantica* in a natural forest. For Ecol Manag 197:181–189

Lander TA, Klein EK, Oddou-Muratorio S et al (2014) Reconstruction of a windborne insect invasion using a particle dispersal model, historical wind data, and Bayesian analysis of genetic data. Ecol Evol 4:4609–4625

Lefèvre F, Boivin T, Bontemps A et al (2013) Considering evolutionary processes in adaptive forestry. Ann For Sci 71:723–739

Lewinsohn TM, Novotny V, Basset Y (2005) Insects on plants: diversity of herbivore assemblages revisited. Annu Rev Ecol Evol Syst 36:597–620

Liebhold A, Tobin P (2008) Population ecology of insect invasions and their management. Annu Rev Entomol 53:387–408

Lodos N, Onder F (1979) Contribution to the study on the Turkish Pentatomoidea (Heteroptera), IV. Family: Acanthosomatidae Stal 1864. Turk Bitki Derg 3:139–160

Löfstedt C, Svensson GP, Jirle EV et al (2011) 3Z, 6Z, 9Z, 12Z, 15Z)-pentacosapentaene and (9Z, 11E)-tetradecadienyl acetate: sex pheromone of the spruce coneworm *Dioryctria abietella* (Lepidoptera: Pyralidae). J Appl Entomol 103:1216–1221

Lucchetta P, Bernstein C, Thery M et al (2008) Foraging and associative learning of visual signals in a parasitic wasp. Anim Cogn 11:525–533

Luchi N, Mancini V, Feducci M et al (2012) *Leptoglossus occidentalis* and *Diplodia pinea*: a new insect-fungus association in Mediterranean forests. Forest Pathol 42:246–251

Mangini AC, Duerr A, Taylor JW (2003) Seed and cone insect pest management: challenges and solutions. In Proceedings of the society American foresters national convention, pp 170–175

Maron JL, Crone E (2006) Herbivory: effects on plant abundance, distribution and population growth. Proc R Soc B 273:2575–2584

Martin H (1949) Contribution à l'étude du balanin des noisettes (*Balaninus nucum* L.). Rev Pathol Veg Entomol Agric Fr 28:3–28

McClure M, Quiring DT, Turgeon JJ (1998) Proximate and ultimate factors influencing oviposition site selection by endoparasites on conifer seed cones: two sympatric dipteran species on larch. Entomol Exp Appl 87:1–13

Médail F, Quézel P (1997) Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. Ann Missouri Bot Garden 84:112–127

Mehrnejad MR, Linnavuori RE, Alavi SH (2013) Hemipteran bugs associated with pistachio trees and notes on major species. Zool Ecol 23:29–41

Menu F, Roebuck JP, Viala M (2000) Bet-hedging diapause strategies in stochastic environments. Am Nat 155:724–734

Moegenburg SM (1996) Sabal palmetto seed size: causes of variation, choices of predators, and consequences for seedlings. Oecologia 106:539–543

Mosseler A, Roberts BA, Tricco P (1992) The effects of fir coneworm, *Dioryctria abietivorella* (Grote) (Lepidoptera, Pyralidae), on seed production in small, isolated populations of red pine, *Pinus resinosa* Ait. For Ecol Manag 53:15–27

Moulet P (1995) Hémiptères Coreoidea euro-méditerranéens. Faune de France 81:1–58

Mouna M (2013) Les insectes du cèdre de l'Atlas (*Cedrus atlantica* Manetti) dans le Nord de l'Afrique. Travaux de l'Institut Scientifique, Série Zoologie, Université Mohamed V – Agdal. Rabat, Institut Scientifique

Mourikis PA, Tsourgianni A, Chitzanidis A (1998) Pistachio nut insect pests and means of control in Greece. In: Ferguson L, Kester D (eds) Proceedings of 2nd international symposium on pistachios and almonds, Davis, 24–29 Aug 1997. Acta Hort 470:604–611

Owens JN, Blake MD (1985) Forest tree seed production: a review of literature and recommendations for future research. Petawawa National Forestry Institute, Chalk River

Paparatti B, Speranza S (2004) Management of chestnut weevil (*Curculio* spp.) insect key-pest in Central Italy. Proc III Int Chestnut Congress 693:551–556

Pélisson PF, Bernstein C, François D et al (2013) Dispersal and dormancy strategies among insect species competing for a pulsed resource. Ecol Entomol 38:470–477

Philippi T, Seger J (1989) Hedging one's evolutionary bets, revisited. Trends Ecol Evol 4:41–44

Primack RB (1987) Relationships among flowers, fruits, and seeds. Annu Rev Ecol Syst 18:409–430

Quézel P, Médail F (2003) Ecologie et biogéographie des forêts du Bassin Méditerranéen. Elsevier, Paris

Rappaport NG, Mori S, Roques A (1993) Estimating effect of *Megastigmus spermotrophus* (Hymenoptera: Torymidae) on Douglas-fir seed production: the new paradigm. J Econ Entomol 86:845–849

Roques A (1981) Biology and distribution of *Megastigmus spermotrophus* Wachtl. (Hymenoptera Chalcidoidea Torymidae) and other insects related to cones in forest stands and seed orchards of Douglas fir Pseudotsuga menziesii (Mirb.) Franco. Acta oecol, Oecol Appl 2:161–180

Roques A (1983) Les Insectes Ravageurs des Cônes et Graines de Conifères en France. INRA, Paris

Roques A (1987) Interaction between visual and olfactory signals in cone recognition by insect pests. In: Labeyrie V, Fabres G, Lachaise D (eds) Proceedings of international symposium on insect-plant relationships. Junk, Dordrecht

Roques A (1988) New results and some thinking about significance and induction of prolonged diapause in cone insects with particular references to the larch cone fly (*Lasiomma melania*) and to the Douglas-fir seed chalcid (*Megastigmus spermotrophus*). In: Miller GE (ed) Proceedings 3rd cone and seed insects IUFRO working party conference (IUFRO S2.07–01). Forestry Canada, Pacific Forestry Centre, Victoria, pp 64–81

Roques A (1991) Structure, specificity and evolution of insect guilds related to cones and conifers in Western Europe. In: Baranchikow YN, Mattson WJ, Hain FP, Payne TL (eds) Forest insect guilds: patterns of interactions with host trees. US Forest Service, Radnor, Gen Tech Rep NE-153:300–315

Roques A, Battisti A (1999) Cypress pests. In: Teissier du Cros E, Ducrey M, Barthélémy D, Pichot C, Giannini R, Raddi P, Roques A, Sales Luis J, Thibaut B (eds) Cypress. A practical handbook. Studio Lenonardo, Firenze, pp 75–95

Roques A, El Alaoui El Fels MA (2005) Overview of the arthropod fauna that colonises seed cones in the Mediterranean region. In: Lieutier F, Ghaioule D (eds) Entomological research in Mediterranean forest ecosystems. INRA, Versailles, pp 59–78

Roques A, Raimbault JP (1986) Cycle biologique et répartition de *Megastigmus wachtli* (Seitn.) (Hymenoptera: Torymidae), chalcidien ravageur des graines de cyprès dans le Bassin Méditerranéen. J Appl Entomol 101:370–381

Roques A, Skrzypczyńska M (2003) Seed-infesting chalcids of the genus *Megastigmus* Dalman, 1820 (Hymenoptera: Torymidae) native and introduced to the West Palearctic region: taxonomy, host specificity and distribution. J Nat Hist 37:127–238

Roques L, Auger-Rozenberg MA, Roques A (2008) Modelling the impact of an invasive insect via reaction–diffusion. Math Biosci 216:47–55

Rose KE, Louda SM, Rees M (2005) Demographic and evolutionary impacts of native and invasive insect herbivores on *Cirsium canescens*. Ecology 86:453–465

Rosenberg O, Nordlander G, Weslien J (2014) Effects of different insect species on seed quantity and quality in Norway spruce. Agric For Entomol. doi:10.1111/afe.12091

Rouault G (2002) Biologie et répartition des punaises du genre *Orsillus* (Heteroptera: Lygaeidae) associées aux Cupressaceae: une étude de l'impact d'un pathogène introduit sur les interactions cônes-insectes. PhD Thesis, University of Orléans (in French)

Rouault G, Turgeon J, Candau J-N et al (2004) Oviposition strategies of conifer seed chalcids in relation to host phenology. Naturwissenschaften 91:472–480

Roux G, Roques A, Menu F (1997) Effect of temperature and photoperiod on diapause development in Douglas fir seed chalcid, *Megastigmus spermotrophus*. Oecologia 111:172–177

Sallabanks R, Courtney SP (1992) Frugivory, seed predation, and insect-vertebrate interactions. Annu Rev Entomol 37:377–400

Samin N, Sakenin H, Linnavuori RE et al (2011) A faunistic survey of Heteroptera (Insecta) from western Iran. Calodema 146:1–12

Singh H (1978) Embryology of gymnosperms. Gebrüder Borntraeger, Berlin

Snyder RE (2006) Multiple risk reduction mechanisms: can dormancy substitute for dispersal? Ecol Lett 9:1106–1114

Soula B, Menu F (2005) Extended life cycle in the chestnut weevil: prolonged or repeated diapause? Entomol Exp Appl 115:333–340

Speranza S (1999) Chestnut pests in central Italy. Proc 2nd Int Symp Chestnut 494:417–424

Stojanova A, Civelek H, Yörük B, Sarı S, Atahan T (2012) Checklists of Turkish Eurytomidae Walker, 1832 and Torymidae Walker, 1833 (Hymenoptera, Chalcidoidea). Turk J Entomol 36:69–82

Strauss SY, Whittall JB (2006) Non-pollinator agents of selection on floral traits. In: Harder LD, Barrett SCH (eds) Ecology and evolution of flowers. Oxford University, Oxford, pp 120–138

Strauss SY, Zangerl AR (2002) Plant-insect interactions in terrestrial ecosystems. In: Herrera CM, Pellmyr O (eds) Plant–animal interactions: an evolutionary approach. Blackwell, Oxford

Suckling DM, Gibb AR, Dentener PR et al (2005) *Uraba lugens* (Lepidoptera: Nolidae) in New Zealand: pheromone trapping for delimitation and phenology. J Econ Entomol 98:1187–1192

Suez M, Gidoin C, Lefèvre F, Candau J-N, Chalon A, Boivin T (2013) Temporal population genetics of time travelling insects: a long term study in a seed-specialized wasp. PLoS one 8(8): e70818

Takács S, Bottomley H, Andreller I et al (2009) Infrared radiation from hot cones on cool conifers attracts seed-feeding insects. Proc R Soc 276:649–655

Tapias R, Climent J, Pardos JA et al (2004) Life histories of Mediterranean pines. Plant Ecol 171:53–68

Thomas PA, Polwart A (2003) *Taxus baccata* L. J Ecol 91:489–524

Toper Kaygin A, Kavakli Z, Yiğit B et al (2014) Major pests and diseases identified in pine cones in turkey. Paper presented at the Joint IUFRO 7.03.01, 7.03.06 and 7.03.14 working party meeting, Antalya, 9–14 Apr 2014

Trudel R, Guertin C, Grant GG (2006) Potential for mating disruption to reduce cone damage by the spruce seed moth, *Cydia strobilella*, in spruce seed orchards. J Appl Entomol 130:245–250

Turgeon J (1994) Insect exploiting seed cones of *Larix* spp., *Picea* spp., and *Pinus* spp.: species richness and patterns of exploitation. In: Turgeon JJ, de Groot P (eds) Biology, damage and management of seed orchard pests. Canadian Forestry Service, Sault Sainte Marie, pp 15–30

Turgeon JJ, Roques A, De Groot P (1994) Insect Fauna of coniferous seed cones: diversity, host plant interactions and management. Annu Rev Entomol 39:172–212

Turnbull LA, Crawley MJ, Rees M (2000) Are plant populations seed-limited? A review of seed sowing experiments. Oikos 88:225–238

Ulgenturk S, Canakcioglu H (2004) Scale insect pests on ornamental plants in urban habitats in Turkey. J Pest Sci 77:79–84

von Aderkas P, Rouault G, Wagner R et al (2005) Seed parasitism redirects ovule development in Douglas fir. Proc R Soc B 272:1491–1496

Wilcock C, Neiland R (2002) Pollination failure in plants: why it happens and when it matters. Trends Plant Sci 7:270–277

Witzgall P, Trematerra P, Liblikas I et al (2010) Pheromone communication channels in tortricid moths: lower specificity of alcohol vs. acetate geometric isomer blends. Bull Entomol Res 100:225–230

Xenopoulos SG, Diamandis S (1985) A distribution map for *Seridium cardinale* causing the cypress canker disease in Greece. Eur J For Pathol 15:223–226

Zangerl AR, Berenbaum MR (1997) Cost of chemically defending seeds: furanocoumarins and Pastinaca sativa. Am Nat 150:491–504

Chapter 5
Native Sap-Sucker Insects in the Mediterranean Basin

Aurélien Sallé and Andrea Battisti

Abstract Several native species of aphids, coccids and bugs can affect trees in the Mediterranean Basin. The prominent species on broadleaved trees are Phylloxera quercus and Kermes vermilio for evergreen oaks, and Phloeomyzus passerinii for poplars. On conifers, Haematoloma dorsatum and three species of Leucaspis could be considered as pine pests. Most of these species are occasional pests. They generally affect the vigour of their host tree by consuming host resources. In addition, resources may be further depleted by indirect effects, resulting from a reduced photosynthesis due to sooty molds development and early leaf fall. These insects can also cause significant aesthetic damage for ornamental trees. Phloeomyzus passerinii however can be considered as a primary pest killing mature poplar stands during outbreaks, probably through dramatic modifications of resources allocations within their host trees. The economical impact of most of these species has increased recently, and some of them have spread northwardly, while they were previously restricted to the Mediterranean Basin. Climate change and/or changes in silvicultural practices could explain these recent modifications of geographical ranges and damage incidence.

5.1 Introduction

Several sap-sucker insects may be considered as tree pests in the Mediterranean Basin. The most damaging pests are often invasive species, like *Matsucoccus feytaudi* Duc., *Matsucoccus josephi* Bodenheimer et Harpaz, *Cinara cedri* Mimeur or *Cedrobium laportei* Remaudière, which are therefore presented in a separate chapter. Besides *Phloeomyzus passerinii* (Signoret), native Heteroptera are mostly occasional pests which rarely significantly affect the vigor or survival of their host tree.

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Direct damage occurs generally through resource depletion affecting tree growth or seed production (Dixon 1971; Wood and Tedders 1986; Wood et al. 1987; Smith and Schowalter 2001). Tree growth might be further reduced by the development of sooty molds on the honeydew which accumulates on leaves or needles, affecting light penetration and therefore photosynthesis (Wood et al. 1988). Growth reduction can be associated with early leaf or needle fall (Dixon 2005). Some species can induce more conspicuous symptoms like the chlorosis or misshaping of host tissues. This can be related to plant manipulation of host tissue by the insect, like for instance during gall induction (Dixon 2005), an alteration of host physiology as a consequence of insect feeding (Quisenberry and Ni 2007), or the injection of salivary toxins (Miles 1989). Contrary to crop pests, Heteroptera living on trees are rarely vectors of phytovirus (Blackman and Eastop 1994). Besides a reduction of tree vigor, the chloroses, leaf misshaping and early leaf or needle fall can have aesthetic after-effects on ornamental trees, hedges or even forest stands.

A common feature among several of the species presented below is that their damage increased a few years or decades ago. This might result from climate change, which can affect insect development but also host suitability. The meta-analyses performed by Koricheva et al. (1998) and Huberty and Denno (2004) concluded that water deficit can negatively affect or favor sap-suckers and generally negatively affect the survival or colonization density of gall-formers, unless it interferes with tree resistance mechanisms (Björkman 2000). For the woolly poplar aphid, a combination of global warming shortening nymphal development and the plantation of susceptible poplar genotypes over large areas have probably favored the damage expansion to northern latitudes (Pointeau 2011). Changes in silvicultural practices may have also favored the incidence of other species. For the oak phylloxera and the berry kermes, the use of evergreen oaks, holm oak in particular, in urban context or in plantations for truffle production may have also favored the infestations (Martin-Santafé et al. 2014a). For the red-black pine bug, pine plantations in old pastures or changes in grasses communities, as a consequence of increased nitrogen deposition, could have favored this insect since its nymphs develop on grasses roots (Masutti et al. 2005; Moraal 1996; Roversi et al. 1991).

5.2 Pests of Broadleaved Trees

Phylloxera quercus Boyer de Fonscolombe (Hemiptera: Phylloxeridae), the oak phylloxera, is a phylloxerid developing of the lower side of oak leaves. *Phylloxera florentina* Targ., *P. coccinea*, Targ., *P. signoreti* Targ., *P. lichtensteini* Balb. and *P. balbiani* Lich. are generally considered synonyms of *P. quercus*. For some authors however two separate species should be considered: *P. quercus* and *P. florentina*, the first species colonizing *Quercus coccifera* L. and *Q. robur*, while the second develops on *Q. ilex* L. and *Q. robur* L. (Grassé 1951; Tremblay 1981). *Phylloxera quercus* is a Mediterranean species encountered in Southern Europe and Northern Africa, but also mentioned in Southwest Asia (Blackman and Eastop 1994). It is also present in the Middle East, especially in Iraq where it has caused significant damage (Mohammad and Abdullah 1985). The species has been also intercepted several times on imported *Q. ilex* in Great Britain (Reid and Cannon 2010).

The life cycle is quite complex. It has been detailed by Grassi et al. (1912, in Antonelli 1989) and more recently reviewed by Antonelli (1989). Overwintering usually occurs as eggs, and occasionally young nymphs, on evergreen oaks which are the primary hosts. In spring, after hatching, nymphs settle on the lower face of a young leaf and develop to yellow, apterous, fundatrix females. These females lay hundreds of eggs under the infested leaf. In late spring, from the eggs, similar apterous fundatrix females are produced, but also winged morphs. The apterous females will continue to lay eggs under the leaves of the primary host while the winged morphs will colonize deciduous oaks. On these secondary optional hosts, winged morphs will lay eggs on the lower side of the leaves, during summer months. On the primary host, a third generation is produced in summer which gathers apterous fundatrix females, winged fundatrix females which migrate to secondary hosts, and winged sexuparae which lay eggs on the primary host. These eggs will give birth to sexual winged morphs. The following generations will gather sexual winged morphs, winged sexuparae and apterous fundatrix. Up to eight generations have been reported on the primary host (Grassi et al. 1912, in Antonelli 1989). On the secondary host however, only three generations are performed. The eggs laid by the winged fundatrix morphs will produce apterous fundatrix females, similar to those occurring on the primary host. These females give birth to apterous virginoparae females and winged sexuparae which migrate on the primary host. The apterous virginoparae females will only give birth to winged sexuparae which will also fly back to the primary host to lay eggs. The sexual winged morphs have no functional mouthparts. After mating, at the end of summer or autumn, they lay overwintering eggs on the primary host, in bark crevices close to buds.

The aphid develops on the leaves of evergreen oaks, *Q. ilex*, *Q. suber* L., and *Q. coccifera*, which are primary hosts (Martelli and Arru 1957). Deciduous oaks like *Q. robur*, *Q. pubescens* Willd., *Q. faginea* Lam. and *Q. petraea* (Matt.) Liebl. can be secondary, facultative hosts (Antonelli 1989; Fernandez de Cordova 2002; Martelli and Arru 1957). The oak phylloxera has also been mentioned on *Q. lusitanica* Lam. and *Q. pyrenaica* Willd. (Nieto 1974).

All aphid morphs, except the sexual ones, feed on the underside of leaves (Fig. 5.1a). The fundatrix preferentially insert their stylets in veins. It induces a necrotic area affecting leaf growth and resulting in misshaping on young, developing leaves (Antonelli 1989). On the limb, chlorotic and necrotic spots develop at the feeding sites. Bronze colored spots sometimes merge together and become visible on the upper leaf surface (Fig. 5.1b). This leaf damage may lead to early leaf fall during heavy infestations (Reid and Cannon 2010). In addition to direct damage, honeydew can also favor the development of sooty molds on leaves, impairing photosynthesis (Ubaldo et al. 2008). These alterations can be quite frequent on oaks since during a survey in Apulia (Italy) Ubaldo et al. (2008) detected attacks of *P. quercus* on 43 % of the 3360 *Quercus* sp. investigated. Antonelli (1989) noted that damage was more frequent on trees regularly pruned, in hedges for instance, on which novel shoots are abundant. The leaf damage may cause growth reduction during heavy infestations, mostly for evergreen oaks, the primary hosts, which suffer

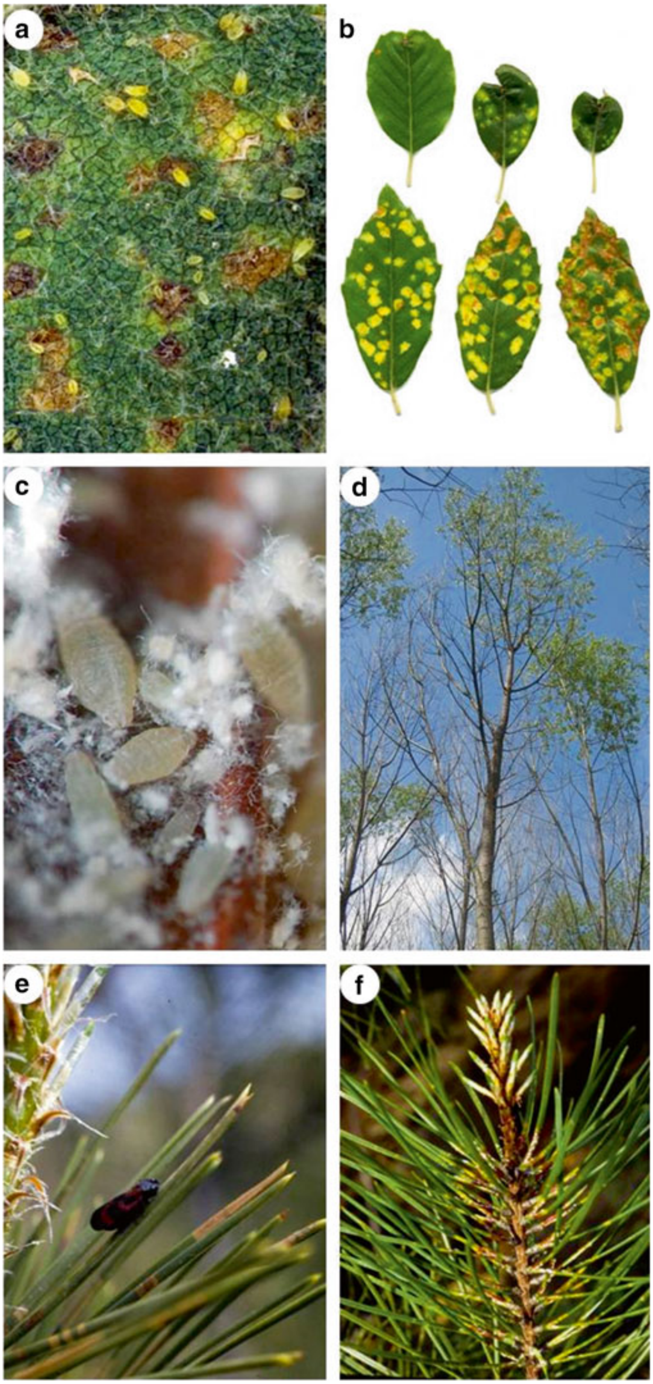

Fig. 5.1 Native sap-suckers damaging forest trees in the Mediterranean Basin. (**a**) lower side of a *Quercus pubescens* leaf showing the damage caused by the Phylloxera aphids in different developmental stages, (**b**) Different types of damage on *Quercus ilex* leaves caused by Phylloxera aphids, (**c**) a colony of *Phloeomyzus passerinii* on the bark of a poplar, (**d**) a poplar in the spring following a heavy infestation by *P. passerinii*, with only a partial bud break, (**e**) *Haematoloma dorsatum* mating on a needle pair, with damage caused by sucking the needles (yellow circular spots and dry apex), (**f**) scales and damage of *Leucaspi*s sp. on needles of *Pinus nigra* (Photo credits: **a**, **b**, **e** and **f** A. Battisti, **c** and **d** A. Sallé)

from a longer infestation by the aphid (Antonelli 1989). In addition to growth reduction, oak phylloxera attacks also lead to significant aesthetic damage, especially relevant for urban trees or hedges (Antonelli 1989, Niccoli in Reid and Cannon 2010). In Iraq, *P. quercus* has also been reported to kill young oaks during years of severe infestation (Mohammad and Abdullah 1985).

The aphid is preyed on by various predators including ladybirds (Coleoptera: Coccinellidae), hoverflies (Diptera: Syrphidae), mirids (Heteroptera: Miridae) and lacewings (Neuroptera: Chrysopidae) (Antonelli 1989).

Population control can be achieved through chemical spraying. Several insecticides, reviewed in Antonelli (1989), have been recommended. The spraying should be preferentially performed early in spring. Mineral oils could also be used in winter to kill overwintering eggs or nymphs. However, since this parasite rarely affects tree survival, chemical spraying and mineral oils should be restricted to heavy infestations, in nurseries only (Antonelli 1989).

Kermes vermilio Planchon (Hemiptera: Kermesidae), the berry kermes, is a coccid developing on oak twigs. It occurs all over the Mediterranean basin (Portugal, Spain, France, Italy, Greece, Turkey, Algeria, Morocco, Sicily, Crete, Corsica and Sardinia) (Malumphy 2008; Pellizzari et al. 2012 and references therein), and has been introduced recently in Great Britain (Malumphy 2008). This insect is well-known for the red dye, the vermilion, which can be extracted from the eggs located beneath the venter of females. This dye has been widely used during antiquity and Middle Ages and was then considered an important economic resource of the Mediterranean Basin. Since the sixteenth century, it has been replaced by synthetic dyes and pigments from another coccid, *Dactylopius coccus* Costa (Foldi 2003).

This coccid is univoltine, oviparous and overwinters as first instar nymphs. First instars are active and mobile until they find a feeding site. First and second instars are orange or bright red, with white wax secretions. For females there is also a third nymphal instar. Adult females appear in spring. They are sessile, legless, reddish-brown, and covered with a grey-white wax. They are usually settled on a wax pad. They produce up to 2000 eggs, laid in a brood chamber located beneath females' venter. Eggs hatch and larvae leave the brood chamber in summer (Leonardi 1920; Malumphy 2008; Marotta et al. 1999; Martin et al. 2007; Martin Bernal and Ibarra Ibanez 2011). These instars, and the female, have been described in detail by Balachowsky (1950) and Pellizzari et al. (2012). For the males, following the second instar, sessile prepupal and pupal stages occur. Adult males appear in spring (Marotta et al. 1999). They exhibit a single pair of wings, and legs, but mouthparts are not functional (Ibarra et al. 2001; Malumphy 2008). This insect is a parasite of evergreen oaks. It colonizes the branches, preferentially the young ones, of *Q. ilex*, *Q. coccifera* and *Q. suber* (Pellizzari et al. 2012).

Several species have been found preying on *K. vermilio*. The predators include the caterpillar of *Eublemma scitula* (Rambur) (Panis 1974) and the ladybird *Exochomus quadripustulatus* L. (Belcari and Minnocci 1989; Martin Bernal and Ibarra Ibanez 2011). Some chalcids are also parasitoids of this coccid: *Metaphycus hirtipennis* Mercet, *M. hispanicus* Mercet, *Encyrtus infidus* Rossi, *Cheiloneurus claviger* Thomson, *Pachyneuron muscarum* L. and *Sauleia* sp. (Del Bene and Landi 1992; Japoshvili and Karaca 2002; Marotta et al. 1999; Martin et al. 2007). In Italy, reported parasitism rates rose up to 37 % and 75 % (Del Bene et al. 1992; Marotta et al. 1999).

The species has only been reported rarely as a pest but, since 1987, it has become more abundant on ornamental *Q. ilex* trees in Italy and heavy infestations have been recorded in urban environments, mainly in Central and Southern Italy (Andreatta 1996; Belcari 1991; Belcari and Minnocci 1989; Del Bene and Landi 1992; Marotta et al. 1999). Heavy infestation has also been reported on ornamental *Q. ilex* in England (Malumphy 2008). In Spain infestations have been detected in isolated trees in gardens, in urban plantations but also in holm oak forests and truffle plantations (Ibarra et al. 2001; Martin et al. 2007; Martin Bernal and Ibarra Ibanez 2011; Martin-Santafé et al. 2014b). During heavy infestation the coccid can induce the yellowing of leaves, leaf loss and the drying of apical stems (Ibarra et al. 2001; Malumphy 2008; Martin et al. 2007; Pellizzari et al. 2012). This may result in partial or total defoliation and oak dieback, but trees can generally recover (Ibarra et al. 2001; Martin et al. 2007; Martin Bernal and Ibarra Ibanez 2011). However it results in significant aesthetic damage. Heavy infestations are apparently linked with climatic conditions and/or decreased tree vigor (Martin Bernal and Ibarra Ibanez 2011). Another scale species, *Kermes ilicis* L., can also cause similar damage on evergreen oaks when population levels are high (Martin-Santafé et al. 2014a, b). Spores of the phytopathogenic fungus *Diplodia mutila* (Fr.) Mont., have been found on the wax of *K. vermilio* nymphs, suggesting that they might vector the fungus (Ibarra et al. 2001), but it still need to be demonstrated.

During heavy infestations, insecticide spraying has been performed in Spain. Several products induced high mortality rates and might be efficient for managing *K. vermilio* outbreaks when natural enemies fail to control coccid populations (Martin et al. 2007). However considering the low incidence of the coccid on tree health, and the possible incidence of chemicals on the associated fauna, insecticide treatments should be restricted to particularly important infestations (Martin Bernal and Ibarra Ibanez 2011).

Phloeomyzus passerinii (Signoret) (Hemiptera: Aphididae: Phloeomyzinae), the woolly poplar aphid, develops on the trunk of different poplar species. *Phloeomyzus passerinii* is the only known species within the Phloeomyzinae sub-family (Blackman and Eastop 1994; Nieto-Nafria and Mier-Durante 1998), but a subspecies, *P. passerinii zhangwuensis*, has been described in China (Zhang and Zhong 1982). *Phloeomyzus dubius*, *P. redelei* and *P. dearborni* are considered synonyms of *P. passerinii* (Eastop and Hille Ris Lambers 1976; Masutti 1982). The species has been described for the first time at the end of the nineteenth century in France and since it has been recorded in several European countries, Russia, throughout the Mediterranean Basin, the Near East and Middle East and Asia, and has therefore probably a Palaeartic distribution (see Pointeau 2011 and references therein). It has also been introduced in Northern and Southern America (Ortego et al. 2004; Smith 1974). Although the geographical range of this aphid is wide, damage mostly occurred in the Mediterranean Basin until recently. The first outbreaks were reported in 1934 in Italy (Della Beffa 1936), in 1940 in Spain (Aparisi 1971), in 1980 in Iran (Rajabi Mazhar et al. 2003), and in 1996 in the South of France (Maugard 1996).

Since then outbreaks have spread up to the North of France (Baubet and Goudet 2010), and it is considered an emerging pest of poplar stands.

This aphid is monoecious and develops only on *Populus* species, on the trunk or main branches. There is apparently no alternate host. Throughout the year grayish or greenish round apterous females can be observed within the bark crevices of mature trees where they produce an abundant white woolly wax (Fig. 5.1c). They lay viviparous nymphs through parthenogenetic reproduction. The first instar is quite mobile while the three following instars are rather sessile (Charles et al. 2014). Under field conditions, in Italy, 10–12 parthenogenetic generations per year have been reported (Della Beffa 1936), but under optimal laboratory conditions up to 33 generations occurred (Arzone and Vidano 1984). In autumn slender black and winged sexual morphs may occur. The nymphal development producing these sexual winged morphs starts with two nymphal instars, similar to those occurring at the beginning of parthenogenetic morphs development, followed by two active nymphal instars with wing buds (Charles et al. 2014). Sexual reproduction produces eggs which may overwinter (Arzone and Vidano 1984; Blackman and Eastop 1994; Vala et al. 2011). Population genetics studies based on mitochondrial and nuclear markers, including microsatellites (Pointeau et al. 2012a), indicate that genetic diversity can be observed at different scales, from region to tree within an infested stand, suggesting that sexual reproduction maintain a certain level of genetic mixing (Pointeau 2011). The feeding strategy of *P. passerinii* has been unraveled only recently. It feeds in the shallow tissues of the cortical parenchyma of poplar bark where it induces the formation of a pseudogall (Dardeau et al. 2014a, b; Pointeau et al. 2012b). This pseudogall enhances both aphid development and feeding behavior of the aphid (Dardeau et al. 2014a). It suggests an improvement of the nutritional value of poplar tissues, probably through carbohydrates and amino acids mobilization from the surrounding tissues (Dardeau et al. 2014b, 2015).

Several species and hybrids of poplars can be colonized by the woolly poplar aphid: *Populus nigra* L., *P. deltoides* (Bartr.) Marsh., *P. suaveolens* Fisher, *P. ciliata* Wall., *P. maximowiczii* Henry, *P. tremuloides* Michx. and *P. x canadensis* Michx. (Blackman and Eastop 1994; Habib and Ghani 1970; Smith 1974). It has also been reported on *P. alba* L. (Theobald 1929), but subsequent susceptibility assessments did not support this observation (Karahroodi et al. 2006; Lapietra and Allegro 1990; Rajabi Mazhar et al. 2003). Susceptibility tests have been developed in Italy, Iran and France and indicate an important variability in resistance among cultivated poplar species and hybrids (Allegro et al. 1996; Pointeau et al. 2011; Sadeghi et al. 2007).

In Italy and Iran many generalist predators have been found preying on the woolly poplar aphid. In these countries, more than 30 predators belonging to Anthocoridae (Heteroptera), Miridae (Heteroptera), Pentatomidae (Heteroptera), Chrysopidae (Neuroptera), Hemerobiidae (Neuroptera), Syrphidae (Diptera), Chloropidae (Diptera), Chamaemyiidae (Diptera), Coccinellidae (Coleoptera) or Thrombiididae (Acarina) have been described (Arzone 1987; Raspi 1996; Raspi 2005; Vidotti 1960). The prominent species were *Orius minutus* L. (Anthocoridae), *Chrysopa perla* (L.) and *Chrysoperla carnea* (Steph.) (Chrysopidae), *Sphaerophoria scripta* (L.), *Syrphus ribesii* (L.), *Episyrphus balteatus* (Deg.), *Metasyrphus corolla* (Fabr.) and *Melliscaeva auricollis* (Syrphidae), and *Exochomus quadripustulatus*, *Scymnus ferrugatus* (Muls.), *Coccinella septempunctata* L., *Adalia bipunctata* (L.), *Synharmonia globata* (L.), *Propylaea quatuordecimpunctata* (Ws.) (Coccinellidae) (Arzone 1987). Nonetheless this associated fauna apparently does not exert a significant control on aphid populations at the beginning of outbreaks and is generally not considered sufficient to prevent outbreaks and their damage.

Damage occurs in poplar stands following outbreaks, during which trunks can be covered with aphid colonies. Mature stands are usually affected when tree circumference is above 90 cm (DSF 2006; Maugard and Baubet 2004). Outbreaks can be detected at the end of spring, but can also start later, until autumn. Massive colony development generally begins in the upper third of the trunks, just below the crown, and aphid colonies then extend downwards. Trunks can become blackish due to sooty molds development on aphid honeydew. Major symptoms mostly occur the spring following the outbreak. Barks cracks, referred as “lizard skin”, bark necroses and dark exudations can be observed on formerly infested trunks. The most striking symptom is the absence of bud break on some or all of the branches of the canopy (Fig. 5.1d). This results in reduced growth and sometimes massive mortality. Following an outbreak, up to 70 % of a susceptible stand, often close to harvest age, can be killed (Arzone and Vidano 1984; Della Beffa 1936; Maugard and Baubet 2004). Stand environment may buffer or aggravate damage levels. For instance, damage is usually more significant in fertile stands (Maugard and Baubet 2004). These symptoms have been attributed to the injection by the aphid of salivary toxins in the tree (Lapietra and Allegro 1990). However detailed histological investigations did not support this assertion, as no extended necroses were observed in the probing area (Dardeau et al. 2014b; Pointeau et al. 2012b). It seems more likely that the nutrient sinks induced by the numerous pseudogalls induced in the bark during outbreaks significantly alter nutrient allocations within infested trees, and in turn affect host growth and survival (Dardeau et al. 2014a, b).

Since natural biological control is not considered efficient, aphid populations are usually controlled through insecticide fogging on infested trees (Charles et al. 2014). Considering that poplar stands are generally located in alluvial areas this may generate environmental issues. An alternative is the selection of resistant poplar genotypes. The susceptibility tests allow an early discrimination of susceptible versus resistant genotypes which may affect either aphid settlement and/or development (Allegro et al. 1996; Pointeau et al. 2011, 2013; Sadeghi et al. 2007).

5.3 Conifer Pests

Haematoloma dorsatum Ahrens (Hemiptera: Cercopidae), the red-black pine bug, is a spittle bug developing on conifers. Moraal (1996) has reviewed the bionomics of this species. Two subspecies have been described *H. dorsatum quinquemaculatum* and *H. dorsatum lugens* (Nast in Moraal 1996, De Jong and Gravestein in Moraal 1996). Until the beginning of the twentieth century this species was restricted to the Mediterranean basin (Portugal, Spain, France, Switzerland, Italy, Greece, Turkey and Algeria) (Nast in Moraal 1996) but since then it has spread to the North and East of Europe and has been recorded in Belgium, the Netherlands, Germany, Austria, Poland, Hungary, Czech republic, Romania and Russia (Moraal 1996 and references therein, Holzinger et al. 1996).

Adults are red with black spots (Fig. 5.1e). Sub-species can be distinguished according to their color pattern, *H. dorsatum lugens* being almost black, while the other sub-species is more red. This insect is univoltine. Reproduction occurs at the end of spring on trees. Eggs are laid within a nick at the base of grass stems and hatch in autumn. Nymphs overwinter until next spring. They feed in group of two to five individuals on the basal stem parts or roots of various grasses (Roversi and Baccetti 1994). They are commonly found on *Deschampsia flexuosa* L. in the Netherlands and Austria, *Festuca elegans* Boiss., *Brachypodium* sp. and *Dactylis* sp. in Spain (Alonso et al. 1992; Cobos 1995; Moraal 1996). A few individuals were also collected from *Molinia caerulea* (L.) Moench and *Calamagrostis epigejos* (L.) Roth in Austria, but it was not found on *M. caerulea* in the Netherlands (Körner et al. 2001; Moraal 1996). There are four nymphal instars which develop within a protective mass of white spittle. Adults migrate on conifer needles where they feed, preferentially on old needles. Young and mature pine stands can be infested (Moraal 1996). The insects insert their stylets in the stomatal openings, and are reported to suck sap (Roversi et al. 1989). They are also reported to inject saliva which presumably induces typical yellowish or brownish discoloration rings on the needles (Fig. 5.1e). This results in needles drying and early fall in summer. The insect might also be a potential vector of *Sphaeropsis sapinea* (Fr.) Dyko and Sutton as it was found carrying conidia of the fungi (Feci 2000). This pathogenic fungus is also associated with another pine spittle bug, *Aphrophora parallela* Say, occurring in Northern America (Haddow and Newman 1942).

Damage occurs on tree only. The species has been observed on several conifer species including *Pinus nigra* (Arnold), *P. pinaster* (Aiton), *P. sylvestris* L., *P. halepensis* Mill., *P. jeffreyi* Balf., *P. brutia* Ten., *P. ponderosa* Dougl. ex Laws. and also *Abies*, *Cedrus*, *Cupressus*, *Juniperus*, *Picea* and *Pseudotsuga* species (Cobos 1995; Covassi et al. 1989; Notario et al. 1981). Major problems have been reported on pines mostly (Cobos 1995; Moraal 1996; Notario et al. 1981; Roversi et al. 1991), and occasionally on cypress (Binazzi et al. 1998).

The insect has been mostly harmful to pine stands in Spain, Italy and the Netherlands (Alonso et al. 1992; Cobos 1995; Covassi et al. 1989; Masutti et al. 2005; Moraal 1996). Partial defoliation due to adult feeding may weakened pines and makes them prone to colonization by secondary pathogens or pests. There is no known parasite, predator or environmental factor that would significantly affect the populations of *H. dorsatum*. There is only one observation of an unidentified Diptera larva entering the spittle mass to prey on nymphs (Roversi and Baccetti 1994). Populations have been monitored in Spain with insecticide spraying (Notario et al. 1981), but silvicultural practices reducing the grass cover might prove useful to control the populations of this insect, as for *Aphrophora saratogensis* (Fitch) in Northern America (Baker 1972; Moraal 1996).

Leucaspis pusilla Loew, *L. pini* (Hartig) and *L. lowi* Colvée (Hemiptera: Diaspididae) are three armored scale species infesting pine needles. *Leucaspis* *leonardi* Coleman, *Actenaspis pusilla* Leonardi, *Leucodiaspis pusilla* Lindinger, *L. perezi* Green, *Diaspis perezi* Lindinger, *Pusillaspis pusilla* Lindinger are synonyms of *Leucaspis pusilla. Aspidiotus pini* Hartig, *A. flavus* Hartig, *Diaspis candida* Targioni Tozzetti, *Leucaspis affinis* Leonardi, *L. candida* Targioni Tozzetti, *L. löwii* Löw, *L. löwi* Lindinger, *L. loewi* Cockerell, *Leucodiaspis candida* Lindinger and *L. pini* Zahradnik are synonyms for *Leucaspis pini. Anamaspis loewi* Leonardi, *Fiorinia sulcii* Newstead, *Leucaspis sulci* Lindinger, *Leucodiaspis loewi* Lindinger and *L. sulci* Lindinger are synonyms of *Leucaspis lowi* (Miller and Gimpel 2013). The three species have a Palaeartic distribution and occur from Western Europe to Russia and throughout the Mediterranean Basin (Miller and Gimpel 2013; Raspi and Antonelli 1987 and references therein). *Leucapsis pusilla* has also been introduced in Argentina, and occurs in the Middle East (Miller and Gimpel 2013 and references therein).

These scale insects generally develop at the base of the internal face of pine needles (Fig. 5.1f). Females are protected by a white waxy scale, incorporating the hardened exuviae of the second instar, which is generally elongated, pear-shaped and yellowish, but sometimes blackish (Raspi and Antonelli 1987; Soria et al. 2000). They are small, up to 3.2 mm long for *L. lowi*, and rather inconspicuous at low density. The three species are very similar, and misidentification frequently occurs. Damage due to *L. pusilla* or *L. lowi* has probably been frequently wrongly attributed to *L. pini* (Soria et al. 2000).

Leucaspis pusilla is bivoltine in Italy (Raspi and Antonelli 1987), and apparently *L. pini* and *L. lowi* also have two generations in Spain, in the warmer locations (Casado Alvarez and Soria Carreras 2007). In central Europe however, these species exhibit only one annual generation as *L. pusilla* and *L. pini* in Hungary or *L. lowi* in Germany (Kosztarab and Kozar 1988; Schmutterer et al. 1957). The development of *L. pusilla* has been described in detail by Raspi and Antonelli (1987). Eggs and nymphs are covered by typical curvy waxy secretions. The first instar nymphs occur at the end of spring and summer for the first generation and autumn for the second generation. They are crawlers, which search for a feeding site. They are followed in summer, or in winter for the second generation, by a second nymphal instar, sessile, which produces the waxy cuticle. Apparently *L. lowi* and *L. pusilla* also overwinter as second nymphal instar in Spain (Casado Alvarez and Soria Carreras 2007). The shape of the cuticle is different between female and male nymphs. For males, this instar is followed by violaceous prepupal and pupal stages. Males are winged and possess a long copulatory organ. They are active in summer and spring for the second generation, but do not feed. Females occur in summer and autumn, and in spring. Following reproduction, eggs are laid in autumn, or at the end of spring for the second generation, under the protective scale of the mother. *Leucaspis pini* can lay up to 50 eggs, 26 for *L. lowi* (Schmutterer et al. 1957; Kosztarab and Kozár 1988). The three species apparently develop on most pines species. The three species have been described on *Pinus halepensis*, *P. pinaster*, *P. sylvestris*, *P. pinea* L., *P. mugo* Turra, *P. nigra. Leucaspis lowi* and *L. pusilla* have also been described on *P. radiata* D. Don and *L. pusilla* and *L. pini* on *P. brutia*. In addition *L. pini* can develop on *P. ponderosa* and *L. pusilla* on *P. canariensis* C. Sm., *P. strobus* L., *P.*

roxburghii Sarg. and *Cedrus atlantica* (Manetti ex Endl.) Carrière (Raspi and Antonelli 1987 and references therein, Ben-Dov 2012 and references therein, Miller and Gimpel 2013 and references therein).

Each of these armored scale species has a complex associated fauna. The predators are mostly ladybirds like *Neomysia oblongoguttata* (L.), *Chilocorus bipustulatus* (L.), *C. renipustulatus* (Scriba), *Exochomus flavipes* (Thunberg), *Myrrha octodecimguttata* (L.), *Vibidia duodecimguttata* (Poda) (Coccinellidae), and a *Leucopis* sp. (Chamaemyiidae). The three species share common parasitoids belonging to different families of Hymenoptera: Aphelinidae, Encyrtidae, Eulophidae, Signiphoridae, Trichogrammatidae. A complete list is provided by Miller and Gimpel (2013).

Sap-sucking by the nymphs and females induce chlorotic lesions at the base of infested needles. During heavy infestations, needles can dry out and fall. Heavy infestations have been reported for the three species in the Mediterranean Basin, for instance in Spain, Corsica and Italy (Masutti et al. 2005; Normand 2005; Raspi and Antonelli 1987; Soria et al. 2000), but also in Central Europe (Kosztarab and Kozar 1988; Kozar et al. 2013). These heavy infestations can lead to massive defoliation. For instance in Corsica, in 2003, 40 % of a maritime pine forest have been defoliated over 1,000 ha (Normand 2005). As mentioned earlier, since species identification is quite difficult, it seems however that damage attributed to *L. pini* would rather be due to the two other species, which are more abundant in Spain and Italy (Blay 1992; Casado Alvarez and Soria Carreras 2007; Raspi and Antonelli 1987; Soria et al. 2000). An additional species, *Leucaspis signoreti* (Signoret), with a similar geographical distribution and colonizing pine needles, has apparently also caused extensive damage to pine stands in Ukraine, but, to our knowledge, has never been reported as a pest in the Mediterranean Basin (Tropin 1950).

References

Allegro G, Picco F, Bianco B (1996) Resistance behaviour to *Phloeomyzus passerinii* of some recently-selected Italian poplar clones. In: Proceedings of the 20th session of the International Poplar Commission, Budapest, pp 199–208

Alonso RH, Martin Bernal E, Perez Fortea V (1992) *Haematoloma dorsatum* (Ahrens) en Aragón. Ecologia 6:335–340

Andreatta G (1996) Attacchi di *Kermococcus vermilio* Planch su leccio (*Quercus ilex* L) nella pineta di Lido di Volano. Monti e Boschi 47:38–41

Antonelli R (1989) La *Philloxera quercus* afide dannoso a varie specie di quercie. Inf Fitopatol 39:27–33

Aparisi C (1971) Noticia sobre el afido lanigero del chopo *Phloeomyzus passerinii* Signoret, y ensayos para su tratamiento. Plag For 14:3–11

Arzone A (1987) Contributo alla conoscenza dei limitatori di *Phloeomyzus passerinii* Sign. Ann Accad Agric Torino 129:139–158

Arzone A, Vidano C (1984) Investigations on *Phloeomyzus passerinii* (Sign) in Piedmont. Ann Fac Sci Agr Univ Stud Torino 13:337–356

Baker WL (1972) Eastern forest insects. US Dept Agric, Misc Publ 1175

Balachowsky A (1950) Les Kermes (Hom, Coccoidea) des chênes en Europe et dans le bassin Méditerranéen. In: Proceedings of the International Congress of Entomology, Stockholm, pp 739–754

Baubet O, Goudet M (2010) Situation du puceron lanigère en 2009. For Entrep 194:50–53

Belcari A (1991) Ulteriori acquisizioni sulla biologia e sulle possibilità di controllo in Toscana di *Kermes vermilio* (Planchon) (Rhynchota: Kermesidae). Disinfestazione 8:23–26

Belcari A, Minnocci A (1989) Attacchi di *Kermes vermilio* (Planchon) (Rhynchota: Kermesidae) su *Quercus ilex* L. Toscana Disinfest 6:48–52

Ben-Dov Y (2012) The scale insects (Hemiptera: Coccoidea) of Israel–check list, host plants, zoogeographical considerations and annotations on species. Isr J Entomol 41:21–48

Binazzi A, Covassi MV, Roversi PF (1998) Role of Cinara (*Cupressobium*) cupressi (Buckton) and other sap-sucking insects in the decay of the common cypress (*Cupressus sempervirens* L). Ann Accad Ital Sci For 47:55–66

Björkman C (2000) Interactive effects of host resistance and drought stress on the performance of a gall-making aphid living on Norway spruce. Oecologia 123:223–231

Blackman RL, Eastop VF (1994) Aphids on the world's trees: an identification and information guide. CABI, Wallingford

Blay A (1992) La familia Diaspididae Targioni-Tozzetti, 1868 de España peninsular y Baleares (Insecta: Hemiptera: Coccoidea). Dissertation, University of Madrid

Casado Álvarez J, Soria Carreras S (2007) Descripcion del ciclo biologico y distribucion de las principales cochinillas que afectan a las aciculas de los pinos en la Comunidad Autonoma de Madrid. Bol Sanid Veg Plag 33:195–207

Charles JG, Nef L, Allegro G et al (2014) Insect and other pests of poplars and willows. In: Richardson J, Isebrands JG (eds) Poplars and willows, trees for society and the environment. CABI, Oxford, pp 459–526

Cobos JM (1995) Nota sobre la presencia de *Haematoloma dorsatum* (Ahrens) en pinares del Sistema Central. Bol Sanid Veg Plag 21:133–137

Covassi M, Roversi PF, Toccafondi P (1989) Danni da *Haematoloma dorsatum* (Ahrens) su conifere (Homoptera, Cercopidae) I Alterazione macroscopiche degli apparati fogliari. Redia 72:259–275

Dardeau F, Pointeau S, Ameline A et al (2014a) Host manipulation by a herbivore optimizes its feeding behaviour. Anim Behav 95:49–56

Dardeau F, Deprost E, Laurans F et al (2014b) Resistant poplar genotypes inhibit pseudogall formation by the wooly poplar aphid, *Phloeomyzus passerinii* Sign. Trees 28:1007–1019

Dardeau F, Body M, Berthier A, Miard F, Christidès JP, Feinard-Duranceau M, Brignolas F, Lieutier F, Sallé A (2015) Effects of fertilisation on amino acid mobilisation by a plant-manipulating insect. Ecol Entomol 40:814–822

Del Bene G, Landi S (1992) *Kermes vermilio* (Planch) ei suoi nemici naturali in Toscana. Atti G Fitopatol 1:229–236

Della Beffa G (1936) Contributo alla conoscenza degli insetti parassiti dei pioppi Il *Phloeomyzus passerinii*. Boll Lab Sper R Oss Fitopatol Torino 13:17–23

Dixon AFG (1971) The role of aphids in wood formation II The effect of the lime aphid, *Eucallipterus tiliae* L (Aphididae), on the growth of lime, *Tilia* x *vulgaris* Hayne. J Appl Ecol 8:393–399

Dixon AFG (2005) Insect herbivore-host dynamics: tree-dwelling aphids. Cambridge University Press, Cambridge

DSF, Département de la Santé des Forêts (2006) Information santé des forêts Puceron lanigère du peuplier Ministère de l'Agriculture et de la Pêche, Paris

Eastop VF, Hille Ris Lambers D (1976) Survey of the world's aphids. W Junk, The Hague

Feci E (2000) Indagini su aspetti eziologici di *Sphaeropsis sapinea* in Provincia di Bolzano Provincia Autonoma di Bolzano-Alto Adige, Ripartizione 32, Foreste Bolzano

Fernandez de Córdova J (2002) Insectos que atacan a los encinares cordobeses (Homoptera: Aphidinea). Bol Soc Andal Entomol 3:40–47

Foldi I (2003) Les cochenilles – 2ème partie. Insectes 130:1–3

Grassé PP (1951) Traité de zoologie: Anatomie, systématique, biologie Tome X: insectes supérieurs et hémiptéroïdes Fasc II. Masson et Cie Editeurs, Paris

Habib R, Ghani MA (1970) Eriosomatinae on poplars and their natural enemies in West Pakistan. Tech Bull Comm Inst Biol Contr 13:43–58

Haddow WR, Newman FS (1942) A disease of Scots pine caused by *Diplodia pinea* associated with the pine spittle bug. Trans R Can Inst 24:1–17

Holzinger WE, Jantscher E, Remane R (1996) Erstnachweise von Zikaden aus Österreich, mit Bemerkungen zu weiteren Arten (Ins: Homoptera, Auchenorrhyncha). Linzer Biol Beitr 28:1149–1152

Huberty AF, Denno RF (2004) Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology 85:1383–1398

Ibarra N, Lastanao C, Pelegrin EG, Bernal EM (2001) Kermes vermilio Planchon, parasito de quercineas en Aragon. Primeras observaiones. In: III Congreso Forestal Espanol, Granada, 25–28 Sept 2001

Japoshvili G, Karaca I (2002) Coccid (Homoptera: Coccoidea) species of Isparta Province, and their parasitoids from Turkey and Georgia. Turk J Zool 26:371–376

Karahroodi ZR, Sadeghi E, Azdo Z (2006) Study of differences between populations of mummy aphid, *Phloeomyzus passerinii* Sign on 21 clones of *Populus* in nursery. In: Lafortezza R, Sanesi G (eds) Patterns and processes in forest landscapes consequences of human management, IUFRO meeting 80103, Accademia Italiana di Scienze Forestali 80, 6

Koricheva J, Larsson S, Haukioja E (1998) Insect performance on experimentally stressed woody plants: a meta-analysis. Annu Rev Entomol 43:195–216

Körner M, Nickel H, Sayer M (2001) Zikaden an Gräsern eines norddeutschen Kiefernforstes– Abundanz, Phänologie und ein Vergleich der Fangmethoden. Beitr Zikadenkunde 4:33–43

Kosztarab M, Kozar F (1988) Scale insects of Central Europe. Kluwer, Dordrecht

Kozar F, Benedicty ZK, Fetyko K et al (2013) An annotated update of the scale insect checklist of Hungary (Hemiptera, Coccoidea). ZooKeys 309:49–66

Lapietra G, Allegro G (1990) Suscettibilita a *Phloeomyzus passerinii* Sign dei cloni di pioppo coltivati in Italia. Inf Fitopatol 40:41–44

Leonardi G (1920) Monografia delle cocciniglie Italiane. E Della Torre, Portici

Malumphy CP (2008) First British outbreak of *Kermes vermilio* Planchon (Hemiptera: Kermesidae), a Mediterranean pest of evergreen oaks. Br J Entomol Nat His 21:75–79

Marotta S, Ripullone F, Tranfaglia A (1999) Bio-ethological observations on *Kermes vermilio* (Planchon) (Homoptera Coccoidea Kermesidae) harmful to *Quercus ilex* in the Basilicata region (Italy). Phytophaga 9:63–83

Martelli M, Arru GM (1957) Ricerche preliminari sull'entomofauna della Quercia da sughero ("*Quercus suber*" L) in Sardegna. Francia 140:5–49

Martin Bernal E, Ibarra Ibanez N (2011) Kermes vermilio Planch; cochinilla de las encinas. Plagas y Enfermedades de las masas forestales espagnolas 25

Martin L, Goula M, Rojo M (2007) Estudi d'una plaga : Kermococcus vermilio (Insecta, Homoptera, Kermesidae), la caparreta de l'alzina. In: Congrés forestal Catala, Tarragona, 27 Sept 2007

Martin-Santafé M, Sanchez-Duran S, Batlle-Durany A et al (2014a) First identification of the pathogen causing tumor malformations in evergreen oaks in Spain. For Syst 23:357–363

Martin-Santafé M, Perez-Fortea V, Zuriaga P et al (2014b) Phytosanitary problems detected in black truffle cultivation. A review. For Syst 23:307–316

Masutti L (1982) The insects of Euroamerican poplars and their original food-plants ecological aspects of problems of prevention and control. Arboric Legno 25:1–8

Masutti L, Battisti A, Faccoli M (2005) Insect fauna of the *Pinus nigra* group in Italy. In: Lieutier F, Ghaioule D (eds) Entomological research in Mediterranean forest ecosystems. INRA Editions, Versailles, pp 79–87

Maugard F (1996) Attaque d’un ravageur inhabituel dans le Sud-Ouest de la France: le puceron lanigère du peuplier. Cah DSF 1:19–20

Maugard F, Baubet O (2004) Le puceron lanigère du peuplier accentue sa présence dans le Sud-Ouest et étend sa zone d’épidémie vers le Nord Bilan de la Santé des Forêts en 2003. Ministère de l’Agriculture et de la Pêche, Paris

Miles PW (1989) Specific responses and damage caused by Aphidoidea. In: Minks AK, Harrewijn P (eds) Aphids – their biology, natural enemies and control. Elsevier, Amsterdam, pp 23–47

Miller DR, Gimpel ME (2013) ScaleNet: a database of the scale insects of the world. Retrieved from http://www.sel.barc.usda.gov/scalenet/scalenet.htm

Mohammad MA, Abdullah AA (1985) Ecological studies on acorn aphid, *Phylloxera quercus* Boyer (Phylloxeridae, Homoptera). Iraqi J Agric Sci (Zanco) 3:69–76

Moraal LG (1996) Bionomics of *Haematoloma dorsatum* (Hom, Cercopidae) in relation to needle damage in pine forests. Anz Schädl Pflanzensch Umweltschutz 69:114–118

Nieto JM (1974) Recopilacion de las citas de pulgones (Aphidinea) de Espana. Graellsia 28:45–102

Nieto-Nafria JM, Mier-Durante MP (1998) Fauna Iberica Hemiptera, Aphididae I. CSIC Press, Madrid

Normand S (2005) Etat sanitaire du pin maritime en région méditerranéenne. For Mediterr 26:17–22

Notario A, Castresana L, Baragano JR (1981) Nota sobre un cercopido, *Haematoloma dorsatum* (Arhens), que ataca a los pinos. Bol Sanid Veg Plag 7:157–160

Ortego J, Difabio ME, Durante M, Pilar M (2004) Nuevos registros y actualización de la lista faunística de los pulgones (Hemiptera: Aphididae) de la Argentina. Rev Soc Entomol Argentina 63:19–30

Panis A (1974) Action prédatrice d'*Eublemma scitula* [Lepidoptera Noctuidae, Erastriinae] dans le Sud de la France. Entomophaga 19:493–500

Pellizzari G, Porcelli F, Convertini S, Marotta S (2012) Description of nymphal instars and adult female of *Kermes vermilio* Planchon (Hemiptera, Coccoidea, Kermesidae), with a synopsis of the European and Mediterranean species. Zootaxa 3336:36–50

Pointeau, S (2011) Interactions peuplier – puceron lanigère (*Phloeomyzus passerinii* (Sign)) et processus à l’origine de l’émergence et de l’expansion des pullulations. Dissertation, University of Orléans

Pointeau S, Sallé A, Lesieur V et al (2011) Estimating the effect of poplar resistance on the performance of the woolly poplar aphid, *Phloeomyzus passerinii*, in various experimental conditions. Can J For Res 41:1233–1241

Pointeau S, Martin C, De Feraudy D et al (2012a) Characterization of twelwe mocrosatellite loci in the woolly poplar aphid, *Phloeomyzus passerinii* (Hemiptera: Aphididae: Phloeomyzinae). Mol Ecol Res 12:374–376

Pointeau S, Ameline A, Laurans F et al (2012b) Exceptional plant penetration and feeding upon cortical parenchyma cells by the woolly poplar aphid. J Insect Physiol 58:857–866

Pointeau S, Ameline A, Sallé A et al (2013) Characterization of antibiosis and antixenosis to the woolly poplar aphid (Hemiptera: Aphididae) in the bark of different poplar genotypes. J Econ Entomol 106:473–481

Quisenberry S, Ni X (2007) Feeding injury. In: van Emden HF, Harrington R (eds) Aphids as crop pests. CABI, Wallingford, pp 331–352

Rajabi-Mazhar N, Moharamipour S, Sadeghi SE (2003) Antixenosis resistance to woolly poplar aphid *Phloeomyzus passerinii* Sign (Hom: Aphididae) of different poplar clones. J Entomol Soc Iran 22:31–44

Raspi A (1996) *Thaumatomyia elongatula* (Becker) (Chloropidae) and *Leucopis annulipes* Zetterstedt (Chamaemyiidae): two Diptera preying on *Phloeomyzus passerinii* (Signoret) (Homoptera: Phloeomyzidae) in Italy. Proc Entomol Soc Wash 98:509–516

Raspi A (2005) *Leucopis* (*Xenoleucopis*) *rajabimazhari*, new species from Iran (Diptera Chamaemyiidae). Bol Soc Entomol Italiana 137:219–222

Raspi A, Antonelli R (1987) Alcune note sulla *Leucaspis pusilla* Loew (Homoptera Diaspididae), parlatorino dannoso sui pini in Toscana. Frustula Entomol 10:127–152

Reid S, Cannon R (2010) Rapid assessment of the need for a detailed pest risk analysis for *Phylloxera quercus* group. Retrieved from https://secure.fera.defra.gov.uk/phiw/riskRegister/planthealth/documents/phylloxeraQuercus.pdf

Roversi PF, Baccetti C (1994) On the ecology and ethology of *Haematoloma dorsatum* (Ahrens) (Homoptera, Cercopidae). Redia 77:133–150

Roversi PF, Covassi M, Toccafondi P (1989) Danni da *Haematoloma dorsatum* (Ahrens) su conifere (Homoptera, Cercopidae) II Indagine microscopica sulle vie di penetrazione degli stiletti boccali. Redia 72:595–608

Roversi PF, Covassi M, Toccafondi P (1991) Distribuzione e bioecologia di *Haematoloma dorsatum* in Italia In: Atti delle giornate di studio sull' avversita del pino Regione Emilia Romagna, Assessorato Agricoltura e Alimentazione, Bologna

Sadeghi SE, Rajabi-Mazhar NA, Moharramipour S (2007) A study on the incidence of woolly poplar aphid, *Phloeomyzus passerinii* (Hom: Aphididae), on poplar species and clones in Hamedan Province, Iran. J Entomol Soc Iran 26:47–59

Schmutterer H, Kloft W, Liidicke M (1957) Coccoidea, Schildläuse, scale insects, cochenilles. In: Sorauer P (ed) Handbuch der Pflanzenkrankheiten, Tierische Schädlinge an Nutzpflanzen. Paul Parey, Berlin

Smith CF (1974) The genus *Phloeomyzus* with the description of *P. dearborni* N. sp. from *Populus tremuloides* Michx (Homoptera: Aphididae). Proc Entomol Soc Wash 76:66–72

Smith JP, Schowalter TD (2001) Aphid-induced reduction of shoot and root growth in Douglas-fir seedlings. Ecol Entomol 26:411–416

Soria S, Moreno M, Vinuela E et al (2000) Scale insects on *Pinus* spp. in Spain. Bol Sanid Veg Plag 26:335–348

Theobald FV (1929) Genus *Phloeomyzus* Horvath. The plant lice or Aphididae of Great Britain 3:268–272

Tremblay E (1981) Entomologia applicata Vol II. Liguori Ed, Napoli

Tropin IV (1950) A forest pest-the pine needle scale *Leucaspis signoreti*. Lesnoe Khozyaistvo 3:84–85

Ubaldo D, Gatto A, Mannerucci F et al (2008) Indagini fitosanitarie in giovani impianti forestali in Puglia. Italia For Mont 63:259–274

Vala JC, Pointeau S, Lambert M et al (2011) *Phloeomyzus passerinii* (Signoret, 1875) dit Puceron lanigère du Peuplier (Hemiptera Sternorrhyncha Aphididae). L'Entomologiste 67:49–55

Vidotti G (1960) Osservazioni sull'etologia ed ecologia del *Phloeomyzus passerinii* Sign nella zona di Este (Hemiptera Aphididae Aphidinae). Atti Inst Veneto Sci Let Art 118:203–218

Wood BW, Tedders WL (1986) Reduced net photosynthesis of leaves from mature pecan trees by three species of pecan aphid. J Entomol Soc 21:355–360

Wood BW, Tedders WL, Dutcher JD (1987) Energy drain by three pecan aphid species (Homoptera: Aphididae) and their influence on in-shell pecan production. Environ Entomol 16:1045–1056

Wood BW, Tedders WL, Reilly CC (1988) Sooty mold fungus on pecan foliage suppresses light penetration and net photosynthesis. Hortscience 23:851–853

Zhang GX, Zhong TS (1982) New species and subspecies of Chinese Aphidoidea. Sinozoologica 2:19–28

Chapter 6
Bark Beetles of Mediterranean Conifers

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Abstract Bark beetles of conifer trees in the Mediterranean basin play a relevant ecological and economic role in forest ecosystem functioning. Their activity often reflects the health conditions of the stands, while some species may become tree killers causing large outbreaks. Making the first impact toward wood decomposition, they are crucial components of the trophic nets. This group is extremely diversified, in relation to a wide variety of host tree species and displays a high level of endemism. The particular behavioral, biological and demographic traits of the species are largely the outcome of typical climate of the Mediterranean basin and the long history of human activity in the region. Much less knowledge has however been accumulated on these species than on those of temperate and boreal forest ecosystems; many gaps still exist, even regarding basic biology of many of the species and their common associates. This chapter is a synthetic presentation of the present knowledge of different aspects of biology, ecology, population dynamics, and management of conifer bark beetles in the Mediterranean basin, while underlying the essential information still missing. The particularities and originality of the most important species are discussed. The associated organisms and their relationships with beetles and host trees are presented. The population dynamics of the major species is discussed in relation to the biological, ecological and demographic characteristics. The economic importance of the pest species and their management are addressed. Observed and anticipated effects of climate change are elaborated and research needs are suggested in that context.

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6.1 Introduction

Bark beetles (Coleoptera: Curculionidae: Scolytinae) form about half of the 7500 species of the Scolytinae subfamily (Wood 1982; Bright 1993). They appeared 280 million years ago, as indicated by findings of fossils of petrified wood that show galleries characteristic of their feeding habits as early as the Triassic period (Ross 1965). They are distributed in more than 250 genera and are considered the most damaging pests of conifer forests worldwide. The Mediterranean basin gathers about 40 species living in typical Mediterranean conifers. Their attacks on branches or trunk for reproduction usually occur on weakened trees only, the reasons for weakness being much diversified. For that reason, they are called "secondary" pests or weakness pests. Only in case of epidemic populations during outbreaks, can their attacks succeed on healthy trees. Aggressiveness of Mediterranean conifer bark beetles does not reach levels comparable to those of some temperate or boreal species such as *Ips typographus* L. in Europe or *Dendroctonus ponderosae* Hopk. in North America, but the success of their attacks always means tree death, and they have been involved in dramatic conifer mortalities for a long time. Their economic importance varies depending on regions and years but the outbreaks of their epidemic populations can locally cause serious economic loss (Knížek and Beaver 2004). Moreover, with global warming, there is a risk of increasing damage in the Mediterranean basin and of northward extension of some species in presently temperate regions. Ecologically, their endemic populations play an important role by preparing the substrate for a high diversity of saproxylic organisms. As in temperate and boreal regions, life cycles of Mediterranean bark beetles are very diverse with various types of voltinism, existence of sister broods and various type of feedings, but the Mediterranean areas are the only regions where bark beetle activity, at least for some species, occurs all year round. Another important particularity of bark beetles in the Mediterranean basin is their high level of narrow endemism.

This chapter begins with a presentation of species diversity, distribution and host trees of bark beetles in the Mediterranean basin, allowing settling the list of species considered as Mediterranean in the chapter. The biological particularities of the Mediterranean bark beetles are then discussed, followed by the life history traits of the different species. Then the various types of biotic associations are presented, before the population dynamics and its factors. Economic and ecological importance follow, preceding population management. Observed and expected climate change effects are then discussed, and the chapter ends with suggestions of research directions.

6.2 Species Diversity, Distribution and Host Species

6.2.1 Morphological Characteristics and Species Diversity

Bark beetles are small or very small insects, always less than one centimeter in length, with short legs, and an elongated and cylindrical body typically dark and shiny in colour. The back end of the elytra, *i.e.* the hardened anterior wings typical of beetles, frequently shows a marked declivity with small cusps, spines or other more or less pronounced tegument structures and processes. The larvae are all very similar to each other morphologically: small, white, hairless and legless, and curved in a characteristic C-shape. Different bark beetle species are very similar to each other morphologically, with small or very small adults, which are difficult to see outside the host and generally short-lived, and larvae often indistinguishable among species. The combination of these features results in an effective difficulty in species identification, with possible confusion and mistakes. The only information available is usually the host tree and shape of the mating system, which remains impressed between the bark and sapwood or on the wood, also for months after insect emergence. Therefore, in many cases the mating system layout – which has a constant shape within the same species – and the host tree allow the insect species to be easily identified (Faccoli 2015).

There are currently about 350 known species in Western Europe and North Africa (Pfeffer 1995) which, added to the about 480 from North and Central America (Wood 1982) and about 900 from Asia (Knížek 2011), only account for around 25 % of the whole subfamily. Most species of bark beetles are in the equatorial rain forests. The main species living on Mediterranean conifers are only about 42, corresponding to about 11 % of the West Palaearctic fauna (Sect. 6.2.3).

6.2.2 Specificity and Host Exploitation

Bark beetles are particularly demanding about the physiological conditions of the host tree. To identify the most suitable trees in a forest, bark beetles follow blends of volatiles released by stressed trees. The molecules released by physiologically altered plants are intercepted by specific olfactory sensilla located on the adult antennae, allowing the insect to select the potential host species, e.g. a beech rather than a pine. These volatiles can also be perceived at considerable long distances, even a few kilometers. Recently dead or stressed trees may thus be found and infested by a first group of individuals called “pioneers”. In many species, frass coming out from the early boring activity of pioneers contains beetle produced volatiles – aggregation pheromones – attractive to other conspecifics. By this mechanism, in a very short time the tree is occupied by a large number of adults overcoming tree defenses (Sect. 6.6.1.2). In order to prevent overcrowding, bark beetles produce a different set of volatiles – anti-aggregation pheromones – that repel the arrival of new individuals on already saturated host tissues.

The ability to distinguish between different tree species allows bark beetles to specialize on one or few closely related host species, often belonging to the same genus. Actually, bark beetles include species that can feed on different plant organs of both hardwoods and conifers. The majority of species that develop on conifer trees feed and bore their galleries in the cortex layers, *i.e.* the innermost part of the bark that is rich in sugar – of woody plants. The pattern of tree colonization by bark beetle species is shaped by the bark characteristics of host trees, which must be thick enough to harbor the adults boring the mating system. Hence, medium-large species usually infest the lower-middle parts of trunks of large trees, while smaller species are more frequent in the mid-high parts; small size species are often found in twigs and branches or in young trees with thin bark. Stem sections covered by thick rhytidome are rarely colonized by small bark beetles. Within the same host tree there is hence a spatial distribution of the different species according to their size. This mechanism enables bark beetle guild to exploit all the available bark area, facilitating the rapid death of the tree, with little competition for space or food of other wood boring species. The first steps of bark colonization are generally performed by particularly aggressive species. In the succeeding days, however, they are joined by other – larger or smaller – less aggressive species that infest the unclaimed bark surface still available on the dying trees. These secondary species are called "satellite species" because they generally associate with and usually depend on more aggressive species for host colonization.

6.2.3 Host Species and Distribution

Mediterranean countries may host both strictly Mediterranean conifers, such as many coastal pine, juniper and cypress species, and conifers growing in mountainous areas exposed to continental climatic conditions, such as firs, cedars and black pines. Although they usually grow at high elevations, firs and cedars species are endemic of one or few Mediterranean countries (for instance, *Cedrus atlantica* Endlicher, *Cedrus libani* A. Rich., *Abies pinsapo* Boissier, *Abies nebrodensis* (Lojac.) Mattei, *Abies numidica* de Lannoy, *Abies cephalonica* Loudon, and others). The long geographic and evolutionary isolation of these trees, which have induced the formation of endemic species, in turn, also often led to a creation of a specific, endemic – and hence Mediterranean – fauna of associated insect species. Differently, black pine growing at high elevations of Mediterranean countries in many cases represent only local varieties or subspecies of *Pinus nigra* Arnold, such as *P. n. leucodermis* (Antoine), *P. n. balcanica* (Beissn.), *P. n. bosniaca* Elwes, *P. n. laricio* (Poiret), *P. n. corsicana* (Loudon), *P. n. mauretanica* (Maire et Peyerimhoff) and others. These subspecies of black pine host a generic fauna of bark beetles occurring throughout most Europe, often shared with other continental pine species (Pfeffer 1995). For these reasons bark beetles infesting black pines in Mediterranean countries cannot be defined as strictly Mediterranean species, and they are not considered in the present review.

Bark beetles living only or mainly in Mediterranean conifers belong to about 42 species (Table 6.1). Actually, the scientific literature reports a greater number of bark beetles potentially developing on Mediterranean conifers, although most cases refer to single records of continental species occasionally infesting Mediterranean conifers. Among bark beetles associated to Mediterranean conifers there are species (such as *Carphoborus bonnairei*, *Carphoborus henscheli*, *Carphoborus marani*, *Crypturgus cedri, Hylurgops bonvouloiri*, *Phloeosinus acatayi*, *Phloeosinus cedri*, *Pityophthorus cephalonicae*, *Pityophthorus pinsapo* and *Scolytus numidicus*) monophagous on a specific host-tree, as well as species able to infest a greater number of hosts, although usually all belonging to the same genus (*Pinus*, *Thuja*, *Abies* or *Cedrus*) (Table 6.1). *Cryphalus numidicus*, *Crypturgus numidicus*, *Orthotomicus erosus* and some *Phloeosinus* spp. are the only species known to infest hosts belonging to different genera in the Mediterranean basin.

Mediterranean pines are the conifers infested by the largest number of bark beetles (Table 6.2). In many cases, these insect species show some degree of polyphagia and may be found also on continental pines or even on other conifers. Firs and cedars are instead colonized by a lower number of characteristic bark beetle species, only occasionally shared with other conifers (such as for instance some *Cryphalus* and *Crypturgus*). Trees and shrubs belonging to the cypress family are infested by very few species of extremely specific bark beetles of the genus *Phloeosinus* (Table 6.2).

The geographic distribution of bark beetles infesting Mediterranean conifers may extremely heterogeneous according with the different species (Table 6.1). Some species are strictly endemic of specific Mediterranean countries or regions (e.g., *C. marani*, *C. cedri, H. bonvouloiri, Orthotomicus tridentatus, Phloeosinus acatayi, Ph. cedri, Pityophthorus cephalonicae, Pityophthorus pinsapo,* and *S. numidicus*); they are usually species infesting endemic host trees (mainly cedars and firs) growing in small or isolated forests. Another group of species is instead largely spread in many Mediterranean countries or even in the whole Mediterranean basin (e.g., *Tomicus destruens*, *Phloeosinus* spp., *C. numidicus, Crypturgus mediterraneus, C. numidicus, Pityogenes calcaratus* and others). They are species infesting conifers commonly growing in most Mediterranean areas either naturally, such as the junipers, or because largely planted in the past, such as the pines. Finally, there is a last group of species which is extremely common in the Mediterranean regions, but occurring also in central-eastern Europe where they may infest either the same tree species growing in other climatic conditions (e.g., *Pityokteines* spp. on silver fir) or different continental host-plants, *i.e.* continental conifers (e.g., *Hylastes* spp., *Hylurgus* spp., *Orthotomicus erosus*, *Pityophthorus pityographus*, and others) (Table 6.1).

Table 6.1 Main bark beetles living on Mediterranean conifers, their Mediterranean host species and distribution

Bark beetle species	Main Mediterranean host trees	Mediterranean distribution[a]
Carphoborus bonnairei Brisout[b]	*Pinus halepensis* Miller	AG, MO, TU, CY
Carphoborus henscheli Reitter[b]	*Pinus brutia* Tenore	CY, IS, SY, TR
Carphoborus marani Pfeffer[b]	*Pinus halepensis* Miller	GR
Carphoborus pini Eichhoff[b]	*Pinus halepensis* Miller, *P. pinaster* Aiton, *P. pinea* L., *P. brutia* Tenore	BH, CR, FR, GR, IT, SP, AG, TU, CY, TR
Cryphalus numidicus Eichhoff[b]	*Abies numidica* de Lannoy ex Carrière, *A. pinsapo* Boissier, *Cedrus atlantica* Endlicher, *Pinus halepensis* Miller	BU, FR, GR, IT, SP, AG, EG, LB, MO, TU, TR
Cryphalus piceae (Ratzeburg)	*Abies alba*, *A. borisii-regis* Mattfeld, *A. cephalonica* Loudon, *A. bornmuelleriana* Mattfeld	BH, BU, CR, FR, GR, IT, MC, SL, SP, YU, AG, TR
Crypturgus cedri Eichhoff[b]	*Cedrus atlantica* Endlicher	AG
Crypturgus cribrellus Reitter[b]	*Pinus pinea* L., *P. brutia* Tenore, *P. halepensis* Miller, *P. pinaster* Aiton	BU, CR, FR, IT, MC, PT, SL, SP, YU
Crypturgus mediterraneus Eichhoff[b]	*Pinus pinaster* Aiton, *P. brutia* Tenore, *P. halepensis* Miller, *P. pinea* L., *Abies pinsapo* Boissier, *A. numidica* de Lannoy	CR, FR, GR, IT, PT, SP, AG, MO, TU, CY, IS, TR
Crypturgus numidicus Ferrari[b]	*Pinus brutia* Tenore, *P. halepensis* Miller, *P. pinaster* Aiton, *P. pinea* L., *Abies pinsapo* Boissier, *A. numidica* de Lannoy, *Cedrus libani* A. Rich.	BH, BU, CR, FR, GR, IT, MA, SP, AG, TU, TR
Crypturgus parallelocollis Eichhoff[b]	*Abies borisii-regis* Mattfeld, *A. cephalonica* Loudon	GR, TR
Hylastes angustatus (Herbst)	*Pinus pinaster* Aiton, *P. pinea* L.	BU, CR, FR, GR, IT, MC, PT, SL, SP, TR, YU
Hylastes ater (Paykull)	*Pinus pinaster* Aiton, *P. pinea* L.	AZ, BH, BU, CR, FR, GR, IT, MC, PT, SL, SP, YU, AZ, TR
Hylastes attenuatus Erichson	*Pinus halepensis* Miller, *P. pinaster* Aiton, *P. pinea* L.	AZ, BH, CR, FR, GR, IT, MC, PT, SL, SP, YU, MR, TR
Hylastes batnensis anatolicus Knizek and Pfeffer[b]	*Cedrus libani* A. Rich.	TR
Hylastes batnensis batnensis Brisout[b]	*Cedrus atlantica* Endlicher	AG, MO

(continued)

Table 6.1 (continued)

Bark beetle species	Main Mediterranean host trees	Mediterranean distribution[a]
Hylastes linearis Erichson	*Pinus brutia* Tenore, *P. canariensis* Smith, *P. halepensis* Miller, *P. pinaster* Aiton, *P. pinea* L.	CR, FR, GR, IT, MC, PT, SL, SP, YU, AG, CI, MO, MR, TU, CY, IS, SY, TR
Hylurgops bonvouloiri (Chapuis)[b]	*Cedrus atlantica* Endlicher	AG
Hylurgus ligniperda (F.)	*Pinus pinaster* Aiton, *P. brutia* Tenore, *P. halepensis* Miller, *P. pinea* L.	AZ, BH, BU, CR, FR, GR, IT, MC, PT, SL, SP, YU, AG, CI, MO, MR, TU, CY, TR
Hylurgus miklitzi Wachtl[b]	*Pinus halepensis* Miller, *P. pinaster* Aiton, *P. pinea* L.	CR, FR, GR, IT, MA, SP, AG, EG, LB, MO, TU, IS, TR
Orthotomicus erosus (Wollaston)	*Pinus brutia* Tenore, *P. canariensis* Smith, *P. halepensis* Miller, *P. pinaster* Aiton, *P. pinea* L., *Cedrus atlantica* Endlicher, *C. libani* A. Rich.	AZ, BU, CR, FR, GR, IT, MA, MC, PT, SL, SP, YU, AG, EG, LB, MO, MR, TU, IS, JO, SY, TR
Orthotomicus tridentatus Eggers[b]	*Cedrus libani* A. Rich., *Pinus brutia* Tenore	TR
Phloeosinus acatayi Schedl[b]	*Cedrus libani* A. Rich.	SY, TR
Phloeosinus armatus Reitter[b]	*Cupressus sempervirens* L., *Juniperus* sp.	GR, IT, CY, IS, JO, LE, SY, TR
Phloeosinus bicolor (Brullé)	*Cupressus sempervirens* L., *Juniperus communis* L., *J. excelsa* Bieb, *J. foetidissima* Willd., *J. macrocarpa* (Sibthorp and Smith), *J. phoenicea* L., *J. sabina* L., *Tetraclinis articulata* (Vahl) Mast., *Thuja occidentalis* L., *Th. orientalis* L.	AL, AR, BH, BU, CR, FR, GR, IT, MC, PT, SP, YU, AG, CI, EG, LB, MO, TU, CY, IS, SY, TR
Phloeosinus cedri Brisout[b]	*Cedrus atlantica* Endlicher	SP, AG, MO
Phloeosinus henschi Reitter[b]	*Cupressus sempervirens* L., *J. oxycedrus* L., *J. phoenicea* L.	BH, CR, GR, MC, LE, SY
Phloeosinus rudis Blandford[b,c]	*Thuja orientalis* L.	FR
Phloeosinus thujae serrifer Wichmann[b]	*Juniperus communis* L., *Cupressus sempervirens* L.	SL
Phloeosinus thujae thujae (Perris)	*Juniperus communis* L., *J. sabina*, *Thuja occidentalis* L., *Th. orientalis* L., *Cupressus sempervirens* L.	AL, BH, BU, CR, FR, GR, IT, MA, MC, PT, SL, SP, YU, AG, CI, EG, LB, MO, TU, TR
Pityogenes calcaratus (Eichhoff)[b]	*Pinus halepensis* Miller, *P. brutia* Tenore, *P. pinaster* Aiton	CR, FR, GR, IT, MA, PT, SP, AG, MO, TU, IS, SY, TR

(continued)

Table 6.1 (continued)

Bark beetle species	Main Mediterranean host trees	Mediterranean distribution[a]
Pityogenes pennidens (Reitter)[b]	*Pinus brutia* Tenore, *P. halepensis* Miller, *P. pinea* L.	GR, CY, IS, SY, TR
Pityokteines vorontzowi (Jacobson)	*Abies alba* Miller*, A. bornmuelleriana* Mattfeld	BH, BU, CR, FR, GR, IT, MC, SL, SP, YU, TR
Pityokteines curvidens (Germar)	*Abies alba* Miller, *Abies borisii-regis* Mattfeld, *A. cephalonica* Loudon, *A. cilicica* (Antoine and Kotschy), *A. bornmuelleriana* Mattfeld	BH, BU, CR, FR, GR, IT, MC, PT, SL, SP, YU, TR
Pityokteines spinidens (Reitter)	*Abies alba* Miller	BH, BU, CR, FR, GR, IT, LS, SP, YU, TR
Pityophthorus cephalonicae Pfeffer[b]	*A. cephalonica* Loudon	GR
Pityophthorus pinsapo Pfeffer[b]	*Abies pinsapo* Boissier	SP
Pityophthorus pityographus cribratus Pfeffer[b]	*Abies alba* Miller, *A. cephalonica* Loudon, *A. bornmuelleriana* Mattfeld	GR, TR
Pityophthorus pityographus pityographus (Ratzeburg)	*Abies alba* Miller	BH, BU, CR, FR, GR, IT, MC, SL, SP, YU
Pityophthorus pubescens (Marsham)	*Pinus halepensis* Miller, *P. pinaster* Aiton, *P. pinea* L.	CR, FR, GR, IR, IT, SL, SP, AG, EG, LB, MO, TR, CY, IS
Scolytus numidicus Brisout[b]	*Cedrus atlantica* Endlicher	AG, MO
Tomicus destruens (Wollaston)[b]	*Pinus pinea* L., *P. brutia* Tenore, *P. canariensis* Smith, *P. pinaster* Aiton, *P. halepensis* Miller	CR, BH, SL, YU, FR, GR, IT, PT, SP, AG, MR, TU, CY, IS, TR

Modified after Pfeffer (1995) and Knížek (2011)

[a] Legend: *AG* Algeria, *AL* Albania, *BH* Bosnia Herzegovina, *BU* Bulgaria, *CI* Canary Islands, *CR* Croatia, *EG* Egypt, *FR* France, *GR* Greece, *IT* Italy, *JO* Jordania, *LB* Libya, *LE* Lebanon, *MA* Malta, *MC* Macedonia, *MO* Morocco, *MR* Madeira archipelago, *PT* Portugal, *SL* Slovenia, *SP* Spain, *SY* Syria, *TR* Turkey, *TU* Tunisia, *YU* Serbia and Montenegro

[b] Species endemic of the Mediterranean basin or its regions

[c] Species native to Japan, accidentally introduced in Southern France

6.3 Biological Particularities of Mediterranean Conifer Bark Beetles

As most Mediterranean forest insects, conifer bark beetles of the Mediterranean basin exhibit a number of life traits and behaviours that distinguish them from their temperate and boreal counterparts.

They are firstly characterized by a high level of narrow endemism. Twenty eight species or sub-species of bark beetles are indeed specifically localized in the

Table 6.2 Bark beetle species recorded for the main Mediterranean conifers (Modified after Pfeffer 1995)

Host tree species	Bark beetle species
Abies alba	*Cryphalus piceae*, *Pityokteines curvidens*, *P. spinidens*, *P. vorontzowi*, *Pityophthorus pityographus pityographus, P. pityographus cribratus*
Abies borisii-regis	*Cryphalus piceae*, *Crypturgus parallelocollis*, *Pityokteines curvidens*
Abies bornmuelleriana	*Cryphalus piceae*, *Pityokteines curvidens*, *P. vorontzowi*, *Pityophthorus p. cribratus*
Abies cephalonica	*Cryphalus piceae*, *Crypturgus parallelocollis*, *Pityokteines curvidens*, *Pityophthorus cephalonicae*, *P. pityographus cribratus*
Abies cilicica	*Pityokteines curvidens*
Abies numidica	*Cryphalus numidicus, Crypturgus mediterraneus*, *C. numidicus*
Abies pinsapo	*Cryphalus numidicus*, *Pityophthorus pinsapo, Crypturgus mediterraneus*, *C. numidicus*
Cedrus atlantica	*Cryphalus numidicus*, *Crypturgus cedri*, *Hylastes batnensis batnensis*, *Hylurgops bonvouloiri*, *Orthotomicus erosus*, *Phloeosinus cedri*, *Scolytus numidicus*
Cedrus libani	*Hylastes batnensis anatolicus*, *Orthotomicus tridentatus*, *O. erosus*, *Phloeosinus acatayi, Crypturgus numidicus*
Cupressus sempervirens	*Phloeosinus armatus*, *Ph. bicolor*, *Ph. thujae*, *Ph. th. serrifer, Ph. henschi*
Juniperus communis	*Phloeosinus bicolor*, *Ph. thujae, Ph. th. serrifer*
Juniperus *excelsa*	*Phloeosinus bicolor*
Juniperus foetidissima	*Phloeosinus bicolor*
Juniperus macrocarpa	*Phloeosinus bicolor*
Juniperus oxycedrus	*Phloeosinus henschi*
Juniperus phoenicea	*Phloeosinus bicolor*, *Ph. henschi*
Juniperus sabina	*Phloeosinus bicolor*, *Ph. thujae*
Pinus canariensis	*Hylastes linearis*, *Orthotomicus erosus*, *Tomicus destruens*
Pinus halepensis	*Carphoborus bonnairei*, *C. marani*, *C. pini*, *Cryphalus numidicus*, *Crypturgus cribrellus*, *C. mediterraneus*, *C. numidicus*, *Hylastes attenuatus*, *H. linearis*, *Hylurgus ligniperda*, *H. miklitzi*, *Orthotomicus erosus*, *Pityogenes calcaratus*, *P. pennidens*, *Pityophthorus pubescens*, *Tomicus destruens*
Pinus brutia	*Carphoborus henscheli*, *C. pini, Crypturgus cribrellus*, *C. mediterraneus*, *C. numidicus*, *Hylastes linearis*, *Hylurgus ligniperda*, *Orthotomicus erosus*, *O. tridentatus*, *Pityogenes calcaratus*, *P. pennidens*, *Tomicus destruens*
Pinus pinaster	*Carphoborus pini*, *Crypturgus cribrellus*, *C. mediterraneus*, *C. numidicus*, *Hylastes angustatus*, *H. ater*, *H. attenuatus*, *H. linearis*, *Hylurgus ligniperda*, *H. miklitzi*, *Orthotomicus erosus*, *Pityogenes calcaratus*, *P. pubescens*, *Tomicus destruens*
Pinus pinea	*Carphoborus pini*, *Crypturgus cribrellus*, *C. mediterraneus*, *C. numidicus*, *Hylastes angustatus*, *H. ater*, *H. attenuatus*, *H. linearis*, *Hylurgus ligniperda*, *H. miklitzi*, *Orthotomicus erosus*, *Pityogenes pennidens*, *Pityophthorus pubescens*, *Tomicus destruens*
Tetraclinis articulata	*Phloeosinus bicolor*
Thuja occidentalis	*Phloeosinus bicolor*, *Ph. thujae*
Thuja orientalis	*Phloeosinus bicolor*, *Ph. thujae*, *Ph. rudis*

Only native conifers are considered

Mediterranean basin, corresponding to a 67 % level of endemism, and among them about half (13) are highly localized (Table 6.1). Tree diversity combined with insect specificity for their hosts certainly contribute to explain such a high endemism level, as 60 % of the conifers native from the Mediterranean basin are also endemic from that area. This is especially true for most highly localized species which are often specific for a localized host tree species. Conversely, endemic species largely distributed in the Mediterranean basin are often polyphagous or specialized on a largely distributed tree species (Table 6.1). Nevertheless, some of these highly localized monophagous species, such as *C. marani* on *Pinus halepensis* and *Phloeosinus thujae serrifer* on *Cupressus sempervirens* feed on hosts that are widely distributed in the Mediterranean basin. Similarly, the largely distributed endemic bark beetle species *Pityophthorus pityographus cribratus* feed on *Abies alba*, a non-endemic tree species, and *Tomicus destruens* also endemic from the Mediterranean basin, is able to develop on most European pines (Lieutier et al. 2015). Factors other than host trees thus interfere; of which climate is certainly an important one, as demonstrated for *T. destruens* (Horn et al. 2014).

Considering the particularities of the Mediterranean climate, it may be trivial to specify that Mediterranean insects are adapted to warmer conditions that temperate species. Nevertheless, it is one of their characteristics. As example, the comparison of temperature requirements of *Tomicus piniperda* L. with those of *T. destruens*, its Mediterranean counterpart, demonstrates that the second is particularly well adapted to the Mediterranean climate (Horn et al. 2014 and Fig. 6.1). Temperature appears as the main factor of *T. destruens* localization in the Mediterranean basin, which means that climate warming may allow its northward extension (see below). In *O. erosus*, beetle development still accelerates with temperature increase until 36 °C, with oviposition followed by egg development still occurring at that temperature, which demonstrates the good adaptation of *O. erosus* to high temperatures (Mendel and Halperin 1982). Mild winter temperatures and hot dry summers that characterize the Mediterranean climate make temperatures to be favorable to beetle development practically all year round, at least at low elevation and on the southern and eastern areas of the Mediterranean basin. These conditions allow, for example, larval development of *T. destruens*, *H. micklitzi* and *H. linearis* during winter (Halperin 1966; Mendel et al. 1985; Graf and Mzibri 1994; Ben Jamâa et al. 2000). Overwintering conditions in the Mediterranean basin can also differ from that in other European latitudes. The southernmost populations of *T. piniperda* overwinter in shoots, while the temperate and boreal ones overwinter under the bark at the base of the trees, where they are better protected from cold (Escherich 1923; Chararas 1962; Långström 1983).

The consequences of these climate characteristics are longer annual activities and accelerated development of Mediterranean bark beetles compared to temperate and boreal ones. These are particularly evident when considering species of which the geographical range extends largely across Europe. *T. piniperda* is known from Scandinavia to some localities of the northern rim of the Mediterranean Sea (Lieutier et al. 2015). The reproductive flight of this univoltine species generally occurs in April in Scandinavia (Långström 1983), whereas it occurs in February in Central

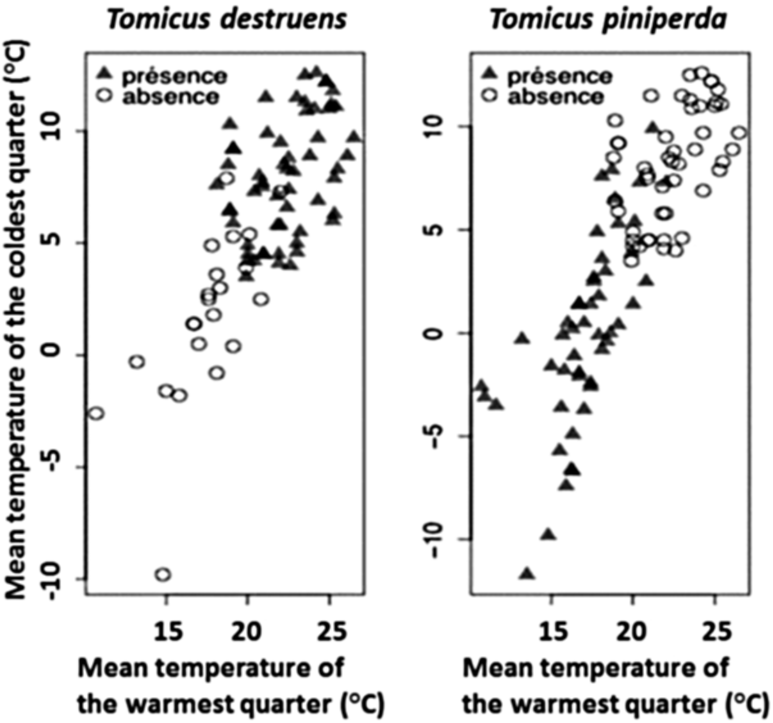

Fig. 6.1 Relationships between the presence of *Tomicus destruens* and *T. piniperda* and mean temperatures of the warmest quarter and the coldest quarter (From Horn et al. 2014, with permission)

France (Sauvard 1989) and in January in its southernmost localities. The corresponding flight of the vicariant Mediterranean congener *T. destruens* even occurs from October-November to February, depending on latitudes and elevation of localities (Faccoli et al. 2005; Sarikaya and Avci 2010). As the southern limit of *T. piniperda* distribution approximately coincides with the northern limit of *T. destruens* distribution (Horn et al. 2012), the difference between dates of reproductive flights results in temporal segregation between the two species in the localities where they cohabit. The geographical range of the multivoltine species *O. erosus* extends from central and southern Europe until North Africa and the Atlantic islands (Balachowsky 1949). In Morocco, this species flies from February-March to November-December (Ghaioule et al. 1998), whereas in central France, its flight period extends from April-May to October only. The Mediterranean *P. calcaratus* also reproduces from February to November (Mendel et al. 1985). Longer annual activity combined with accelerated development lead to higher numbers of main generations for the multivoltine species and higher numbers of sister broods for all species, compared with related species or with populations of the same species in temperate areas. Most temperate multivoltine bark beetle species have only one or two generations per year whereas their Mediterranean counterparts can have up to five to seven generations from early spring to late autumn. *Ips sexdentatus* Boern. is typically bivoltine in Northern France while it has three annual generations in Southern France and sometimes even five in Turkey (Chararas 1962). The Mediterranean populations of *O. erosus* can have five to seven generations per year and up to seven sister broods for the post-winter generation, while its continental populations have only three main generations (the last one not complete) with a maximum of five sister broods for the post-winter generation (Carle 1975; Mendel et al. 1985; Özkazanç et al. 1985; Ghaioule et al. 1998). Five to seven annual generations have also been reported for *P. calcaratus* (Mendel et al. 1985).

Although bark beetles may benefit from forest fires under all European latitudes [see for example Långström et al. (1999) for northern Europe], their higher frequency in the Mediterranean basin has often been a crucial factor in bark beetle population dynamics. Fires in Portugal facilitate attacks by *I. sexdentatus*, *O. erosus*, *Pityogenes bidentatus*, *Hylurgus ligniperda* and *T. piniperda* on *Pinus pinaster* (Ferreira and Ferreira 1987). In Spain, fire-scorched stands of *P. pinaster*, *P. nigra*, *Pinus sylvestris* and *Pinus radiata* have been attacked by *T. destruens*, *T. piniperda*, *Tomicus minor* Hartig, *H. ligniperda*, *H. ater* and *I. sexdentatus* (Fernandez and Salgado 1999; Gallego et al. 2004; Fernandez 2006; Santolamazza Carbone et al. 2011), with the two *Tomicus* species and *I. sexdentatus* being the most abundant species (Santolamazza Carbone et al. 2011). Attacks by *Orthotomicus longicollis, O. erosus, T. piniperda, C. numidicus, I. sexdentatus and P. calcaratus* have also been reported on *Pinus brutia*, *P. halepensis* and *P. nigra* in Greece after forest fires (Markalas 1997). Parasites and predators may also benefit from fires, as observed for the North America bark beetle *Ips pini* and its clerid predator *Thanasimus dubius* Fab. (Santoro et al. 2001). Moreover, tree mortality caused by bark beetles and other xylophagous insects on surviving trees creates fuel for future fires.

6.4 Life History

6.4.1 General Considerations

Bark beetles, similarly to other wood boring insects, have specific tools for exploiting bark tissues, which would otherwise be difficult to penetrate and digest. Small size and flexibility of biological rhythms, availability of specific enzymes, symbioses with fungi, and the presence of suitable tegumental structures – such as strong jaws, chewing stomachs, and organs for maintenance and transport of symbiotic fungi – are some of the evolutionary adaptations adopted by bark beetles to feed on woody tissues. Moreover, unlike some other xylophagous species, these insects are very demanding in the quality of the host trees, colonizing only living but strongly weakened plants or recently dead but not debarked trees with tissues still fresh. In general, when the populations of aggressive bark beetle species reach epidemic levels, their attacks can succeed on healthy trees. However, such a situation rarely occurs in the Mediterranean basin.

The general development pattern is fairly uniform among species. Adults of bark beetles land on the trunk or branches of trees suitable for colonization and drill an entrance hole through the bark which, in the phloem, is widened to form an area – called nuptial chamber or vestibule – where mating usually occurs. The nuptial chamber and gallery system is the result of a species-specific mating system. Polygamy, typical for many of the species, may range between 2 (e.g. *O. erosus*) and 10 females (e.g. some *Pityogenes* and *Pityokteines* species) per male. Each female then bores her own egg gallery (sometime named – arm) and the eggs are usually laid on both side of the tunnel. Egg galleries are recognizable as having a constant diameter – generally slightly greater than the width of the adult insect – for their whole length and being clean of frass (excrement and sawdust) removed outside the gallery system. In a few species, females die inside the egg galleries or in the opening after egg laying, thus limiting the entry and movement of predators feeding on the immatures. In most species, each larva excavates a gallery perpendicular to the egg gallery and characterized by increasing diameter as the larva grows by feeding on bark tissues. Unlike the egg tunnels, larval galleries are packed with frass derived from the feeding-excavating activity. The mature larvae burrow a pupation chamber into the bark or in the outer wood layers in which to metamorphose into pupae and then adults. The immature adults are characterized by clear colours and soft tegument; their maturation requires a feeding period before beginning the reproductive period. Polygamous species, those with more females per male, usually nourish on the phloem left from larval feeding. Monogamous species, with just one female per male, instead emerge immediately from the tree where they developed and perform the maturation feeding on buds, shoots or twigs of healthy and vigorous trees, belonging to their host species. Some species inflict their major injury by killing large number of twigs in which they dig short galleries. After maturation, adults look for new trees suitable for colonization and reproduction. During bark colonization, males of polygamous species penetrate the bark first and are later joined by females, while in monogamous species, excluded some rare cases, the reverse is true.

Unlike xylem-boring insects, the development of bark beetles is very fast and – from egg to adult – generally takes about 7–10 weeks, except for slowdowns or interruptions due to a drop in temperature or change of season. This is mainly due to the feed quality. Bark beetle species consume fresh bark tissues, rich in sugars and nitrogen compounds. The colonized bark area becomes an ephemeral niche and the newly emerged adults move on to other hosts to carry out the next generation, as their breeding host no longer suitable further colonization and reproduction. The general cortex and wood characteristics make the tree also unsuitable for the development of beetle symbiotic fungi. A colonized tree may, however, be re-attacked and allow a second consecutive generation when some bark area was not colonized during the first one. In these situations, different bark beetle species – usually less aggressive and demanding in terms of food quality – may infest still live bark area of the same tree.

6.4.2 Life History of the Main Bark Beetle Species Living on Mediterranean Conifers, Presented in Alphabetic Order

6.4.2.1 *Carphoborus pini* Eichhoff

World Distribution Central and Southern Europe; Northern coasts of Africa; South-Western Mediterranean regions of Asia (Pfeffer 1995).

Mediterranean Distribution Bulgaria, Croatia, France, Greece, Italy, Spain, Algeria, Tunisia, Cyprus, Turkey (Knížek 2011).

Main Hosts Found mainly on *P. pinea*, *P. halepensis* and *P. pinaster* (Pfeffer 1995); occasionally on *P. brutia* (Chararas 1962).

Biology and Ecology *C. pini* is a small polygamous species breeding mainly in small branches and tiny twigs of pines, with diameter also smaller than 0.5 cm. The breeding system is composed of a central mating chamber from which depart two to four egg galleries strongly engraving the wood surface. The egg galleries are long, with a winding, spiral and irregular development. The larval galleries are short (1–2.5 cm) and terminate with a large pupal chamber. Galleries systems appear very confusing. Sexual maturation takes place before adult emergence in the same host tree where the larvae developed. *C. pini* tolerates phloem degradation and bark drying better than other bark beetle species. The species overwinters as adults under the bark of the branches infested during the previous summer. The adults emerge at the beginning of April starting the first generation, followed by a second in June and a third in August–September (Chararas 1962).

Possible Damage Although *C. pini* is a common species widely distributed in the Mediterranean basin, it breeds mainly in small branches and tiny twigs, with diameter also smaller than 0.5 cm, of pines dying for unsuitable climatic or environmental conditions (drought, fire, cold winter winds) or in trees already infested by more aggressive species. *C. pini* is hence a secondary species not requiring any management considerations.

6.4.2.2 *Cryphalus numidicus* Eichhoff

World Distribution Southern Europe and South-Western Asia, from Spain to Turkey; Northern Africa (Pfeffer 1995).

Mediterranean Distribution Bulgaria, France, Greece, Italy, Spain, Algeria, Egypt, Libya, Morocco, Tunisia, Turkey (Knížek 2011).

Main Hosts In Europe is found mainly on *P. halepensis* although in Spain infests also Spanish fir (*A. pinsapo*). In North Africa is recorded from Algerian fir (*A. numidica*), Moroccan fir (*A. pinsapo marocana*) and *C. atlantica* (Barbey 1925; Peyerimhoff 1919; Chararas 1974).

Biology and Ecology The adults bore very irregular galleries (often invaded by fungi) within the phloem of thin barks on small branches of healthy trees. The species develops quickly and produces one to two generations per year depending on climatic conditions (Chararas 1962). *C. numidicus* often coexists with *Ph. cedri*, another primary species, due to their similar host preferences (Fabre et al. 1999). The species can cause primary damage according with the colonisation density. In case of massive attacks the bark falls off from the sapwood, branches and the tree decline progressively (Chararas 1974).

Possible Damage *C. numidicus* largely spreads on the mountains of the circum-Mediterranean regions; the beetle is common in many Algerian forests of cedar and *Abies numidica* (Peyerimhoff 1919). *C. numidicus* is listed among the most common cedar pests (Rungs 1940). It is a primary and extremely dangerous pest because of its ability to infest and reproduce massively mainly in young healthy trees. The species infests and kills apparently healthy hosts, causing in recent years the death of a large numbers of trees.

6.4.2.3 *Crypturgus mediterraneus* Eichhoff

World Distribution Circum-Mediterranean regions of Southern Europe (including Portugal); Northern Africa; South-Western Asia (Pfeffer 1995).

Mediterranean Distribution Croatia, France, Greece, Italy, Portugal, Spain, Algeria, Morocco, Tunisia, Cyprus, Israel, Turkey (Knížek 2011).

Main Hosts On Mediterranean pine species, mainly *Pinus halepensis, P. brutia* and *P. pinaster*, but also *P. pinea* (Pfeffer 1995). Recorded also from *A. pinsapo* and *A. numidica* in Spain and Algeria (Chararas 1962).

Biology and Ecology Monogamous species developing in weakened trees where it bores irregular galleries. *Crypturgus* adults exploit the penetration holes made by other species to penetrate the bark of the host tree. The sinuous highly branched egg galleries disperse in the bark thickness, usually beginning from breeding system of larger and more aggressive species. *C. mediterraneus* lives on dying trees which it abandons when the bark is dry. In the Mediterranean region *C. mediterraneus* develops at least three complete generations per year.

Possible Damage Species very abundant throughout the whole Mediterranean basin, but largely secondary, infesting only trees heavily stressed or already infested by more aggressive species. *C. mediterraneus* has no economic relevance; high population density of this species may interfere with the development of associated more aggressive species, often observed together with *O. erosus*.

6.4.2.4 *Crypturgus numidicus* Ferrari

World Distribution Circum-Mediterranean regions of Southern Europe; Northern Africa; South-Western Asia (Pfeffer 1995).

Mediterranean Distribution Bosnia Herzegovina, Bulgaria, Croatia, France, Greece, Italy, Malta, Spain, Algeria, Tunisia, Turkey (Knížek 2011).

Main Hosts In the Mediterranean countries living mainly on the Aleppo pine (*P. halepensis*), but also on *P. brutia* and *P. nigra mauretanica* (Pfeffer 1995); found on *P. pinaster* along the Atlantic coast of France, and on *P. pinea* in Turkey (Schimitschek 1944; Selmi 1989). Reported also from *A. pinsapo* in Spain and from A. *numidica* and *Cedrus libanotica* in Algeria.

Biology and Ecology Species very common throughout the whole Mediterranean area, with biology and ecology very similar to *C. mediterraneus*. Breeding in the bark of the trunk and branches of decaying pines previously infested by more aggressive species such as *O. erosus* and *P. calcaratus*. Egg galleries forming a confused system partially bored into the bark thickness which rapidly dries up and fall down from the stem.

Possible Damage No economic importance.

6.4.2.5 *Hylastes ater* Paykull

World Distribution Whole Europe; Asia from Siberia to Korea; introduced in New Zealand, Australia Chile, Japan and South Africa (Pfeffer 1995).

Mediterranean Distribution Azores, Bosnia Herzegovina, Bulgaria, Croatia, France, Greece, Italy, Macedonia, Portugal, Slovenia, Spain, Serbia and Montenegro, Azores, Turkey (Knížek 2011).

Main Hosts Species largely polyphagous on *Pinus*, infesting both native (*P. sylvestris*, *P. pinea*, *P. nigra laricio*, *P. nigra nigra*, *P. pinaster*) and exotic pine species (*P. radiata* and *P. ponderosa*). Other conifers may be occasionally attacked, including *Larix*, *Abies*, *Taxus baccata*, *Thuja*, *Picea* and *Pseudotsuga menziesii* (Grüne 1979; Gil and Pajares 1986; Pfeffer 1995).

Biology and Ecology *H. ater* usually infests the base of trunks, collars and thick exposed roots of weakened or felled pines (Milligan 1978). The adults are commonly found also in the moist bark occurring in the lower part of fallen trees laid on the soil. In these conditions, large numbers of individuals frequently aggregate in large roots or in freshly cut logs to reach sexual maturation or hibernate. With favorable weather conditions the adults beginning to flight in March looking for new hosts where they mate and start to reproduce in June (Fernández 1997). *H. ater* is a monogamous species, and after mating the female bores a uniramous simple longitudinal egg gallery about 8–14 cm long, slightly oblique to the wood fibers and with a dilated basal chamber, where 5–15 eggs are laid. Larval galleries are very irregular in shape, frequently intersecting and overlapping each other. The subcortical system impresses the wood surface only weakly. The newly emerged adults carry out broad and irregular cortical feedings directed upwards in the bark of young pine stems to reach sexual maturation. Maturation feeding often causes death of the young seedlings. Usually there is only one generation per year, although two generations may be complete in years when favorable conditions persist.

Possible Damage *H. ater* is a secondary species infesting stressed and dying trees. Nevertheless it can cause economic losses in reforested areas due to bark and crown damage resulted from the maturation feeding carried out by immature adults in young seedlings. Significant damage is reported in nurseries and young plantations. In some areas of Chile, about 70 % of *P. radiata* seedlings died due to *H. ater* attack (Ciesla 1988). Older trees are usually less sensitive, being protected by the bark thickness. Moreover, the association with pathogenic fungi makes *H. ater* the most harmful species of the genus (Fernández 1997). In this respect, in Spain was found associated with the pine pathogen *Leptographium wingfieldii* (Romón et al. 2007), and other *Leptographium* and *Ophiostoma* species (Kirisits 2004).

6.4.2.6 *Hylurgus ligniperda* Fabricius

World Distribution Central, Eastern and Southern Europe; Crimea and Caucasus; Northern Africa; introduced in the United States (California), South Africa, Australia, New Zealand, Chile, Brazil, Uruguay, Sri Lanka and Japan (Pfeffer 1995).

Mediterranean Distribution Azores, Bulgaria, Croatia, France, Greece, Italy, Macedonia, Portugal, Slovenia, Spain, Serbia and Montenegro, Algeria, Canary Islands, Morocco, Madeira Islands, Tunisia, Cyprus, Turkey (Knížek 2011).

Main Hosts Oligophagous on both Mediterranean (*P. halepensis*, *P. brutia*, *P. pinaster*, *P. pinea*) and continental (*P. sylvestris*, *P. nigra*) pine species (Pfeffer 1995).

Biology and Ecology Monogamous species with usually two generations per year. Adults start to flight in late May and in early June they mate and infest the host trees. At the end of July the new adults of the first generation emerge and begin a second generation. The adults are large (5–5.5 mm) and usually dig the mating system in the lower part of trunk, root collar and emerging roots of large recently dead, weakened or cut trees (Gil and Pajares 1986). The female bores longitudinal uniramous system consisting of a very irregular, single, large (3–4 mm) and long egg gallery, often bifurcated, which develops sinuously and longitudinally for several decimeters without a precise pattern. Many long (up to more than 8 cm), irregular, and sinuous larval galleries often intertwined in a confused way. Mating system entirely excavated in the bark thickness without affecting sapwood (Faccoli 2015).

Possible Damage Although secondary and aggressive, *H. ligniperda* is a very common species in pine forests where it infests only strongly decaying trees or fresh stumps. It is also common in log piles in the bark portion in contact with soil. Although with no economic importance, sometimes it can becomes a pest in stressed and dying pine plantations (Viedma 1964).

6.4.2.7 *Hylurgus miklitzi* Wachtl

World Distribution Mediterranean regions of Europe; Asia Minor; Caucasus; Northern Africa (Pfeffer 1995).

Mediterranean Distribution Croatia, France, Greece, Italy, Malta, Spain, Algeria, Egypt, Libya, Morocco, Tunisia, Israel, Turkey (Knížek 2011).

Main Hosts *H. miklitzi* lives exclusively on *Pinus* species and mainly on *P. halepensis* and *P. brutia*, but found also on *P. pinaster* and *P. pinea*, and occasionally on *P. nigra* (Grüne 1979; Pfeffer 1995).

Biology and Ecology Very similar to *H. ligniperda* and often considered just as a southern form, from which differs mainly for the smaller size. The general behaviour and biology of this species is very similar to that of *H. ligniperda*.

Possible Damage No economic importance because its attacks occurs only in dying trees or in plants already infested by other more aggressive species such as *T. destruens*. In Algeria *H. miklitzi* is widely distributed along the coast, in the Aleppo pine plantations.

6.4.2.8 *Orthotomicus erosus* Wollaston

World Distribution Throughout central and southern Europe including Atlantic and British Islands; North Africa; Western and central Asia until China and Korea. Introduced in Northern Europe, South Africa, Chile, Fiji Islands and the United States (Pfeffer 1995).

Mediterranean Distribution Azores, Bulgaria, Croatia, France, Greece, Italy, Malta, Macedonia, Portugal, Slovenia, Spain, Serbia and Montenegro, Bosnia Herzegovina, Algeria, Egypt, Libya, Morocco, Madeira Islands, Tunisia, Israel, Jordan, Syria, Lebanon, Cyprus, Turkey (Knížek 2011).

Main Hosts *O. erosus* is virtually able to infest all *Pinus* species (*P. radiata*, *P. pinea*, *P. pinaster*, *P. halepensis*, *P. brutia*, *P. canariensis*, *P. sylvestris*, *P. nigra*, *P. nigra cevennensis*, *P. nigra mauretanica*, *P. nigra pallasiana*); recorded also from *C. libani* and *C. atlantica* (Pfeffer 1995), and occasionally from *P. menziesii*, *Cupressus arizonica*, and *Picea* spp., although these hosts are usually used for maturation feeding or hibernation (Lee et al. 2005).

Biology and Ecology *O. erosus* is a polygamous species in which each male mates with three to five females; in East Mediterranean countries this species is bigamous. Host colonization occurs from March to October on weakened trees. In spring, the adults start to flight with mean air temperature of about 12–14 °C (Haack 2004). The species has medium size (2.5–3.5 mm) and the adults infest main branches and trunk by an irregular multiramous system consisting of three to five irregular egg galleries engraved irregularly, undulated, longitudinal, with no clear pattern. In East Mediterranean, the gallery design is one line of two egg arms along the wood grains. Number of egg galleries and their length vary in relation to species and colonization density (4–8 cm), but they are generally shorter than 10 cm. Females usually lay 26–75 eggs each, and larvae have three instars (Lee et al. 2005). Larval galleries are close to each other, numerous, longer and more sinuous than egg galleries. Only egg gallery weakly affects the sapwood (Faccoli 2015). Before emergence, young adults feed on phloem to reach sexual maturation. There may be 1 to 5–7 generations per year, depending on the geographical area and climatic conditions (Carle 1975; Mendel et al. 1985; Özkazanç et al. 1985; Ghaioule et al. 1998). Mountain populations living on *P. sylvestris* develop a single annual generation, while Mediterranean populations infesting *P. halepensis* may reach four generations per year.

Possible Damage Very common scolytid infesting all pine species. *O. erosus* is however a secondary species, very frequent in recently felled trees and non-debarked logs or in trees attacked and killed by more aggressive bark beetle species. It may also attack living trees affected by some kind of stress, such as fire and drought. In situations of high population levels, *O. erosus* can launch massive attacks against healthy trees, causing their death. Moreover, the adults can transmit blue stain fungi of the genus *Ophiostoma* and *Leptographium* (Kirisits 2004). In Israel, mainly *Ophiostoma ips*, but also *Graphilbum rectangulosporium* and *Geosmithia* sp. 24 were isolated from adult *O. erosus* (Dori-Bachash et al. 2015). In Spain *O. erosus* has been found associated also to the phoretic fungus *Fusarium culmorum* (Romón et al. 2007).

6.4.2.9 *Orthotomicus tridentatus* Eggers

World Distribution Endemic from Turkey; introduced in Austria (Pfeffer 1995).

Main Hosts The distribution of this pest closely corresponds to that of *C. libani*, its main host, although the insect was recorded also on *P. nigra* and *P. brutia* (Pfeffer 1995).

Biology and Ecology In the cedar forests of the Mediterranean regions of Turkey *O. tridentatus* shows two generations per year (Avci and Sarikaya 2009), with the first mating season at the end of April and the second during the second half of August. Following trunk colonization, dense resin flows occur on the bark around the entry holes drilled by the males. After mating, the egg galleries bored by the females within the inner bark are generally two- or three-branched, usually running longitudinally in different directions and forming an “S” shape. Egg galleries are 3.5–15 cm long, while larval galleries are about 2.5–4.5 cm long. Females lay eggs into singly niches excavated along both sides of the egg gallery. The number of laid eggs per gallery (*i.e.*, per female) varies between 22 and 48 (Avci and Sarikaya 2009). Pupation of the second generation occurs at the end of September and beginning of October. *O. tridentatus* overwinters as young adults in the bark of the infested trees. After overwintering, adults emerge in April looking for new host trees.

Possible Damage *O. tridentatus* usually infests trees exposed to biotic and abiotic stress, such as damage due to cedar defoliators, drought, poor site conditions, and related factors (Avci and Sarikaya 2009). Nonetheless, *O. tridentatus* is the most aggressive bark beetle species on Turkish cedar forests, and the main cause of cedar mortality in this country.

6.4.2.10 *Phloeosinus armatus* Reitter

World Distribution Eastern Mediterranean countries and Middle East. Introduced in Italy in 1991 and in the USA (California) in 1992 (Pfeffer 1995).

Mediterranean Distribution Greece, Italy, Cyprus, Israel, Jordan, Lebanon, Syria, Turkey (Knížek 2011).

Main Hosts Infesting mainly *C. sempervirens* (Schimitschek 1944; Balachowsky and Chararas 1961; Pfeffer 1995). In Israel, *Ph. armatus* was detected also on *Cupressus macrocarpa*, *Cupressus glabra* and *Juniperus* sp. (Mendel 1984), while in Italy occasionally found on *Cupressus arizonica* (Covassi 1991).

Biology and Ecology *Ph. armatus* is an oligophagous, with a clear preference for dying stressed cypress trees. No sexual dimorphism in body size was observed, with mean body width of about 1.7 mm (Baruch et al. 2005). The adults colonize stem and small branches, up to about 2 cm in diameter, for oviposition. *Ph. armatus* is a monogamous species boring an egg gallery system composed of two asymmetric longitudinal egg tunnels, with a mean length of about 16 cm. In Israel, the pair arms were identical in width; female excavates a great deal of a first egg tunnel before beginning to elongate the second one. After emergence, the new immature adults colonize cypress shoots where they perform a maturation feeding. In this phase of its life history, *Ph. armatus* plays an active role in the spread of the pathogenic fungus *Seiridium cardinale* (Wagener), responsible of a pandemic disease known as cypress canker. *Ph. armatus* is often associated with *Ph. bicolor*, in the same host tree. Studies carried out on the voltinism of *Ph. armatus* reported the occurrence of two generations in Greece, Turkey and Italy (Schimitschek 1944; Balachowsky and Chararas 1961; Pennacchio et al. 2013), while three to four partially overlapping generations in Israel (Mendel 1984), with adults active throughout the year in the coastal areas. The species overwinters mainly as adults.

Possible Damage This species usually does not cause any economic losses, although large infestations were recently recorded in central Italy (Pennacchio et al. 2013). In Israel, however, the maturation feeding by great number of beetles developed after drought periods may inflict a serious damage by defoliating large masses of twigs.

6.4.2.11 *Phloeosinus bicolor* Brulle

World Distribution Central and Southern Europe; Caucasus; Asia Minor; China; North Africa (Pfeffer 1995).

Mediterranean Distribution Albania, Bosnia Herzegovina, Bulgaria, Croatia, France, Greece, Italy, Macedonia, Portugal, Spain, Serbia and Montenegro, Algeria, Canary Islands, Egypt, Libya, Morocco, Tunisia, Cyprus, Israel, Syria, Turkey (Knížek 2011).

Main Hosts Largely polyphagous insect living on many genera of the cypress and juniper family, including Cupressus (*C. sempervirens*), *Juniperus* (*J. communis*, *J. excelsa*, *J. foetidissima*, *J. macrocarpa*, *J. phoenicea*, *J. sabina*), *Thuja* (*Th. occidentalis* and *Th. orientalis*), *Tetraclinis* (*T. articulata*) and *Callitris* (C. *articulata*). It is able to develop also on *Cephalotaxus* and *Sequoiadendron* (Pfeffer 1995).

Biology and Ecology The infestation occurs in branches and stems of much weakened trees growing both in hedges and as isolated trees. Although *Ph. bicolor* is a monogamous species (Zocchi 1956), in spring the female begin the first generation (April) boring a longitudinal biramous system consisting of two egg galleries of different length. Leaving from a central nuptial chamber, the egg galleries run parallel to wood fibers for about 2.5–7 cm. The nuptial chamber, of about 0.3–0.4 cm in diameter, often has short non-reproductive arms. The numerous (50–60) and often intertwined larval galleries, about 2–7 cm long, are initially perpendicular to the egg galleries, and then oblique or even parallel to them. Both larval and egg galleries deeply engrave the sapwood surface (Faccoli 2015). As in all monogamous species, to reach sexual maturation adults need a period of feeding carried out boring short tunnels in shoots or twigs 2–3 year old, of preferably young and vigorous plants. *Ph. bicolor* produces at least two generations per year, and generally overwinters as adults of the second generation within the shoots infested during the maturation feeding (Zocchi 1956).

Possible Damage Species extremely common in gardens, parks and nurseries, and everywhere the host plants occur. *Ph. bicolor* infests plants recently dead or severely weakened by pathogens or adverse weather conditions. Healthy trees infested during maturation feeding may be infected by plant pathogens, such as *S. cardinale*, causing a slow and progressive tree decline making them suitable to be infested by the following insect generations. Although killing trees, the economic importance of *Ph. bicolor* deals mainly with its impact at ornamental level. Reduction of the plant value may be recorded in trees growing in gardens and parks, mainly when cultivated in hedges; significant economic damage was reported also in nurseries in France and North Africa.

6.4.2.12 *Phloeosinus thujae* Perris

World Distribution Southern and Central Europe including England; Caucasus; Northern Africa (Pfeffer 1995).

Mediterranean Distribution Albania, Bosnia Herzegovina, Bulgaria, Croatia, France, Greece, Italy, Malta, Macedonia, Portugal, Slovenia, Spain, Serbia and Montenegro, Algeria, Canary Islands, Egypt, Libya, Morocco, Tunisia, Turkey (Knížek 2011).

Main Hosts Developing mainly on *Juniperus* (*J. communis* and *J. sabina*) and *Thuja* (*Th. occidentalis* and *Th. orientalis*) (Pfeffer 1995). Recorded occasionally also from the genus *Cupressus* (*C. sempervirens* and *C. thurifera*), *Sequoia*, *Tetraclinis*, *Callitris* and *Wellingtonia*.

Biology and Ecology Species rarer than *Ph. bicolor*, *Ph. thujae* has a similar reproductive behaviour but usually overwinters as larvae (and not as adult) in the infested barks, so adult emergence begins later in spring (June) with a mean air temperature of about 23 °C (Zocchi 1956). *Ph. thujae* breeds mainly in young trunks, twigs and small branches (often less than 1 cm diameter). Mating system of the same type as *Ph. bicolor*, but shorter, less engraving the wood surface, with irregular and intertwined larval galleries. *Ph. thujae* produces only one generation per year (Zocchi 1956).

Possible Damage Species with no economic importance, infesting dead or weakened trees, frequently associated with *Ph. bicolor* on the same trees. Maturation feeding carried out on healthy trees which may be infected by plant pathogens.

6.4.2.13 *Pityogenes calcaratus* Eichhoff

World Distribution Southern and Mediterranean Europe from Portugal to Crimea; South-Western Asia; Northern Africa (Pfeffer 1995).

Mediterranean Distribution Croatia, France, Greece, Italy, Malta, Portugal, Spain, Morocco, Algeria, Tunisia, Israel, Syria and Turkey (Knížek 2011).

Main Hosts Species infesting preferably on the Aleppo pine (*P. halepensis*); also found in *P. pinaster* and *P. brutia*, more rarely in *P. nigra* and *P. sylvestris* (Pfeffer 1995).

Biology and Ecology *P. calcaratus* is a polygamous species which flies in spring, with a mean air temperature of about 18–19 °C, colonizes branches of trees killed or already attacked by more aggressive species. *P. calcaratus* is chiefly associated

Fig. 6.2 (**a**) Early galleries of *Pityogenes calcaratus*; (**b**) Gallery systems of *Tomicus destruens* (Photos Z. Mendel)

with *O. erosus*, always occupied the upper stem sections above those colonized by the latter species. Adults of medium-small size (2-2.6 mm) occurring in small branches of dying pines. True stellate system consisting of three to seven, generally four to five, egg galleries developing radially from a central nuptial chamber for 4–8 cm, up to a maximum of about 10 cm (Fig. 6.2a). Colonizing small branches, the last portion of the egg galleries often bends longitudinally, running parallel to the main axis of the twig. Larval galleries thin, numerous, short, 1–3.5 cm long. Both egg and larval galleries clearly affect sapwood (Faccoli 2015). In rather high elevations, usually there are two generations per year with adults of the second generation overwintering under the bark of the trees infested during the previous summer. In Israel, the beetle carries out three to four annual generations.

Possible Damage Being a secondary species, *P. calcaratus* has a scarce economic importance. It is associated with the fungus *Leptographium guttulatum* in Spain (Romón et al. 2007) and with *Graphilbum rectangulosporium* and *Geosmithia* sp. in Israel (Dori-Bachash et al. 2015).

6.4.2.14 *Pityokteines curvidens* Germar

World Distribution Distribution range extended from the whole Central-Southern Europe to the Eastern Siberia and Japan. Introduced in the Neotropical and Afrotropical regions (Pfeffer 1995).

Mediterranean Distribution Bosnia Herzegovina, Bulgaria, Croatia, France, Greece, Italy, Macedonia, Portugal, Slovenia, Spain, Serbia and Montenegro, Turkey (Knížek 2011).

Main Hosts Insect infesting various species of firs (*A. alba*, *Abies cephalonica*, *Abies borisii-regis*, *Abies bornmüelleriana*, *Abies cilicica*, *Abies firma*, *Abies sachalinensis*) (Pfeffer 1995).

Biology and Ecology Tree colonisation usually occurs in early in spring (April) on thin barks of the upper part of stem and large branches (Chararas 1962). The medium size adults (1.8–3.2 mm) infest stressed fir trees or stacks of non-debarked logs. The females bore transverse multiramous system composed of three to eight egg galleries about 6 cm long and 1.5–2 mm wide. Egg galleries are often only four – two lower and two upper – distributed to form a characteristic cross brace system. Larval galleries are up to about 7 cm long, numerous, regular, closely spaced and perpendicular to egg galleries. Many egg niches occurring very close each other. Egg galleries and egg niches deeply excavated in sapwood, while larval galleries bored within the bark without engraving wood surface (Faccoli 2015). *P. curvidens* may produce one or two generations per year according with elevation and local climatic conditions (Chararas 1962). The species usually overwinters as adults within characteristics hibernation chambers bored in the phloem of the middle-upper part of trunks of apparently healthy firs. In the following spring the new breeding systems will be excavated starting from these chambers.

Possible Damage Species common in mature fir forests suffering from drought or root pathogen infections. Although considered as secondary species that only attacks weakened or recently felled trees, *P. curvidens* is one of the most common bark beetle species infesting firs; often associated with *P. vorontzowi*.

6.4.2.15 *Tomicus destruens* Wollaston

World Distribution Southern Europe; North-Western Africa; South-Western Asia (Pfeffer 1995).

Mediterranean Distribution Croatia, Slovenia, Bosnia Herzegovina, Serbia and Montenegro, France, Greece, Italy, Portugal, Spain, Algeria, Tunisia, Morocco, Madeira Islands, Cyprus, Israel, Turkey (Knížek 2011).

Main Hosts Olygophagous on Mediterranean pine species (*P. halepensis*, *P. pinaster*, *P. pinea*, *P. brutia* and *P. canariensis*).

Biology and Ecology *T. destruens* is a univoltine species developing in winter (October–March) in most of its distribution area. The adults, although of medium-large size (4–4.8 mm), infest the middle-upper part of stem and large branches. In Israel, the beetle always colonize the lower part of the stem, or mid stem of big size trees, usually share the same tree with *O. erosus* and *P. calcaratus*. Females bore longitudinal uniramous systems composed of a regular egg gallery developing parallel to wood fibers; about 8–10 cm long and 3–4 mm wide, only weakly affecting the sapwood surface (Fig. 6.2b). A roundish nuptial chamber is located in the lower part of the egg gallery, often inclined laterally and easily identifiable. Larval galleries are numerous, 60–80 mm long and sinuous. They develop mainly in the bark thickness without affecting sapwood (Faccoli 2015). Adults emerge early in spring, with a mean air temperature of about 12 °C, and spend a long period of maturation feeding (about 6–7 months) within shoots of healthy pines, causing shoot desiccation and their fall on litter. High twig consumption may make the tree susceptible to successful colonization by the following insect generations in the next years (Lieutier et al. 2015).

Possible Damage *T. destruens* is widespread in the circum-Mediterranean countries. It is a common species in dense Mediterranean pine forests suffering from drought, fire, or root diseases, causing serious damage in many countries. It also infests piles of fresh and non-debarked logs. Large pine mortality due to *T. destruens* has been observed in the last decades in many circum-Mediterranean countries. Damage by *T. destruens* has been frequently reported from nearly all southern European countries, Turkey, Tunisia, Algeria, Morocco and Israel (Lieutier et al. 2015). Quantitative data about economic damage caused by *T. destruens* are however scarce and mainly referring to single specific events. For instance, the more than 37,000 m^3 of pine timber harvested from 1988 to 2000 in Algeria following *T. destruens* infestations occurred in pine forests spread in semi-arid areas, over an area of about 20,000 ha (Chakali 2003, 2005). Monleón et al. (1996) reported about 4000 trees killed close to Barcelona (Spain), while Stergulc (2002) assessed tree mortality within a stone pine forest of the northern Adriatic Sea of about 6 % of the whole forest area (52 ha). In southern Europe, 900,000 m^3 of maritime pine was prematurely harvested after the devastating storm in 1999 (Nageleisen 2004), but the role of *T. destruens* as well as other attacking bark beetles was not assessed.

6.4.2.16 *Scolytus numidicus* Brisout

World Distribution Species endemic of North-Western Africa (Algeria and Morocco) (Pfeffer 1995).

Main Hosts Monophagous on *C. atlantica*.

Biology and Ecology *S. numidicus* is an univoltine species developing preferably in branches of average diameter (3–4 cm), although it can be found also in smaller (1.5 cm) and larger branches (6–7 cm) (Balachowsky 1969). Adult emergence occurs in mid to late spring, from May to June according to elevation. In Algeria, adult flight was reported in May (Atlas Blida) and early June (Djurjura) (Peyerimhoff 1919), while in Morocco (Ifrane, Middle Atlas), from late April to late May (Balachowsky 1969) and even in June and July (Chararas 1978). *S. numidicus* is a monogamous species, and the females colonize the host tree first, drilling a penetration hole in the bark of weakened cedar trees; later the male joins the female and mating takes place. The female bores the egg gallery where she will lay eggs singly in small niches along both sides of the gallery (Chararas 1978). The longitudinal egg gallery is about 4–8 cm long and 1 mm wide, often terminating with a diverticulum. The larval galleries shift almost immediately in the same direction of the egg gallery (Peyerimhoff 1919). Pupation chambers are excavated in the external sapwood. The species overwinters as mature larvae or adults under the bark of the trees infested in summer.

Possible Damage *S. numidicus* is a secondary pest infesting mainly decaying or defoliated trees. The species may nevertheless become a primary aggressive pest in case of large and intense infestations (Balachowsky 1969).

6.5 Associated Organisms

Since their appearance some 280 million years ago (Ross 1965) and simultaneously to their species diversification and the development of their adaptations to a diversity of host trees, bark beetles in general have been the central point of the building of a fantastic diversity of associations with other living organisms from many different taxonomic groups, from viruses and bacteria to insects and mites. Their galleries indeed offer a particularly favorable biotope for the development of complex biocenoses involving functions ranging from simple cohabitation and commensalism to parasitism, mutualism and true symbiosis. The functioning of such subcortical biocenoses and their exact relationships with host trees have been only partially exposed; even for long-time studied bark beetles species, such as the North-American *Dendroctonus* and *Ips* and the European *Ips* and *Tomicus* (Lieutier et al. 2004a; Vega and Hofstetter 2015). Only associations between bark beetles and particular taxonomic groups of associates have been studied. Bark beetles of the Mediterranean basin constitute a much diversified group of species (Sect. 6.2) which has been much less deeply studied than their boreal and temperate counterparts. Consequently, a consistent knowledge on associated organisms is available only for few bark beetle species and taxonomic groups of associates.

6.5.1 Virus, Bacteria, Protista, Microsporidia and Pathogenic Fungi

No information is available regarding virus and bacteria associated with Mediterranean bark beetle species. However, the high diversity of virus and bacteria observed in many bark beetle species and genera from European temperate forests (Wegensteiner 2004; Wegensteiner et al. 2015) allows considering that these two groups of pathogens are certainly commonly associated with bark beetles of the Mediterranean basin also. Only very few local observations have been made regarding Protista accompanying Mediterranean bark beetles. In Israel, a species of *Endamoeba* (Rhizopoda) has been reported to parasite the gut of 10 % of the insects in a population of *O. erosus* (Purrini and Halperin 1983). A species of Eugregarinida, *Gregarina* sp., has been found infesting the midgut lumen of *P. spinidens*, *P. curvidens* and *P. vorontsovi* in Croatia (Pernek et al. 2009).

A little more information concerns Microsporidia. In the same Israeli population of *O. erosus* as above, 6 % of the insects were hosting an undetermined Microsporidian species *Menzbieria* sp. in their fat body (Purrini and Halperin 1983; Halperin and Holzchuh 1984). *Menzbieria* sp. has also been isolated from *P. spinidens* populations in Croatian silver fir (*A. alba*) stands, with *Canningia spinidentis* Weiser and Wegensteiner and *Chytridiopsis typographi* Weiser, this latter species being also found in populations of *P. curvidens* and *P. vorontzowi* in the same stands (Pernek et al. 2009). All three species of Microsporidia were infesting the midgut epithelium of their hosts, whereas *C. spinidentis* was also infesting their fat body and gonads. Two other Microsporidian species were reported from Israeli populations of *P. calcaratus*. *Ophryocystis* sp. has been found in the Malpighian tubules of 10 % of the individuals (Purrini and Halperin 1983) and *Nosema calcarati* Purrini and Halperin has been observed infesting all insect stages, especially the adults in their gonads, with a prevalence of 50 % (Purrini and Halperin 1982; Halperin and Holzchuh 1984). *Nosema curvidentis* has also been isolated from *P. curvidens* in Turkey (Selmi 1998, *in* Karaman and Tezcan 2006).

Bark beetle galleries are a favorable medium for the development of entomopathogenic fungi because of their often high humidity level. Many papers refer to bark beetle pathogenic fungi, mostly *Beauveria bassiana* Bals.-Criv., and several assays have even been performed to test their possible use in bark beetle control (Wegensteiner 2004; Wegensteiner et al. 2015). However, very few of those papers refer to bark beetle populations of the Mediterranean basin. *B. bassiana* has been observed naturally killing *P. spinidens* and *P. curvidens* in several silver fir stands of Croatia, with large variations in beetle mortality (1.7–25.2 %) depending on plots (Pernek 2007). This fungus has also been reported to naturally occur in the galleries of *T. destruens* in Italy (Triggiani 1984) and adult *O. erosus* in late summer galleries in Israel (Fig. 6.3a).

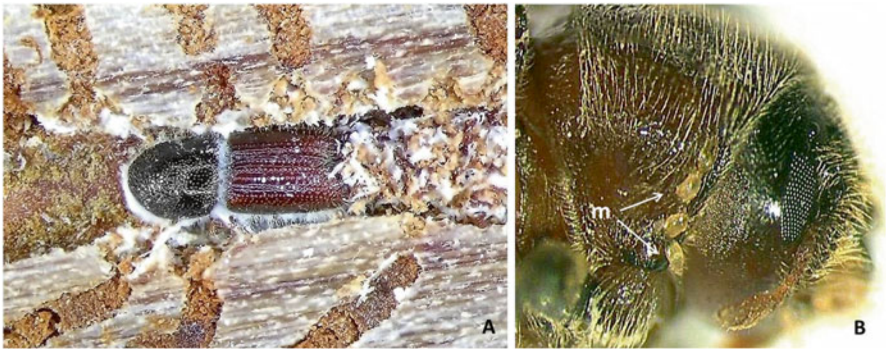

Fig. 6.3 (**a**) Infection of *Orthotomicus erosus* by *Beauveria bassiana*; (**b**) Phoretic mites on *Phloeosinus armatus*. *m*=mites (Photos Z. Mendel)

6.5.2 Non-entomopathogenic Fungi

6.5.2.1 Diversity and Variation of the Associated Fungal Flora

Yeasts are common associates of bark beetles where they have been isolated from breeding galleries, pupal chambers as well as beetle body, but very little information is available about their taxonomy (Six 2003; Kirisits 2004; Hofstetter et al. 2015; Wegensteiner et al. 2015). They are involved in many symbioses involving bark beetles, where they are known to be nutritionally important (Whitney 1982; Six 2003; Kirisits 2004; Hofstetter et al. 2015; Wegensteiner et al. 2015). However, although they are certainly also common there, no yeast has been reported from bark beetles living in the Mediterranean basin. However, yeasts are frequently isolated from the invasive ambrosia beetle *Euwallacea fornicatus* removed from various tree species, including oaks. Basidiomycetes have been isolated from some temperate and boreal bark beetles where they are supposed to play a role in beetles feeding (Whitney 1982; Klepzig et al. 2001a, b; Six 2003; Kirisits 2004; Six and Klepzig 2004; Hofstetter et al. 2015). Nothing is known about possible basidiomycetes associated with Mediterranean bark beetles.

The only non-entomopathogenic fungi reported so far as bark beetles associates in the Mediterranean basin are Ophiostomatoid Ascomycetes. However, only ten bark beetle species (including *Ips acuminatus* and *I. sexdentatus*), linked with these fungi, were recorded; for half of them Mediterranean area is only a part of their geographical range (Table 6.3). All other species presented in Table 6.1 have never been investigated for their fungal associates. Moreover, in spite of the high level of endemism (Sect. 6.3), only one species endemic from the Mediterranean basin (*T. destruens*) has been studied and, in species that have a wide range, the investigations have mainly been carried out outside of the Mediterranean area. Very limited information is thus available on Ophiostomatoid fungi associated with Mediterranean bark beetles, which does not allow drawing definitive tendencies.

The fungal flora of the widely distributed bark beetle species does not seem to differ much between the Mediterranean part of their area and the rest of their geographical range, at least for frequent fungal species. This is especially visible for *Ophiostoma ips* and *Ophiostoma brunneo-ciliatum*, and for the ubiquitous *Ophiostoma minus*. Moreover, Table 6.3 also shows that, as in the other areas (Kirisits 2004), *O. ips* appears to be mainly associated with the "*Ips-Orthotomicus*" group, whereas *O. brunneo-ciliatum* seems to be linked to the genus *Ips*. Very likely, the host tree species plays a major role in these groupings, as reported by Harrington (1993) and Kirisits (2004) for bark beetles in general. The presence of the ubiquitous *O. minus* in the galleries of *H. ater*, *I. sexdentatus*, *I. acuminatus* and *T. destruens*, all species developing on pines, is in agreement with this hypothesis. However, the narrow specificity of *O. brunneo-ciliatum* for the genus *Ips* on pines as well as on larch (Mathiesen 1950; Mathiesen-Käarik 1953; Upadhyay 1981; Kirisits 2004) indicates that certainly the beetle species itself interferes in addition to the tree species. Unfortunately, no data are available regarding the fungal flora associated with beetles developing on Mediterranean tree genera such as *Cedrus*, *Cupressus*, *Juniperus* or *Tetraclinis*. However, two species of *Geosmithia* fungi, *G. flava* and *G.*

langdonii (Ascomycota: Hypocreales) were isolated from *P. thujae* collected in Bohemia (Kolarik et al. 2008). As *O. erosus* is able to develop on cedars as well as on pines (Table 6.1), comparing its fungal flora in these two situations would be interesting. The flora associated with the fir bark beetle *P. spinidens* seems to differ from that of the other beetle species developing on pines, but data are very limited. Especially, *G. cucullata*, the main fungal species associated with *P. spinidens* has been reported associated with *I. typographus* on Norway spruce at many occasions (Kirisits 2004) and its identification needs to be clarified (Kirisits et al. 2009).

As in temperate areas, the occurrence of the beetle-fungus associations is very variable depending on localities and year. In Mediterranean areas, the frequency of association of *O. ips* with *I. sexdentatus* varies from 22 % to 40 % in *P. sylvestris* and from 0 % to 60 % in *P. pinaster* (Lieutier et al. 1991; Bueno et al. 2010). In temperate areas, its occurrence has reported to vary between 30 % and 100 % in *P. sylvestris*, and to be around 70 % *P. radiata* (Lieutier et al. 1989b; Romón et al. 2007), whereas no *O. ips* has been found with *I. sexdentatus* in Sweden (Mathiesen-Käarik 1953). In *I. acuminatus*, the association with *O. ips* concerned 40–50 % of the insects in Mediterranean France (Lieutier et al. 1991) but only 5 % in Sweden (Mathiesen-Käärik 1953). In North Africa, *O. ips* has been found in almost all *O. erosus* populations at an occurrence varying from 0 % to 64 % (Lieutier et al. 2002; Ben Jamâa et al. 2007). Although concerning only *Ips* species, the beetle association with *O. brunneo-ciliatum* is also very variable. Regarding *I. sexdentatus*, the occurrence of this fungus in the Mediterranean area has been reported to range from 40 % to 80 % in *P. pinaster* and to be around 80 % in *P. sylvestris* (Lieutier et al. 1991; Bueno et al. 2010). In temperate areas, its occurrence ranged from 0 % to 70 % and is around 50 % in Sweden (Mathiesen-Käarik 1953; Lieutier et al. 1989b). With *I. acuminatus*, *O. brunneo-ciliatum* has been found only in southern France where it was associated with 15–20 % of the beetles (Lieutier et al. 1991). *L. wingfieldii* has been mainly found with *T. destruens*. It is typically a fungus associated with the European populations of *Tomicus*, although at a rather low frequency (Lieutier et al. 2015). It has however been also reported in the galleries of other species at a low occurrence (see Romon et al. 2007 as an example). Its frequency of association with *T. destruens* varies from 0 % to 86 % in the Mediterranean basin (Lieutier et al. 2002; Sabbatini-Peverieri et al. 2006; Ben Jamâa et al. 2007). *L. wingfieldii* appears to be more adapted to low temperatures than other fungal species associated with *T. destruens*, such as *O. minus* (Lieutier and Yart 1989; Solheim et al. 2001). In laboratory cultures, its optimal temperature was 25 °C (30 °C for *O. minus*). However, as those results have been obtained with temperate and boreal populations of *L. wingfieldii*, it would be interesting to determine if the Mediterranean populations have the same needs.

It is clear from Table 6.3 that each bark beetle species is associated with a diversity of non-entomopathogenic fungal species, even in a same locality. Together, these associations form a complex of species which can interfere with each other, with the beetle, with other organisms present in the galleries and with the host tree (Lieutier et al. 2009). The nature of the interactions and the role of the various participants in such a complex have been studied with some details in the case of *Dendroctonus frontalis* Zimm. in North America (Klepzig et al. 2001b; Klepzig and Six 2004; Six and Klepzig 2004; Hofstetter et al. 2006a, among others). Certainly,

Table 6.3 Non entomopathogenic Ophiostomatoid fungi associated with bark beetle species of the Mediterranean basin

	Bark beetle species									
Fungal species	*Crypturgus cinereus*	*Hylastes angustatus*	*Hylastes ater*	*Hylurgus ligniperda*	*Ips acuminatus*	*Ips sexdentatus*	*Orthotomicus erosus*	*Pityogenes calcaratus*	*Pityokteines spinidens*	*Tomicus destruens*
Ceratocystiopsis minima Olchow and Reid	+7				**+10**					
C. minuta (Siemaszko) Upadhyay and Kendr.	+++ 7				+14	+**2**,7			**+6**	
C. neglecta (Kirschner and Oberw.) De Beer and Wingf.	+8									
Graphium fimbriisporum Morelet									**+6***	
Graphilbum fragrans (Math.-Käärik) De Beer, Seifert, Wingf.						+15	+17			
G. pseudormiticum Mouton and Wingf.						+++ 7				
Grosmannia cucullata (Solheim) Zipfel, De Beer, Wingf.									+++ **6***	

G. olivacea (Math.) Zipfel, De Beer and Wingf.			+17			+17	+17			
G. penicillata (Grosmann) Gold			+13, 15	+15						
G. piceiperda (Rumbold) Gold.	**+++** 7					**+7**				
G. serpens (Goid.)		+ *(23)*	+20	+ *(21)*, *(23)*			+ *(21)*			**+18**
Leptographium guttulatum Wingfield and Jacobs			+17,20	+17		+17	+17	+++ 17		**+18**
L. lundbergii Lagerb. and Melin			+13,15		+13,15		+ *(22)*			**+18**
L. obscurum (Davidson) De Beer and Wingf.						+7				
L. procerum (Kendr.) Wingf.			+ *(12)*	+ *(12)*						
L. wingfieldii Morelet			+17				+17			**+++ 1,11,18**
Ophiostoma ainoae Solheim						+++ 7				
O. araucariae Griffin						+++ 7				
O. brunneo-ciliatum Math.-Käärik					+++ **10**	+++ **2**,5,9,**10**,15				

(continued)

Table 6.3 (continued)

Fungal species	Bark beetle species									
	Crypturgus cinereus	*Hylastes angustatus*	*Hylastes ater*	*Hylurgus ligniperda*	*Ips acuminatus*	*Ips sexdentatus*	*Orthotomicus erosus*	*Pityogenes calcaratus*	*Pityokteines spinidens*	*Tomicus destruens*
O. clavatum Math.					+++ 3,4,13, 14, 15,16	+15				
O. floccosum Math.			+17				+16			
O. ips (Rumbold) Nannf.			+17		+++ **10**,15	+++ **2**,3,5,9, **10**,17,19	+++ **1**, **11**, 17, 20	+17		**+1**
O. japonicum Yamaoka and Wingf.	+++ 7					+++ 7				
O. leucocarpum (Davidson) De Beer and Wingf.	+7									
*O. macrosporum (*Francke-Grosm.) De Beer and Wingf.					+3,4,13					
O. minus (Hedgc.) Syd.			+13,15		+++ **10**,13, 15, 16	+9,17,19				**+1**
O. piceae (Münch) Syd. and P. Syd.	+++ 7		+13,15, 17		+3,13,15		+17		+**6**	
O. piliferum (Fr.) Syd. and P. Syd.					+3,13,15					

O. pluriannulatum (Hedgc.) Syd.			+17			+17*	+17			
O. quercus (Georgev.) Nannf.			+17							
O. stenoceras (Robak) Nannf.	+7		+17			+17	+++ 17			
O. tingens (Lagerb. and Melin) De Beer and Wingf.						+15				

References: (1) Ben Jamâa et al. 2007[a]; (2) Bueno et al. 2010; (3) Francke-Grosmann 1952; (4) Francke-Grosmann 1963; (5) Kirisits et al. 2000; (6) Kirisits et al. 2009; (7) Kirschner 2001 in Kirisits 2004; (8) Kirschner and Oberwinkler 1999; (9) Lieutier et al. 1989b; (10) Lieutier et al. 1991; (11) Lieutier et al. 2002[a]; (12) Mackenzie and Dick 1984; (13) Mathiesen 1950; (14) Mathiesen 1951; (15) Mathiesen-Käarik 1953; (16) Rennerfelt 1950; (17); Romón et al. 2007; (18) Sabbatini-Peverieri et al. 2006; (19) Siemaszko 1939; (20) Wingfield and Gibbs 1991; (21) Wingfield and Knox-Davies 1980; (22) Wingfield and Marasas 1983; (23) Wingfield et al. 1988

Bark beetle species not in the list of Table 6.1 (*I. acuminatus* and *I. sexdentatus*) are taken into account because certain fungal species have been isolated in Mediterranean localities of their range. The nomenclature of Ophiostomatoid fungi proposed by De Beer et al. (2013) is used. Extremely rare fungal species and those with doubtful taxonomic status or determined at the genus level only (Kirisits 2004) are not mentioned

* = taxonomic status to be confirmed; + = Fungal species present in at least one beetle population; +++ = Fungal species very commonly associated with a beetle species (present in all studied populations); **bolt** characters = fungal isolations made in the Mediterranean area; *()* = Fungal isolations made outside the natural geographic range of the beetle species. In all other cases, fungal isolations have been made in the natural area of the beetle species but outside the Mediterranean basin. Numbers indicate references (see above footnote)

[a] Reference to *T. piniperda* in the natural area of *T. destruens* according to Horn et al. (2012) and thus considered to refer to *T. destruens*

comparable organizations exist in other bark beetle systems in Europe and the Mediterranean basin, with a specific role for each fungal species (Lieutier et al. 2009) but very little is known in that field regarding the Mediterranean bark beetle species.

6.5.2.2 Benefits from the Association

The benefits of the association for the fungi include carrying them to a new host. For the vast majority of these fungi, the spores have special adaptations to transportation, such as sticky and thick walls to adhere to the beetle body and to resist desiccation or digestive enzymes during transport (Mathiesen-Käarik 1960; Francke-Grosmann 1966). Some others do not have these adaptations but are transported in mycangia in the beetle body as in the mandibles of *I. acuminatus* (Francke-Grosmann 1963, 1967). Phoretic mites associated with the beetles can also be involved in spore dispersal as observed in *I. sexdentatus* (Lévieux et al. 1989). Facilitation in entering the available hosts through wounding made by the beetles and limited interspecific competition are also advantages for fungi associated with beetles attacking living trees, compared to fungi developing on dead substrates (Lieutier et al. 2009).

The benefits for the beetles are multiple and may depend on fungal species (Lieutier et al. 2009). It has been suggested that nutrition is very likely an important benefit for bark beetles (Adams and Six 2007; Bleiker and Six 2007; Klepzig and Six 2004; Six 2003). Some fungi can serve as source of food for certain bark beetle species. Francke-Grosmann (1966) has separated the phloem-colonizing beetle species in two groups: the phloeophagous species feeding exclusively upon the phloem, and the phloeomycetophagous feeding upon both the phloem and fungi. However, phloeophagous species might use some fungi as additional source of food for larvae or teneral adults (Francke-Grosmann 1967; Whitney 1982; Six 2003; Klepzig and Six 2004; Harrington 2005). Among the species which can be found on the Northern rim of the Mediterranean Sea, *I. acuminatus* belongs to the phloeomycetophagous category, as its mature larvae feed on conidia and mycelium of *Ophiostoma macrosporum* (Francke-Grosmann 1967). Oppositely, *I. sexdentatus* seems a true phloeophagous species since it is able to breed normally and to reproduce successfully in the absence of fungal associates (Colineau and Lieutier 1994). No information is available on feeding habits of the true Mediterranean bark beetles, except for *T. destruens* which has been said to be a phloeophagous species (Lieutier et al. 2015), and it is difficult to predict them from the freshness of the preferred substrate, especially for species that attack living trees. Indeed, for example, in spite of their very different feeding habits, *I. sexdentatus* and *I. acuminatus* can simultaneously attack and develop on the same living trees. On the contrary, it is possible that a given species that can develop on a degraded phloem substrate or on dying trees may feed at least partly on associated fungi. It is the situation of *Carphoborus pini*, *Crypturgus mediterraneus*, *C. numidicus*, *H. ater*, *H. ligniperda*, *H. miklitzi*, *Ph. thuyae*, *P. calcaratus*, and *S. numidicus* (Sect. 6.4).

The association would also considerably benefit to beetles attacking living trees because of the ability of certain fungi to significantly contribute in weakening the host tree and thus in facilitating beetle establishment (Lieutier 2004; Lieutier et al. 2009). Indeed, when artificially and individually inoculated at low density to the host tree of their usual beetle host, some fungi have been demonstrated to considerably stimulate the development of a wound induced hypersensitive reaction by the tree. At the moment of beetle attacks, such reactions would lead the tree to increase its energy expenditure, thus contributing in exhausting its defenses. Regarding the fungal species in Table 6.3, *L. wingfieldii*, *O. brunneo-ciliatum*, *O. ips*, and *O. minus* have been shown to stimulate the tree's wound reaction when artificially introduced into pines, the usual host trees of their beetle hosts (Lieutier et al. 1989b, 2004b, 2005; Solheim et al. 2001; Ben Jamâa et al. 2007). Except for *L. wingfieldii* (Sect. 6.6.1.3), they have also been shown to stimulate tree's defenses when introduced into the tree by their beetle host. If conceivable for beetle attacking living trees with efficient defenses, this benefit from the beetle-fungus association of course does not exist for the very secondary beetle species which develop in trees of which defenses have already been exhausted.

When mass inoculated to their host trees above a certain threshold of inoculation density, *L. wingfieldii*, *O. minus*, *O. brunneo-ciliatum*, and *O. ips* can invade the sapwood and eventually cause blue staining and tree death (Solheim et al. 1993; Långström et al. 1993; Croisé et al. 1998; Guérard et al. 2000; Fernandez et al. 2004; Lieutier et al. 2004b, 2005; Ben Jamâa et al. 2007). This threshold is a measure of the fungal virulence for a given tree species (Lieutier et al. 2009). Expressed in number of inoculations per m^2, it can be estimated at 400–800 for *O. minus* and *O. ips* in *P. sylvestris* (Långström et al. 1993; Solheim et al. 1993; Fernandez et al. 2004), 300–400 for *L. wingfieldii* in *P. sylvestris* (Solheim et al. 1993; Croisé et al. 1998), and around 1000 for *L. wingfieldii* in *P. pinaster* and *P. brutia*, for *O. ips* in *P. pinaster*, and for *O. brunneo-ciliatum* in *P. sylvestris* (Guérard et al. 2000; Lieutier et al. 2005; Ben Jamâa et al. 2007). Sapwood occlusion strongly correlates with loss of hydraulic conductivity (Croisé et al. 1998; Fernandez et al. 2004; Lieutier et al. 2005; Ben Jamâa et al. 2007). In addition to variations resulting from differences between fungal/tree species and localities, fungus ability to stimulate the tree defensive reactions, as well as fungal virulence, can vary among isolates in a same fungal species (Lieutier et al. 2004b, 2005; Ben Jamâa et al. 2007). These experiments demonstrate that the concerned fungal species can be pathogenic under certain conditions, but do not prove that these fungi are the immediate cause of host tree death. In fact, no relation exists between beetle aggressiveness and fungal virulence (Paine et al. 1997; Lieutier 2002; Harrington 2005; Lieutier et al. 2009). It has even been suggested that, in case of beetle attack, blue-stain fungi are able to invade the sapwood only after attack has succeeded (Lieutier et al. 2009).

It is worth mentioning that in addition to carrying fungi involved in true beetle-fungus associations and susceptible to bring benefits for the beetle, some Mediterranean bark beetles species have been found to play role as carriers of tree disease agents. It is especially the case for *P. bicolor* and very likely for *P. armatus* and *P. thuyae* which have been found carrying *S. cardinale*, the causal agent of the cypress canker (Tiberi and Battisti 1998; Pennacchio et al. 2013).

6.5.3 Nematodes

The favorable microclimatic conditions and the much diversified and abundant source of food in the bark beetle galleries have allowed the establishment of a large diversity of nematode species and life cycles, corresponding to a high diversity of nematode-bark beetles relationships (Rühm 1956). Nevertheless, it is possible to recognize three main types of nematode life cycles, defining three types of relationships with the beetle hosts.

Table 6.4 presents the known nematode species associated with Mediterranean bark beetles in their natural areas, with their localization in the adult insect or its galleries and their type of relationships with bark beetles. The simplest type of association, which corresponds to the vast majority of the bark beetle associated nematode species, is that where the whole nematode life cycle takes place in the beetle galleries with no prejudice to the insect, defining the saprophytic species (Rühm 1956; Poinar 1972). The nematode feeds on fungi and decaying wood, and its relations with the bark beetle is limited to transportation from one tree to another. The resistant third instar (L3) nematode larvae ("dauerlarvae") attached themselves at various places of the cuticle of the adult insect (under the elytra, on the back of the mesothorax, in the intercoxal zones, near the spiracles, inside the tracheas …). In all cases however, the L3 are in contact with the sole cuticle and not with internal tissues of the insect. The other two life cycle categories relate to parasitism and alternate between the beetle galleries and internal tissues of the insect, but at different levels (Rühm 1956; Poinar 1972). Some species are found as L3 dauerlarvae in the gut or the body cavity of their host. They do not develop inside the insect body and their relations with the beetle are thus not very far from that of the saprophytic species. However, the presence of many L3 larvae in the same insect, can lead to (generally limited) damage to the harbouring tissues. A typical example is that of *Parasitiorhabdits ipsophila* in the mid-gut of *I. sexdentatus* where the movements of numerous L3 larvae can destroy the epithelial cells and lead to a slight delay in beetle maturation (Lieutier 1984a). These species are thus not considered as truly parasitic and can be considered as semi-parasitic species.

The true parasitic species infect the insect with adult, eggs and/or larval forms and realize part of their development inside the beetle body. The infested organs can be the fat body, the hemocoel, the ovaries, the seminal vesicle, or the Malpighian tubules. For example, in *Contortylenchus diplogaster*, the young females mate in the beetle galleries before entering a beetle larva or pupa, directly through the integument or through oral or anal apertures, to finally reach the hemocoel (Kaya 1984). It is not rare that several infective females enter the same insect. Once there, they locate inside the fat body where they enlarge considerably by using host proteins and amino-acids, while the beetle reaches the adult stage (Lieutier 1985; Lieutier et al. 1985). In the adult beetle, the enlarged females are found inside large fat body capsules made of hypertrophied fat cells (Lieutier and Seureau 1981; Lieutier 1984b). When completely matured, the parasitic females lay hundreds of eggs, which results in bursting of the capsules and invasion of the hemocoel by eggs and first instar larvae (Lieutier 1984b). Larvae develop until the fourth stage in the body cavity, then migrate through the gut and reach the galleries where they moult into

Table 6.4 Main nematode species associated with bark beetle species of the Mediterranean basin and their location in the beetle

	Bark beetle species											
Nematode species	*Cryphalus piceae*	*Crypturg. cinereus*	*Ips sex-dentatus*	*Hyl. angustatus*	*Hylastes ater*	*Hylurgus ligniperda*	*Orthotomi-cus erosus*	*Pityokteines curvidens*	*Pityokteines spinidens*	*Tomicus destruens*	*Tomicus piniperda*	Location in beetle and status
***Allantonema** morosum* Fuchs					15						+24	Hemocoel P
***Bursaphelenchus** sp.*										**+9**		Metathoracic S intercoxas
B. abietinus Braasch and Schmutzenhofer								1	1,17			S ?
B. chitwoodi Rühm					+6,15							L3 under elytra S
B. cryphali Fuchs	+4,15,21, 22											L3 under elytra S
B. hellenicus Skarmoutsos, Braasch and Michalopoulou			**+14**			**+14**				**+18**	**+14**	L3 on beetles S
B. hofmanni Braasch								3; 23				S ?
B. leoni Baujard										**+18**		S ?
B. nuesslini Rühm								+7,15,21, 22				L3 under elytra S
B. piniperdae (Fuchs) Rühm											**+++** 4,12,15	L3 under elytra S
B. sexdentati Rühm			8,16,26				**+14**				+2	L3 on beetles S
B. silvestris (Lieutier and Laumond) Baujard			+11,12									Galleries S

(continued)

Table 6.4 (continued)

	Bark beetle species											
Nematode species	*Cryphalus piceae*	*Crypturg. cinereus*	*Ips sex-dentatus*	*Hyl. angustatus*	*Hylastes ater*	*Hylurgus ligniperda*	*Orthotomi-cus erosus*	*Pityokteines curvidens*	*Pityokteines spinidens*	*Tomicus destruens*	*Tomicus piniperda*	Location in beetle and status
B. teratospicularis Kakulia and Devdariani							**+14**					L3 on beetles S
B. tusciae						**+14**						S ?
Contortylenchus *sp.*			**+14**			**+14**	**+++ 14**					P
C. cryphali Rühm	15											Adult in hemocoel P
C. cunicularii (Fuchs) Filipjev					15							Adult in hemocoel P
C. diplogaster (V. Linstow) Rühm			+++ 11,12									Adult in fat body, P larvae in hemocoel
Cryptaphelenchus *koerneri* Rühm					+15							Larvae in jabot S
C. macrogaster (Fuchs) Rühm			+++ 11,12									L3 under elytra S
C. piceae Rühm	+15											L3 under elytra S
C. piceoides Rühm								+++ 15				L3 under elytra S
C. viktoris (Fuchs) Goodey											+5,15	L3 in body cavity S
Diplogasteroides *halleri* Fuchs			+11									L3 under elytra S
D. sexdentati Visilite			+26									L3under elytra S

***Ektaphelenchus** sp.*			**+14**				**+14**					S ?
E. cunicularii Fuchs					+15							External body S
E. tuerkorum Rühm								+15				External body S
***Macrolaimus** canadensis* Sanwal			+11							**+9**	+12	Metathoracic intercoxas, S
***Micoletzkia** sp.*										**+9**	+12	Galleries S
M. buetschlii Fuchs			+11									L3 under elytra S
M. eutelesa Rühm								+15				L3under elytra S
M. hylurginophila Rühm						+++ 15						L3 under elytra S
M. sexdentati Blinova and Vosilite			+++ 12									L3 under elytra S
M. thalenhorstii Rühm				+15	+++ 15							L3 under elytra S
***Neoditylenchus** abieticolus* Rühm	+15											L3 under elytra S
N. panurgus Rühm					+15							L3 under elytra S
N. pityokteinophilus Rühm								+15				L3 under elytra S
***Neoparasitylenchus** sp.*											+12	Adult in hemocoel P
N. cryphali (Fuchs) Filipjev	15											Endopar. adults P
N. cinerei Fuchs		15										Endopar. adults P

(continued)

Table 6.4 (continued)

Nematode species	Bark beetle species											Location in beetle and status
	Cryphalus piceae	*Crypturg. cinereus*	*Ips sex-dentatus*	*Hyl. angustatus*	*Hylastes ater*	*Hylurgus ligniperda*	*Orthotomi-cus erosus*	*Pityokteines curvidens*	*Pityokteines spinidens*	*Tomicus destruens*	*Tomicus piniperda*	
N. hylastis (Wülker) Filipjev				15	15							Endopar. adults P
N. ligniperdae (Fuchs) Filipjev						15						Endopar. adults P
***Panagrolaimus** sp.*											+12	Galleries S
P. detritophagus Fuchs											**+**4	S
P. subelongatus (Cobb) Thorne			+11									Galleries S
P. tigrodon Fuchs										**+9**	**+**4,24	Metathoracic spiracles; under elytra S
***Parasitaphelenchus** sp.*			+++ **10**,12,**14**			**+14**						Larvae in body cavity; ovaries P
P. ateri (Fuchs) Rühm					+++ 15						**+**24	Larvae in body cavity P
P. papillatus Fuchs										**+9,25**	**+++** 9,12,15,19,24	Larvae in body cavity; seminal vesicle P
P. sexdentati (Fuchs) Rühm			+++ 10, 12, 15									Third instar larvae in body cavity P
***Parasitorhabditis** sp.*			+++ **14**			**+14**	+++ **14**				+14	P ?
P. ateri Fuchs					+++ 15							L3 in gut H

P. curvidentis Fuchs								+++ 15				L3 in gut H
P. cryphalophila Rühm	+15											L3 in gut H
P. crypturgophila Rühm		15										L3 in gut H
P. erosus Kurashvili, Kakulia, Devdariani							8					H ?
P. ipsophila Lieutier and Laumond			+++ 11,12									L3 in gut H
P. ligniperdae						+++ 15						L3 in gut H
P. opaci Rühm				+++ 15								L3 in gut H
P. piniperdae Fuchs										**+9,25**	**+++** 9,12,15,20,24	L3 and adults in body cavity P
Parasitylenchus *curvidentis* (Fuchs) Filipjev								+++ 15				Endopar. adults P
Prothallonema *tomici* Nedelchev, Takov and Pilarska											**+**13	Larvae and adults in body cavity P
Ruidosaphelenchus *janasii* Launond and Carle										**+9**		Metathoracic spiracles S
Sulphuretylenchus *kleinei* Rühm					15							Endopar. adults P

(continued)

Table 6.4 (continued)

References: (1) Braasch and Schmutzenhofer 2000; (2) Braasch et al. 1999; (3) Braasch et al. 2000; (4) Fuchs 1930; (5) Fuchs 1937; (6) Kakulia and Shalibashvili 1976a; (7) Kakulia and Shalibashvili 1976b; (8) Kurawhvili et al. 1980; (9) Laumond and Carle 1971; (10) Lieutier 1980; (11) Lieutier and Laumond 1978; (12) Lieutier and Vallet 1982; (13) Nedelchev et al. 2011; (14) Penas et al. 2006; (15) Rühm 1956; (16) Rühm 1960; (17) Schmutzenhofer 1981; (18) Skarmoutsos et al. 1998[a]; (19) Slobodyanyuk 1973; (20) Slobodyanyuk 1974; (21) Tenkáková and Mituch 1987; (22) Tenkáková and Mituch 1988; (23) Tomiczek 2000; (24) Tomalak et al. 1984; (25) Triggiani 1984[a]; (26) Vosilite 1990

Bark beetle species not in the list of Table 6.1 (*I. sexdentatus* and *T. piniperda*) are taken into account because certain nematode observations have been made in Mediterranean localities of their range

Extremely rare species and those with doubtful taxonomic status are not included

+: species present at least one beetle population or low percentage of beetle contamination; +++: species very commonly associated with a beetle species (present in all studied populations) or high percentage of beetle contamination. *L3* resistant at the third stage, *P* True parasitic species, *H* hemi-parasitic species, *S* saprophytic species

Bolt characters = nematode observations made in the Mediterranean area. In all other cases, nematode observations have been made in the European natural area of the beetle species but outside the Mediterranean basin. Numbers indicate references (see above footnote)

[a] Reference to *T. piniperda* in the natural area of *T. destruens* according to Horn et al. (2012) and thus considered to refer to *T. destruens*

adults (Kaya 1984). Damage by true parasitic nematodes is generally consequent, especially in case of a large number of parasitic nematodes in the same insect. They can delay the beetle maturation considerably; cause insect sterilization or even death.

Data regarding nematodes associated with Mediterranean bark beetles are very dispersed and incomplete. Indeed, compared with those related to *I. sexdentatus* and *T. piniperda* in their temperate area, it is clear that many nematode species are still to discover in the Mediterranean bark beetle systems (Table 6.4). Certain specificity for a particular beetle species can exist at the nematode species level (Lieutier et al. 2015). This is not very clear in Table 6.4 because many beetle species have not been thoroughly investigated, making comparisons between beetle species belonging to the same genus not possible. Nevertheless, the high diversity of the *Bursaphelenchus* species (13 species) parallel to the diversity of the beetle species (11) suggests species specificity. However, *Bursaphelenchus hellemicus* has been found in four different beetle species. On the contrary, nematode genera do not exhibit specificity, even at the genus level, as demonstrated by the fact that all nematode genera of Table 6.4 are found in several beetle genera. This is particularly evident for the genus *Bursaphelenchus*. The true parasitic species are in limited number (18/66) and have been found in the fat body, the hemocoel, the ovaries, or the seminal vesicle. *Parasitorhabditis piniperdae* in *T. piniperda* and *T. destruens* is a particular case. Indeed, as all other *Parasitorhabditis* species are found as hemi-parasites in the digestive tract of their host, *P. piniperdae* behave as a true parasite, its dauerlarvae and even its adults being found in the body cavity of the beetle (Laumond and Carle 1971; Lieutier and Vallet 1982).

6.5.4 Mites

As for fungi and nematodes, bark beetle galleries in general host a very large diversity of mite species playing various diversified functions (Kenis et al. 2004; Hofstetter et al. 2013, 2015). Mites are important components of bark beetles communities. They interfere in bark beetle-tree relationships as well as in bark beetle-fungi relationships, where they can be antagonistic, commensalistic, mutualistic, or competitors, thus being involved in a complex array of interactions and associations (Hofstetter and Moser 2014). Mites are transported from one tree to another by the beetles themselves (Fig. 6.3b) or by associated predatory and commensal insect species. Some species carry fungal spores, simply directly attached to their cuticle or in special structures (sporotheca) of their body (Lindquist 1985; Moser 1985). Sporotheca have been recognized in several mite families (Hofstetter et al. 2015). Fungi are the mites' feed; this may explain why these mites developed the adaptations to carry fungi from one place to another. By doing so, mites play an essential role in bark beetle fungi relationships (Klepzig et al. 2001a; Lombardero et al. 2003). Indeed, the ascomycetes genera reported above to be associated with bark beetles and to play a role in beetle-tree relationships (*Ceratocystis*, *Ceratocystiopsis*, *Ophiostoma*, *Grosmannia*, *Leptographium*), as well as basidiomycetes such as *Entomocorticium*, can all be carried by scolytid associated mites (Hofstetter et al.

Table 6.5 Mite species recorded on bark beetle species or their galleries in the Mediterranean basin, with their phoretic stage and their location on the beetle host

Mite species	Bark beetle species							Phoretic stage	Relations with bark beetles	Location on beetle
	Ips sexdentatus	*Orthotomicus erosus*	*Pityogenes clacaratus*	*Pityokteines curvidens*	*Pityokteines spinidens*	*Pityokteines vorontzowi*	*Tomicus destruens*			
Cercoleipus coelonotus Kinn	+++1, 3, 6						+6	Deutonymph, Females, Males	P	No preference
Dendrolaelaps apopthyseus Hirschmann	+1,								P ?	
D. quadrisetus Berlese	+++ 1, 3			+++ 4, 5	+4	+4		Deutonymph	P, F	Under elytra
Dolicheremaeus dorni Balogh				+5				?		?
Ereynetes scutulis Hunter	+1				+4	+4		Female	P	
Histiostoma abietis Scheucher				2						
H. ovalis Gerv	+++ 1, 3							Female, Deutonymph	F	Under elytra, coxa, legs
H. piceae Scheucher				+4,	+4	+4		Deutonymph	F	Under elytra
H. cf varia Woodring				+5				Deutonymph		Under elytra
I. punctatus Lindquist		2	2						P ?	
Lucoppia burrowsi Michael	+1,									
Paraleius leontonychus Berlese	+1,			+++ 4,5	+4	+4		Female, male		Under elytra; elytral declivity; coxa; ventral thorax; legs
Phauloppia lucorum C. Koch				+5				?		?
Pleuronectocelaeno barbara Kinn				+5				Female	P ?	Under elytra
P. japonica Kinn				+5				Female	P ?	Under elytra

Proctolaelaps hystricoides Lindquist and Hunter					+4	+4			F ?	
Schizostethus simulatrix Athias-Henriot				+5				Deutonymph,	P	Elytral declivity
Schwiebea sp.				+5				Deutonymph	F ?	Under elytra; elytral declivity
Tarsonemus minimax Vitzthum				+++ 4,5	+++ 4	+++ 4		Female	F ?	Elytral declivity; under elytra; ventral thorax
T. subcorticallis Lindquist				2					F ?	
Trichouropoda lamellosa Hirschmann				+4,5	+4			Deutonymph	F	Elytral declivity; dorsal thorax
T. ovalis C.L. Koch										
T. polytricha Vitzthum	+1, 3			2				Deuronymph		No preference
U. ipidis Vitzthum	+1			+++ 4,5	+4	+4		Deutonymph	F	Under elytra; elytral declivity; coxa; ventral or dorsal thorax; legs
U. varians Hirschmann	+++ 3									Elytral declivity
Vulgarogamasus lyriformis Oudemans	+1, 3							Deutonymph	P	Under elytra

References: (1) Fernandez et al. 2013; (2) Hofstetter et al. 2015; (3) Moraza et al. 2013; (4) Pernek et al. 2008; (5) Pernek et al. 2012; (6) Sabbatini-Peverieri and Francardi 2010

I. sexdentatus is mentioned only for the observations made in its Mediterranean localities. + : species weakly present on beetles; +++ : species very abundant on beetles

Numbers indicate references (see above footnote). Relations with bark beetles: *P* predator, *F* carrying Ophiostomatoid spores

2013, 2015). Through their feeding and mobility in relation with fungi, and depending on fungal species, mites can affect negatively or positively bark beetle populations. In addition, some mites behave as predators of bark beetle eggs and young larvae. Through influencing bark beetle-fungi interactions or affecting directly beetle survival, mites probably play an essential but complicated role in bark beetle population dynamics (Klepzig et al. 2001a; Lombardero et al. 2003; Hofstetter et al. 2006a, b; Hofstetter and Moser 2014).

In spite of their large diversity and their often-key role in bark beetle-fungus-tree interactions, mites associated with bark beetles have been the subject of extremely limited investigations in the Mediterranean basin. Mainly the three *Pityokteines* species and *I. sexdentatus* have been investigated, and very occasional data are available for *O. erosus*, *P. calcaratus* and *T. destruens* (Table 6.5). In these conditions, no real discussion on mite specificity for bark beetle or tree species is possible. One can only note that there is a strong resemblance among the acarofauna of the three *Pityokteines* species and that a few of their mite species are also found with *I. sexdentatus*. Based on data from *Pityokteines* species, mite abundance and localization on beetles largely vary depending on the mite species, localities and years (Pernek et al. 2008, 2012), as it is the case for all bark beetle mites associations (Hofstetter et al. 2013). Associations with fungi have also been observed or supposed for several mites of Mediterranean bark beetles (Table 6.5). Some of these scolytid associated mite species display a predacious feeding behaviour, but in most cases, it is not certain whether they actually kill the beetles.

6.5.5 Insect Predators and Parasitoids

6.5.5.1 General Considerations

Two guilds of natural enemies – insect predators and hymenopteran parasitoids – chiefly accompany the phloeophagous bark beetle species. They are known mainly in the Northern Hemisphere. Various aspects of the relationships between bark beetles and their arthropod natural enemies in the Mediterranean basin have been studied, from a diversity of points of view. Four main coniferous tree genera are hosts for bark beetles in the region: *Pinus* and *Cedrus* (Pinaceae), and *Cupressus* and *Juniperus* (Cupressaceae). Most research efforts and the resulting information relate to *Pinus* spp., because pine trees form the major natural and planted coniferous forests of the region. Despite the tremendous effects of the last glaciation period in the Mediterranean basin (Médail and Diadema 2009), the complex of organisms associated with pine bark beetles is no less rich than that associated with southern pines in North America. There is also a remarkable taxonomic similarity among the guilds of arthropod natural enemies of bark beetles in the Nearctic (Overgaard 1968; Moser et al. 1971) and west Palearctic regions (Halperin and Holzchuh 1984; Kozak 1976; Nuorteva 1971; Lieutier et al. 2015) and, most probably, also in other areas of the Northern Hemisphere.

Insect predators of bark beetles in general belong to several different orders. The majority is in the Coleoptera, other are in the Diptera and in the suborder Heteroptera (true bugs). They are mainly associated with phloeophagous species. However, diverse predatory species are associated with the Hylesinini in the subtribes Tomicina and Polygraphina, and with the Scolytini in subtribe Ipina. Rich fauna of these predators characterize bark beetle occurrence on members of the Pinaceae. Almost all parasitoids of bark beetles belong to the Hymenoptera but, unlike the predators, they are common among most groups of phloeophagous bark beetle species. In the Hylesinini their hosts are found in the subtribes Tomicina, Phloeosinina, Polygraphina and Phloeotribina, and to a lesser extent also in the Hypoborina; in the Scolytini they occur in the subtribes Ipina and Scolytina and, to lesser extent, also in the Dryocoetina and Pityophthorina. Almost all species belong to five hymenopteran families, the majority from Braconidae and Pteromalidae, others in Eupelmidae and Eurytomidae.

A general inventory of all kinds of bark beetle natural enemies has been established by Karaman and Tezcan (2006) where predators and parasitoids are largely considered. In addition, there is a large body of literature on parasitoids associated with bark beetles of conifer trees (Bushing 1965; Herting 1973; Mendel and Halperin 1981; Hedqvist 1998; Kenis et al. 2004).

6.5.5.2 Insect Predators of Bark Beetles in Mediterranean Conifers

Several papers have dealt with predators of bark beetles in various Mediterranean localities. In addition, Ferreira (1985) established a list of insect predators of bark beetles in *P. pinaster* in Portugal, Halperin and Holzchuh (1984) gave similar information for bark beetles of Israeli conifers, and Avci and Sarikaya (2009) published an inventory of those associated with various species of conifer bark beetles in Turkish forests. Predatory species associated with Mediterranean bark beetles can also be found in the general inventory by Karaman and Tezcan (2006).

The insect predators associated with conifer bark beetles in the Mediterranean basin comprise about 47 species belonging to four orders, and the great majority of the species are beetles (Table 6.6). Among the nine coleopteran families, members of the Cleridae, Colydiidae, Histeridae, Ostomidae and Monotomidae include the major predatory species, and there is rather ample information about the most conspicuous species. Many predators use the bark beetle aggregation pheromone to find attacked trees, and their arrival at scolytid hot spots occurs during or a few days after the beetle colonization phase (Blomquist et al. 2010). As shown in Table 6.6 only a few species were found together with bark beetle species developing on tree families other than Pinaceae. However, even for those, such occurrences happened very rarely. The patterns of stem colonization by their beetle prey also marked the distribution of the natural enemies along the trunk (Dahlsten 1982). Most of the predators are found at the mid and lower levels of the stem, where the bark is thick enough. They are thus common in galleries of *O. erosus* and *T. destruens*. By contrast, most

Table 6.6 Bark beetle predators associated with bark beetle of conifer trees in the Mediterranean

Order and family	Species	Bark beetle prey[a]		
		on *Pinus*	on *Cupressus*	on broadleaves
Coleoptera				
Cleridae	*Clerus mutillarius* Fabricius	14, 22, 23, 31		
	Thanasimus formicarius L.	5, 6, 7, 11, 12, 13, 14, 15, 19, 22–25, 31, 32, 33		
	T. rufipes (Brahm)	32		
Colydiidae	*Aulonium bicolor*	13, 14	16–17	17
	Aulonium ruficorne Olivier	2, 6, 7, 11,13–15, 19, 20, 22, 31		
	Colydium elongatum Fabricius	14, 15, 22, 31		
Histeridae	*Paramalus parallelepipedus* (Herbst)	5, 12, 14, 31		
	P. parallelipipedus (Herbst)	31, 32		
	Platysoma angustatum Hoffman	7, 13, 14, 19, 20, 31, 33		
	P. cornix Marseul	14, 15, 31, 32		
	P. elongatum (Thunberg)	14, 15, 31, 32		
	P. oblongum F.	7, 13, 14, 19		
	Plegaderus otti Marseul	13, 14, 31		
	P. vulneratus (Panzer)	15, 22		
Laemophloeidae	*Cryptolestes spartii* (Curtis)	28		
	Laemophloeus alternans Erichson	14, 20		9
	L. ater Olivier	14, 20		
	L. testaceus Fabricius	14, 20		
	Lathropus sepicola Mueller	14, 20		
Monotomidae	*Rhizophagus bipustulatus* Linnaeus	14, 20, 21, 32		
	R. depressus (Fabricius)	5, 7, 11, 13, 14, 19, 21, 22, 24, 25, 6, 32, 33		
	R. ferrugineus (Paykull)	32		

(continued)

Table 6.6 (continued)

Order and family	Species	Bark beetle prey[a] on *Pinus*	on *Cupressus*	on broadleaves
Nitidulidae	*Epuraea marseuli* Reitter	32		
	E. thoracica Tournier	32		
	Pityophagus ferrugineus (Linnaeus)	32		
Ostomidae	*Nemosoma elongatum* (Linnaeus)	13, 14, 19, 23, 31		
	N. pliginskyi Reitter	22		
	Temnochila caerulea (Olivier)	13, 14, 22, 24, 31 32		
Silvanidae	*Silvanus unidentatus* Fabricius	14, 20		
Staphylinidae	*Atheta coriaria*	14		
	Metaponctus brevicornis	13		
	Nudobius lentus (Gravenhorst)	22, 29		
	Pholeonomus lapponicus (Zetterstedt)	29		
	Pholeonomus pusillus (Gravenhorst)	29		
	Placusa complanata	13, 23		
	Placusa depressa Maekl.	29		
	Staphylinus spp.	13, 31		
Tenebrionidae	*Corticeus fraxini* Kugelann	11, 12, 13, 14, 15, 31, 32		
	C. linearis (Fabricius)	5, 13, 14, 21, 31		
	C. longulus (Gyllenhal)	32		
	C. pini Panzer	7, 13, 14, 20, 31	16, 17	
	C. rufulus Rosenhauer	14, 20	16, 17	
Diptera				
Dolichopodidae	*Medetera setiventris* Thuneberg	28		
	M. striata Parent	14, 20, 31, 32	16, 17	3
	Medetera spp.	14, 20, 31	16, 17	
Stratiomyidae	*Zabrachia minutissima* Zetterstedt	14	17	18

(continued)

Table 6.6 (continued)

Order and family	Species	Bark beetle prey[a] on *Pinus*	on *Cupressus*	on broadleaves
Heteroptera				
Anthocoridae	*Scoloposcelis pulchella* (Zetterstedt)	13, 14, 20, 31, 33		
	Scoloposcelis spp.	13, 14, 31		
Aradidae	*Aradus* spp.	1, 32		
Raphidioptera				
Raphidiidae	*Raphidia ophiopsis* (Linnaeus)	5, 13, 14, 19, 22, 25 30, 32, 33		
	R. syriaca Steinmann	14, 17, 20		

Associations with broadleaved trees are indicated when they come in addition to associations with conifers

[a] Scolytid prey in the Mediterranean: 1 *Carphoborus henscheli*; 2 *C. minimus*; 3 *C. perrisi*; 4 *Chaetoptelius vestitus*; 5 *Cryphalus piceae*; 6 *H. ater*; 7 *H. ligniperda*; 8 *Hylurgus micklitzi*; 9 *Hypoborus ficus*; 10 *Hypothenemus eruditus*; 11 *Ips acuminatus*; 12 *I. mannsfeldi*; 13 *I. sexdentatus*; 14 *Orthotomicus erosus*; 15 *O. tridentatus*; 16 *Phloeosinus armatus*; 17 *P. bicolor*; 18 *Phloeotribus scarabaeoides*; 19 *Pityogenes bidentatus*; 20 *P. calcaratus*; 21 *P. pennidens*; 22 *Pityokteines curvidens*; 23 *P. spinidens*; 24 *P. vorontzowi*; 25 *Pityophthorus pityographus*; 26 *Scolytus amygdali*; 27 *S. carpini*; 28 *S. kirschi*; 29 *S. mediterraneus*; 30 *S. numidicus*; 31 *Tomicus destruens*; 32 *T. minor*; 33 *T. piniperda*

of them are not associated with *P. calcaratus* or *Carphoborus* spp., those latter scolytids occupying the upper level of the stem or side branches.

Coleoptera

Members of the Cleridae, mainly *Thanasimus formicarius*, feed on the tree, where they attack adult scolytids. Adults and larvae of all five cited above predatory beetle families feed on all immature stages of the bark beetles, including immature adults (Langewald 1989). The clerids are found at high elevations and on the northern margins of the Mediterranean basin, but they are widely associated with *I. typographus* on spruce. Members of the other families, especially the Colydiidae and Histeridae, are common also in the southern areas of the region.

Among the Colydiidae on the Mediterranean pines, *Aulonium ruficorne* is probably the most common. This beetle is most abundant in trees attacked by *O. erosus*, but also in those attacked by *P. calcaratus and T. destruens*. It arrives on attacked trees together with adult scolytids (Podoler et al. 1990). *A. ruficorne* adults are also captured in large numbers by traps baited with commercial pheromone lures of *O. erosus* or *I. typographus* (e.g. Mendel and Opatowski 1997). Its main activity occurs during the early stages of beetle development. The adults feed mainly on eggs and young larvae. Mature larvae of the predators are able to remove small wood particles to reach the pupal chambers of their prey. In Israel, high *A. ruficorne* populations may inflict 90 % mortality on immature of *O. erosus* during spring and late summer (Podoler et al. 1990). *A. ruficorne* exploits colonized thin bark areas usually avoided by other coleopteran predators, but in these parts of the stem it may suffer from heavy competition with parasitoids (Mendel et al. 1990). *A. ruficorne* usually leaves the tree soon after the emergence of its scolytid prey.

In general, histerids (Coleoptera: Histeridae) search for their prey in ephemeral habitats, such as dung, carrion, rotting fungi, or other decaying organic matter (Kovarik and Caterino 2000). Therefore, they are well adjusted to exploit bark-beetle-infested trees. Histerid beetles – adults and larvae – feed primarily within the bark beetle galleries; they typically arrive at trees within a few days of bark beetle colonization (Shepherd and Goyer 2003), by exploiting bark beetle aggregation pheromones as kairomones. They are regarded as facultative predators within a specialized habitat (Shepherd and Goyer 2005), and their main impact on the scolytid population occurs during the last period of activity of their prey. In the Mediterranean basin these species are multivoltine and their predacious activity is common in galleries of mainly *O. erosus* and *T. destruens*; and – at high elevations – also of *T. minor* (Halperin and Holzchuh 1984, Långström and Hellqvist 1990). When they prey on *O. erosus* they tend to remain in the attacked trees as long as the bark remains moist, during several weeks and up to several months (in winter). In the southern USA Shepherd (2005) showed that histerids displayed several attributes of successful biological control agents, including high prey (habitat) specificity, rapid host finding, ecological synchrony with prey, and ability to lower prey populations.

Members of the Ostomidae and Monotomidae prey also on the immatures of mainly *O. erosus* and *T. destruens* in Mediterranean pines. With respect to Ostomidae, detailed biological data have been obtained from *Temnochila virescens* (Mignot and Anderson 1970) and *Nosema elongatum* (Dippel 1996), which respond well to the aggregation pheromones of *O. erosus* and *I. typographus*. However, they usually occur in small numbers among the emerging scolytid associates or are captured in pheromone traps (Mendel and Opatowski 1997). The Monotomidae is a small family of beetles with some 80 described species in the Palearctic region. Most species are saprophagous, living either under bark and/or on fermenting sap of trees (*Rhizophagus*) or in various decaying vegetal substrates (*Monotoma*) (Halperin and Holzchuh 1984). Among the three *Rhizophagus* species mentioned in Table 6.6, *Rhizophagus bipustulatus* feeds chiefly by scavenging on fungi, and is not restricted to conifers (JeLínek and Audisio 2004). It is often found associated with *O. erosus* and *T. destruens*, but usually in very small numbers. *Rhizophagus depressus*, known as a predator of *T. piniperda* (Schroeder 1996), preys on *T. destruens* along the northern margin of the Mediterranean basin, but it may occur in galleries of many species of pine bark beetles. *Rhizophagus ferrugineus* is mainly a scavenger; it is lured by tree volatiles as well as short-chain alcohols and scolytid pheromones (Byers 1992) and its role as a predator is not well understood. The last two *Rhizophagus* species are rare in the Mediterranean basin.

Species of five other beetle families – Laemophloeidae, Silvanidae, Staphylinidae, Tenebrionidae, and Nitidulidae – are associated with pine bark beetles. Most of these species are found as adults and larvae under bark of dead trees, where apparently they are primarily fungivores or scavengers (Dahlsten 1982). In each family, some species associated with bark beetles occur in their galleries and may feed on immature prey individuals. Their role as facultative predators is usually questionable.

Diptera

Species of two Dipteran genera are associated with bark beetles in the Mediterranean basin. Members of the genus *Medetera* Fisher von Waldheim (Diptera: Dolichopodidae) display holarctic distribution. Species associated with the pine bark beetle have attracted much attention in Europe and North America (Bickel 1985). They are among the most common predators of bark beetles that develop on Pinaceae species. Members of the genus *Medetera* are chiefly found in woody habitats. Scolytid-associated *Medetera* species display a strict association with pine bark beetles and often have been observed ovipositing at the entrances to the beetle galleries (Bickel 1985). Adults are active predators of soft-bodied small insects and mites. In the Mediterranean basin, *Medetera striata* adults often prey on sciarid midges which occur also on scolytid-infested pines. These flies inhabit galleries made by scolytid beetles in the bark of trees, as in other areas, feeding on scolytid eggs, larvae, pupae, and immature adults (Bickel 1987; Dippel et al. 1997; Hedgren and Schroeder 2004). *Medetera* species seem to respond to the stage of tree decay and the intensity of bark beetle infestation, as indicated by the ratios of tree volatiles and/or prey pheromones (Hulcr et al. 2005). However, observations in Israel showed that, unlike many other predator species, *Medetera* adults were never found among insects captured in funnel traps baited with the aggregation pheromone of *O. erosus* or *I. typographus* (Mendel and Opatowski 1997). *Zabrachia minutissima* (Stratiomyidae) is the only small soldier fly associated with bark beetles. However, the larvae are mainly found under the bark of dead conifers but also on that of other tree families (Krivosheina and Rozkosny 1985).

Hemiptera

The major true bug guild associated with coniferous bark beetles belongs to the flower bugs of the genus *Scoloposcelis* Fieber, a small genus in the tribe Scolopini (Hemiptera: Heteroptera: Anthocoridae). Similarly to other flower bugs that prey on small arthropods, their predaceous habits have attracted the attention of researchers who work in forest ecosystems (Lattin 1999). The genus contains 12 species, distributed over the tropical and subtropical areas of the world. A few of them are known as predators of bark beetles (e.g., Péricart 1996). Important biological information about their association with pine bark beetles came from the study on

Scoloposcelis mississippensis, in southeastern USA (Schmitt and Goyer 1983a, b). *Scoloposcelis pulchella* occurs in the entire Palearctic region but North America. In the western Palearctic, it is found in several different climatic belts covering vast areas, in which several subspecies were described. The bugs arrive in the colonized trees almost simultaneously with the adult scolytids (Lattin 1999). *S. pulchella* is also captured in large numbers in traps baited with the aggregation pheromone of *O. erosus* or *I. typographus* (Dippel et al. 1997; Mendel and Opatowski 1997). The bug and its five nymphal stages prey on all immature stages of the bark beetle. *S. pulchella* is known to associate with many pine bark beetles (e.g., Péricart 1996) but in the Mediterranean basin it is mainly found with *O. erosus, T. destruens*, and *P. calcaratus*. Observations of the behavior of the bug in *P. halepensis* forests in Israel showed that the female bug arrived soon after the colonization process began (Mendel and Opatowski 1997). The adults feed first on scolytid eggs but later the nymphs and adults consume all development stages. In the absence of accessible scolytid prey they switch to feeding on other predators, such as larvae and pupae of *M. striata* and *A. ruficorne*, or on other associates such as early instars of the cerambycid *Arhopalus syriacus* and immature stages of the parasitoids (Mendel and Opatowski 1997).

Members of the flat bug family Aradidae have been reported from various habitats. Several species are associated with pines, some of them being pest species. However, the role of some species as bark beetle predators is questionable, as is that of snakeflies, *Raphidia* spp. (Raphidioptera: Raphidiidae), which inhabit the outer bark. In Israel *Raphidia syriaca* is mainly found on *Pinus halepensis* stems infested with *Matsucoccus josephi* (Halevy 1995). *Raphidia* larvae enter the scolytid galleries during emergence of the brood. *Raphidia ophiopsis* also occurs on outer bark pine stems, where it is ready to prey on any small insects and spiders (Aspöck 2002). The role of snakeflies as predators of scolytids is not clear.

6.5.5.3 Insect Parasitoids of Bark Beetles in Mediterranean Conifers

Most studies on parasitoids of bark beetles in the Mediterranean basin have been developed in the eastern part of the region, and inventories have been established in Israel (Halperin and Holzchuh 1984; Mendel 1986a). Parasitoid species of Mediterranean bark beetles can also be found in the general inventory by Karaman and Tezcan (2006).

As in other regions, the families Braconidae, Pteromalidae, Eupelmidae and Eurytomidae structure and more or less reflect this guild of natural enemies of bark beetles. As in the case of the predators, there are great similarities between the pictures of the complexes of parasitoid genera in the Mediterranean basin and in central and northern areas of Europe, and the pictures of the parallel complex of genera in North America (Bushing 1965; Herting 1973; Hedqvist 1998). The great majority of the species are ectoparasitoids on larvae and pupae of the scolytids (Dahlsten 1982), while a few are endoparasitoids. None of the endoparasitoid species were recorded from bark beetles of conifer trees in the Mediterranean basin (Table 6.7).

Whereas the endoparasitoids arrive at the bark-beetle hot spots during the colonization phase, ectoparasitoids reach their breeding sites when scolytid larvae already are to be found. Most bark beetle parasitoids oviposit through the bark and use various cues to detect the point of drilling (Mills et al. 1991). The outer bark thickness, mainly the rhytidome structure, which affects the proximity of bark beetle larvae and pupae to the surface, plays a major role in oviposition success (Ball and Dahlsten 1973). The advanced larval stages of bark beetles tend to direct their galleries towards the bark surface and thus making them more accessible to parasitization (Kruger and Mills 1990). Female wasps have been observed to be more numerous during host larval development whereas males were more abundant between the pupal stage and host emergence (Mendel 1986a). The females usually do not distinguish between scolytid species colonizing the same host tree, but borers other than scolytids are seldom attacked. Many parasitoid species may develop on hosts of a wide range of sizes, and this, in turn, reflects the relations between host and parasitoid sizes and parasitoid sex ratios. A wide range of host body lengths was found for most species; sex ratio was male biased when small host larvae were attacked (Mendel 1986b). A few species are known to enter the galleries of bark beetles to search for hosts. In addition to those attacking eggs, species of two genera are known for this behavior: *Cerocephala* on broadleaves and *Roptrocerus* mainly on conifers (Mendel 1986a, b).

Probably, all *Roptrocerus* species search within beetle galleries. Information on their associates is available for eight species among the 12 described congeners. They all occur in bark-beetle-infested conifers (Dahlsten 1982; Mills and Schlup 1989). *Roptrocerus xylophagorum* is the best known. It attacks at least 12 economically important species of bark beetles in North America and the west Palearctic region (Bushing 1965; Mendel 1986a; Mills and Schlup 1989). In the Mediterranean basin, it is mainly associated with *O. erosus* and *T. destruens*. *Roptrocerus brevicornis* is rather rare around the Mediterranean. *Israelius carthami* and *Scleroderma domesticus* (Bethylidae) are also found inside beetle galleries. In Israel, they are rarely found on small bark beetles developing on the high sections of pine stems and on side branches (Halperin and Holzchuh 1984; Mendel 1986a).

Among bark beetle parasitoids of conifer trees in the Mediterranean basin, the Braconids comprise four main genera – *Coeloides, Dendrosoter, Ecphylus*, and *Habrobracon* (Table 6.7) – of which the first two, *Dendrosoter* in particular, are more common. None of the congeners of any of these four is restricted to bark beetles on conifer trees; in fact, the *Ecphylus* species and *Habrobracon palpebrator* are probably more common on bark beetles of broadleaves. The three *Coeloides* species are rare in the Mediterranean. Among the five *Dendrosoter* species, four are restricted to bark beetles of Pinaceae, whereas *D. protuberans* is usually associated with *Phloeosinus* spp. on *Cupressus* or on bark beetles of broadleaves (Table 6.7). In most investigated species of bark beetle parasitoids, females are larger than males. However, the males of *Dendrosoter* spp. are on average significantly bigger than the females and in these cases, the sex ratio is close to 1:1 (Mendel 1986a). This phenomenon could be explained by the courtship behavior of those insects. Indeed, the adult males of *D. caenopachoides* and *D. protuberans* form dense aggregates on certain spots on the bark where a female is expected to emerge (Mendel 1986a), which makes them to compete for the emerging female, and one may assume that the larger males have the upper hand in this struggle.

Among the three main families of Chalcidoidea containing parasitoids of Mediterranean bark beetles, the Pteromalidae has the largest number of species (Table 6.7). The most dominant species in this family are *Metacolus unifasciatus* and *Heydenia pretiosa*, both found in high numbers with pine and cypress bark beetles, these latter attacking also scolytid of broadleaved trees (Mendel 1986a, b).

Table 6.7 Bark beetle parasitoids associated with bark beetle of conifer trees in the Mediterranean

Family	Species	Bark beetle host[a]		
		on *Pinus* or *Cedrus*	on *Cupressus*	on broadleaves
Bethylidae	*Israelius carthami* Richards	2, 20		
	Scleroderma domesticus Klog	20		26, 28,29
Braconidae	*Coeloides abdominalis* (Zetterstedt)	32		[b]?
	C. bostrichorum Giraud	22, 32		
	C. sordidator (Ratzeburg)	32[b]		
	Dendrosoter caenopachoides Ruschka	1,2, 14, 20, 31		
	D. flaviventris Foerster	14, 30		
	D. hartigii Ratzeburg	1,2, 14, 20, 32		
	D. middendorffii Ratzeburg	8, 14, 20, 31, 32		
	D. protuberans Nees	13, 32	16, 17	4, 18, 26,28
	Ecphylus hylesini (Ratzeburg)	32		[b]
	Habrobracon palpebrator (Ratzeburg)	32		[b]
Eupelmidae[c]	*Calosota vernalis* Curtis	29		
	C. aestivalis Curtis	14, 20	16, 17	3
	Eupelmus sp. near *urozonus*		16, 17	
Eurytomidae[c]	*Eurytoma arctica* Thomson	32		[b]
	E. blastophagi Hedqvist	32		
	E. morio Bohemann	5,11, 14, 20, 27, 31, 32	16, 17	1, 18, 26, 29

(continued)

Table 6.7 (continued)

Family	Species	Bark beetle host[a]		
		on *Pinus* or *Cedrus*	on *Cupressus*	on broadleaves
Pteromalidae[c]	*Dinotiscus colon* (Linnaeus)	32		18, 26, 28, 29
	Heydenia pretiosa Foerster	1, 2, 4, 8, 14, 31, 32	16, 17	9, 18, 26
	Metacolus azureas Ratzeburg	1, 5, 14, 19, 20, 32		
	M. unifasciatus Foerster	1, 2, 4, 8, 14, 31, 32	16, 17	26
	Macromesus africanus Ghesquière	30		
	Rhaphitelus maculatus	31	16, 17	4, 9, 18, 28
	Rhopalicus quadratus (Ratzeburg)	32	17	
	R. tutela (Walker)	32		?
	Roptrocerus brevicornis Thomson	32		
	R. xylophagorum Ratzeburg	1, 8, 14, 20, 31		9

Associations with broadleaved trees are indicated when they come in addition to associations with conifers

[a] See foot note in Table 6.6

[b] Occurring on broadleaves or hosts other than bark beetles, but not in the Mediterranean

[c] Important information about host range is based on Noyes (2015)

The genus *Rhaphitelus* is present in the area with three species, two (*R. ladenbergii* and *R. maculatus*) occurring on pine bark beetles, but only the latter species is known from bark beetle of conifers in the Mediterranean (Halperin and Holzchuh 1984; Karaman and Tezcan 2006). *Macromesus africanus* is one of the few species reared from cedar bark beetle *S. numidicus* in North Africa (Noyes 2015). *E. morio* is the most common Eurytomidae in the Mediterranean basin (Table 6.7). This species displays wide ranges of hosts and habitats, and may lay its eggs on scolytid larvae that had been previously parasitized by other species (Mendel 1985b). Experiments compared the parasitoid fauna emerging from *P. halepensis* stem sections colonized by *O. erosus* and submitted or not to deep-freezing treatment, before being exposed to natural parasitization. Only *E. morio* emerged from the treated logs, whereas Braconids and Pteromalids were largely dominant in emergence from untreated logs, suggesting that the set of cues used by *E. morio* to locate its beetle hosts differ from that used by species belonging to the other two families (Mendel 1985b).

6.5.6 Vertebrates

Aside of associated organisms living, at least part of their life cycle, in the beetle galleries, vertebrates and especially birds of the Picidae family can interfere in the survival of bark beetles (Kenis et al. 2004; Wegensteiner et al. 2015). Impacts on bark beetle survival result from direct consumption by the woodpecker and from bark removal exposing brood to desiccation or predation. There is only one study dealing with predation by birds on bark beetles in the Mediterranean basin. It reports on effects of the Syrian woodpecker *Picoides syriacus* Hemprich and Ehrenberg on *O. erosus* in *P. brutia*, *P. calcaratus* and *T. destruens* in pines and *P. armatus* in *C. sempervirens* in Israel (Halperin and Holzchuh 1984; Mendel 1985a). In the case of *O. erosus*, depending on trees, the woodpecker-peeled bark area ranged from 5.2 % to 80.4 % (average 60 %) of the total beetle-infested bark area.

6.6 Population Dynamics

6.6.1 Principles of Population Dynamics and Mediterranean Bark Beetle Species

All European bark beetle species attacking living trees (except *Dendroctonus micans* Kug, see below) can basically be considered as “weakness pests”. Indeed, it has been known for a long time that attacks on living trees by bark beetle endemic populations can succeed only on trees that have already been weakened by some other factor, biotic or abiotic. Only epidemic populations can succeed in establishing on healthy vigorous trees. From these considerations, come the notions of tree resistance and population threshold. In a forest, there is a continuum of tree resistance levels, from already dead trees will null resistance on which even individual attacks succeed, to healthy vigorous trees with very high resistance level on which very high attack densities (epidemic populations) are necessary to allow beetle establishment and progeny production.

6.6.1.1 Tree Resistance

In all cases (except *D. micans*), beetle colonization success means tree death. Tree resistance level is thus the key factor in bark beetle population dynamics. It can be defined as the critical density threshold above which trees succumb the attack (Thalenhorst 1958; Berryman 1976; Raffa and Berryman 1983; Christiansen et al. 1987; Paine et al. 1997; Lieutier 2004; Lieutier et al. 2009). Hence, successful colonization is the outcome of an interaction between two major factors, tree resistance and beetle density. In the latent phase, beetle population level is low and its attack density stays below the critical threshold of healthy trees. The beetle population thus establishes and survives on dying trees or recently cut or and broken ones. In case such breeding material proliferates, the beetle population increases in size and can become sufficiently high to overcome the resistance of healthy trees. Thus, the population shifts from a latent to an outbreak phase (Berryman 1982). The level of that threshold depends on tree's species and vigor and on the aggressiveness of the bark beetle species (Berryman 1976; Raffa and Berryman 1983; Christiansen et al. 1987; Paine et al. 1997; Lieutier 2004).

The mechanisms involved in tree resistance are very diverse. They include physical structures and chemical properties, classically separated in two types: the mechanisms pre-existing in trees before beetle attacks (passive defense mechanisms), and those built by trees in response to beetle attacks (active defense mechanisms). Both interact jointly, but mechanisms induced by beetle attack often play a decisive role. Since the pioneer paper by Berryman (1972), there has been a large amount of studies dealing with the functioning of conifer defense mechanisms against bark beetles, synthesized by Lieutier (2002, 2004) and Krokene (2015). We send the reader to these syntheses for details.

6.6.1.2 Bark Beetle Attack Strategies

When attacking live trees, bark beetles are facing tree resistance. Together, conifer defense mechanisms are generally very efficient in protecting trees, and various strategies have evolved in beetle species to cope with them. It has been proposed to recognize two opposed strategies in conifer bark beetles attacking living trees: the strategy of overcoming host resistance (or exhausting tree defenses) and that of avoiding tree defenses (Lieutier 1992, 2002).

The strategy of exhausting tree defenses refers typically to the existence of a critical threshold of attack density as defined above. This threshold would be the maximum number of attacks that a tree is able to stop, owing to its capacity to rapidly synthesize sufficient quantities of defensive compounds at each site of aggression (Safranyik et al. 1975; Berryman 1976; Raffa and Berryman 1983; Christiansen et al. 1987). The strategy of the beetle population would thus be to rapidly stimulate the synthesis of defensive compounds by the tree until defense exhaustion, resulting in a weakened tree unable anymore to defend itself efficiently, and finally leading to beetle population establishment and tree death. Everything that stimulates the tree's energy expenditure would thus be favorable to that strategy (Lieutier 2004; Lieutier et al. 2009). This would be the role of the aggregation pheromones, stimulating mass attacks and resulting in multiplying the penetration points (Berryman 1972, 1976; Raffa and Berryman 1983; Wood 1982). Association with Ophiostomatoid fungi would also be a considerable benefit for the beetle population, through ability of the fungi to stimulate the tree's defensive hypersensitive reactions at the places where they have been introduced into the tree by the beetles. This indeed would increase the energy the tree needs to invest and would finally result in significantly lowering the critical threshold of attack density (Lieutier 2004; Lieutier et al. 2009). Longitudinal maternal galleries and attacks during the period of tree activity would be complementary factors contributing in stimulation of tree defenses. In this strategy, adopted by most bark beetle species attacking living conifers, tree death would be unavoidable as a result of defense exhaustion (Lieutier 2002; Lieutier et al. 2009).

In the other strategy, everything would be done to avoid stimulating tree defenses. The beetle would behave individually and would not need aggregation pheromone. No association would either be developed with ophiostomatoid fungi, and transversal galleries would be preferred because less stimulating of mechanisms of induced resistance. In such a strategy, since tree defenses are avoided and not exhausted, trees could be attacked successfully without being killed, making bark beetles to be considered as true parasites (Lieutier 2002, 2004). Few bark beetle species attacking conifer trees seem to use the latter strategy, among them only *D. micans* in Europe.

6.6.1.3 The Case of the Mediterranean Bark Beetles

All Mediterranean bark beetle species attacking living trees very likely fit in with the defense exhaustion strategy. When looked for, the presence of aggregation pheromones has been evidenced and the related compounds identified. These are the cases for *O. erosus*, *Pityokteines curvidens*, *P. spinidens*, *P. vorontzowi*, *Pityophthorus pityographus*, *P. pubescens*, *Pityogenes bidentatus*, *P. calcaratus*, *I. acuminatus*, *I. sexdentatus* (www.pherobase.com). In other cases, compounds susceptible to play such a role have been evidenced, as for *Phloeosinus armatus*, *O. erosus*, *H. ligniperda*, *H. micklizi*, and *C. cinereus*. An exception concerns *T. destruens* which has been demonstrated not to have aggregation pheromones (Faccoli et al. 2008; Gallego et al. 2008), a situation common to all species of the genus *Tomicus* (Lieutier et al. 2015), but terpenes emitted by the tree through the wounds made by the pioneer beetles are strong attractants for their conspecifics. Moreover, all Mediterranean bark beetle species that have been investigated for fungi have revealed associations with ophiostomatoid fungi (Table 6.3). The capacity of these fungal species to stimulate the tree's induced defenses during insect attacks has been proved when tested (Sect. 6.5.2). An exception however concerns *L. wingfieldii*. Its isolates from *T. destruens* appear unable to stimulate the tree's defense when introduced into *P. pinaster* by the insect, although it does when artificially introduced (Lieutier et al. 2005). Similar observations have been made with isolates from *T. piniperda* tested on *P. sylvestris*, which has been tentatively explained by too low a number of spores introduced into the tree by the beetle, contrary to an artificial inoculation (Lieutier et al. 1989a, 1995). Certainly thus, as for *T. piniperda* in Scots pine, exhaustion of host tree defenses leading to establishment of *T. destruens* in *P. pinaster* is obtained through aggregation due to terpenes and stimulation of tree's defense by the sole mechanical stress due to beetle's boring activity (Lieutier et al. 1995, 2005).

The critical threshold of attack density of the Mediterranean bark beetles has never been directly evaluated. In Algeria *P. halepensis* killed by *T. destruens* supported averaged density of 178 attacks/m^2 on northern slope and 137 attacks/m^2 on southern slope (Chakali 2007), allowing to estimate the critical threshold at a slightly lower density (Lieutier et al. 2015). This is a very low level, especially for a beetle which overcomes tree defenses without the help of a fungus. These values indeed appear comparable to those obtained with very aggressive beetle species helped by a fungus, such as *I. typographus* L. (200–400 attacks/m^2) on *Picea excelsa* Karlsten in Europe (Mulock and Christiansen 1986) or *D. ponderosae* Hopkins (50–120 attacks/m^2) on *Pinus contorta* Dougl. in North America (Waring and Pitman 1980; Raffa and Berryman 1983). *T. destruens* attacks were however recorded on trees in difficult environmental situations (Chakali 2007), which was not the case for *I. typographus* and *D. ponderosae*.

6.6.2 Factors Involved in Population Dynamics

The factors involved in population dynamics of the Mediterranean bark beetles are the same as for any bark beetle population, but sometimes exacerbated by the particularities of the Mediterranean ecosystems. Much less information about these factors is however available for the Mediterranean bark beetles than for their temperate and boreal counterparts. We below present these factors in three parts: (1) Beetle fecundity and brood productivity; (2) Density dependent factors (intra- and inter-specific competition and natural enemies); (3) Density independent factors, affecting beetle populations directly or indirectly through modifying tree's resistance level.

6.6.2.1 Fecundity and Brood Productivity

Fecundity plays a basic role in population dynamics because it is the only factor that directly affects population increase positively. Brood productivity of a generation is the number of ovipositing daughter females per parent female. However, many bark beetle species have several generations per year and several sister broods per generation. The productivity of a given true generation should thus be calculated by summing the number of ovipositing daughter females of all sister broods and then to divide the result by the number of parent females of the first oviposition period. The annual productivity therefore should then be obtained by multiplying the productivity of all successive true generations. However, separate the first reproduction cycle of a given female from her second brood generation is usually impossible especially in the Mediterranean area where many species have several sister broods and generations overlapping each other's. Practically in the field, fecundity is often measured and brood productivity calculated for generations defined by their date of oviposition, knowing that generation and sister broods may occur on the same breeding part of the bark, except for the first generation. The situation is even more complicated for monogamous species of which adult maturation takes place in shoots of trees and makes thus impossible an evaluation of the ovipositing daughter females. In such cases, immature daughter females emerging from bark are used instead of ovipositing daughter females. Comparing field data of a given species with its fecundity and brood productivity measured under optimal laboratory conditions, may allow evaluating the impact of the major regulating factors.

All multivoltine species such as *O. erosus* or *P. calcaratus,* which carry out several annual generations with few sister broods have a high potential of annual productivity and manifest a rapid build-up of high populations. However, the theoretical rate of annual population increase has never been calculated for these species. In fact, among all Mediterranean bark beetle species, theoretical and field brood productivities were calculated only for *T. destruens,* a typical univoltine and monogamous species. Under optimal conditions, free of major limiting factors, figures for laboratory rearing of *T. destruens* on *P. halepensis* displayed an average fecundity of 90.6 eggs per female and a brood productivity of 30 immature females per parent female for the annual generation (sister broods excluded) (Faccoli 2007). In the same optimal conditions, average fecundity was about 55 eggs per female in both *P. pinea* and *P. pinaster* and brood productivity about 16 immature females per parent female in *P. pinea* and 12.5 immature females per parent female in *P. pinaster*. In a *P. halepensis* stand of southeastern France, a population of *T. destruens* had an averaged fecundity of 60.2 eggs per female (Durand-Gillmann 2014) and, based on provided data, it has been calculated that brood productivity was 19 immature females per parent female (Lieutier et al. 2015).

In all other species, only estimations on fecundity of certain generations are available. On *P. halepensis* and *P. brutia* trap trees in Israel, average egg gallery length of *O. erosus* varied from 35 to 71 mm depending on gallery density (Mendel and Halperin 1982) which, based on the extreme values given for field egg densities should correspond to extreme fecundity values of 17–77 eggs per female. In Tunisia, *P. bicolor* is bivoltine and three sister broods follow the first annual generation with 75 %, 50 % and 50 % of the parent beetles leaving the gallery system to establish a new sister generation (Belhabib et al. 2007). Field average fecundity in *C. sempervirens* logs has been evaluated at 9.8 to 11.1–13.5 eggs per female for the first annual generation, depending on logs and year, while the cumulative fecundity (first generation + three sister broods) averaged 54 eggs per female (Belhabib et al. 2007, 2009). In *C. arizonica* logs however, field fecundity of the first annual generation has been 19.4–19.5 eggs per female (Belhabib et al. 2009). In *C. sempervirens* unpruned trap trees in Israel, fecundity of the first annual generation of *P. bicolor* has been 27 eggs per female, whereas that of *P. armatus* has been 49 eggs per female (Mendel 1984).

6.6.2.2 Density Dependent Regulating Factors

Intraspecific Competition It is a powerful regulating factor which interferes mainly during larval development. High larval densities are indeed a direct consequence of mass attacks needed for overcoming tree resistance. Theoretical models have been proposed to define a maximum brood productivity resulting from a compromise between increasing attack density necessary to overcome host resistance and minimizing resulting larval competition (Raffa and Berryman 1983). Species with high critical attack density thresholds are particularly exposed to larval intraspecific competition, except when they attack much weakened trees of which the attack density threshold is very low. In that respect, by decreasing the level of this threshold, associations with fungi able to stimulate tree's defenses help in moderating larval competition. In monogamous species, competition could also occur during shoot maturation feeding, but this has never been investigated and the competition impact during this period is certainly limited. Larval intraspecific competition can drastically affect brood productivity through reductions of larval and pupal survival and brood quality.

In Mediterranean bark beetles, such effects have been reported only for *T. destruens*, in the field on *P. halepensis* (Chakali 2007) and in laboratory rearing on logs of *P. pinea* (Faccoli 2009). In laboratory, it has been shown that competition affecting all immature stages resulted in dramatically decrease of brood productivity. However, negative effects on brood productivity occurred only above certain attack density threshold estimated at 50–75 female/m^2, whereas increasing female density had positive effects on brood productivity below that threshold (Faccoli 2009 and Fig. 6.4). A reduction of the fecundity of the parent beetles caused by intraspecific competition has also been reported in the case of *T. destruens* (Chakali 2007; Faccoli 2009), which can certainly be explained by a higher rate of re-emergence of the parent beetles, as demonstrated for *T. piniperda* (Sauvard 1989). Similar observations have been made on *P. bicolor* in *C. sempervirens* logs in the field, where female immediate fecundity decreased by one third between 200 and 1700 attacks/m^2 (Belhabib et al. 2007). In *O. erosus* as in most bark beetles species, correlation exists between length of larval galleries and fecundity. During attacks on logs of *P. brutia* and *P. halepensis*, it has been reported that the correlation was lower for high (418 galleries/m^2) than for low (255 galleries/m^2) attack densities (Mendel and Halperin 1982), possibly a consequence of reduction in female fecundity under high densities. In such cases, a decrease in immediate fecundity may however be compensated by increased fecundity in sister broods, possibly finally resulting in few modifications in annual brood productivity.

Interspecific Competition Competition among bark beetle species is generally very limited because of spatial, temporal or trophic segregation. In Israel, *T. destruens*, *H. micklitzi*, *H. linearis*, *O. erosus*, *P. calcaratus*, *C. minimus* and *C. mediterraneus* all develop on *P. halepensis* in the same localities and sometimes on the same trees (Mendel et al. 1985). However, the first three species (univoltine) breed only during winter and early spring in the lower section of trees, with *H. micklitzi*, *H. linearis* tending to infest roots, whereas the other four species (multivoltine) breed from spring to autumn, with *O. erosus* in the thick bark section of trees, *P. calcaratus* in thin bark section, *C. minimus* in the top stem. Only *C. mediterraneus* living inside galleries of the other species may be a competitor, although it probably rather behaves as a commensal. Comparable resource partitioning in time, space and food preferences has been reported in Spain with *P. bidentatus*, *O. erosus*,

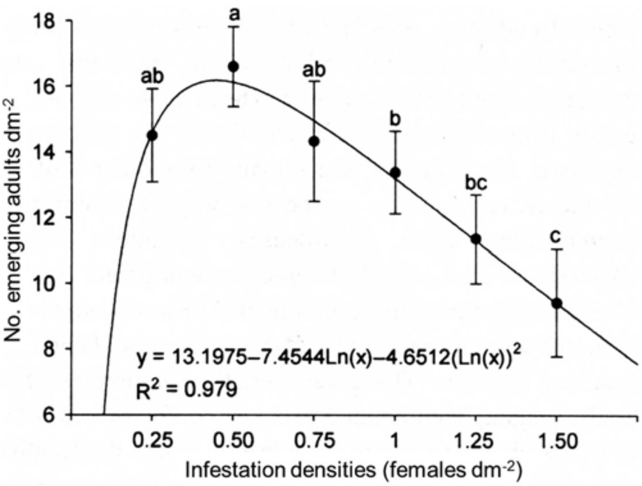

Fig. 6.4 Number (mean ± SEM) of emerging immature adults of *Tomicus destruens* per dm^2 of bark in relation to different infestation densities of females (No/dm^2 of bark). Significant differences among densities of immature adults are indicated by different letters (From Faccoli (2009), with permission by "John Wiley and Sons" (CCA licence 3627200646873))

I. sexdentatus and *T. piniperda* in *P. sylvestris* and *P. radiata* (Amezaga and Rodríguez 1998).

Natural Enemies There is a high diversity of natural enemies of Mediterranean bark beetles (Sect. 6.5) and very likely, acting complementarily, they play in significant role in bark beetle population dynamics, as their counterparts do in temperate and boreal forest ecosystems (Kenis et al. 2004; Wegensteiner 2004; Wegensteiner et al. 2015). However, their impact at the population level is very difficult to quantify for different reasons. Data on pathogenic organisms are scarce, those on nematodes are largely incomplete (Sect. 6.5 and Table 6.4), and the predatory action of mites on bark beetles is uncertain in most cases (Table 6.5). More information is available regarding predatory insects and parasitoids. However, it mainly focuses on inventories and description of biology, without reliable information on impact on bark beetle populations (Sect. 6.5.5). Impact of predators on population dynamics is difficult to appreciate because they are most often polyphagous, leading the different species to sometimes predate upon each other's and even to suffer from cannibalism (Mendel et al. 1990). They also often suffer from competition with parasitoids.

Information on effects of parasitoids on beetle performances mainly relates to particular circumstances and localities, making estimations of their effect on populations speculative. Especially, no study using time series and life tables or enemy exclusion experiments has been carried out for the Mediterranean bark beetles. We are thus far from being able to evaluate the overall effect of these natural enemies on the population dynamics of bark beetles in the Mediterranean basin. Some remarkable local impact can only be mentioned. Based on field observations, Mendel (1984) indicated that more than 95 % of *P. armatus* and *P. bicolor* larvae might be destroyed by hymenopterous parasites in some plantations of *C. sempervirens* in Israel. In some localities of the same country, in absence of competition with parasitoids, *A. ruficorne* populations could predate up to 90 % of the immature stages of *O. erosus* during spring and late summer (Podoler et al. 1990). Predators and parasitoids could in addition be involved in limiting bark beetles outbreak after thinning (Mendel and Opatowski 1997, and see below).

6.6.2.3 Density Independent Factors

Tree Genetics

Genetic constitution of trees interferes very significantly in tree resistance, with consequences on attack success and performances of bark beetles. Most bark beetle species attack several tree species belonging to the same genus and their performances can vary in large proportions among host species. Examples have been given above (Sect. 6.6.2.1) with *P. bicolor* on *C. sempervirens* and *C. arizonica* (Belhabib et al. 2009) and *T. destruens* on *P. halepensis*, *P. pinea* and *P. pinaster* (Faccoli 2007) These variations can have important consequences for the dynamics of the local populations. Even among the same tree species, tree resistance level and defense parameters can largely vary from one tree to another, as shown by artificial inoculations of bark beetle associated fungi in *P. pinaster*, *P. halepensis* and *P. brutia* (Lieutier et al. 2005; Ben Jamâa et al. 2007).

Temperature

Temperature plays a major role in insect survival and development. In winter, the climate typical of the Mediterranean forests does not pose a serious risk for bark beetle survival and several species such as *T. destruens* can even develop during winter. Winter temperature can become very low only in high elevations, but bark beetles in general are rather resistant to such conditions, especially because they overwinter under the bark or in the litter. Winter temperatures are thus not an obstacle for Mediterranean bark beetles. Summer temperatures can reach very high values sometimes not compatible with eggs and larvae survival, leading summer attacks to concentrate on the lower face of fallen trees but many species are well adapted to high temperature, as reported for *O. erosus* (Mendel and Halperin 1982) and *T. destruens* (Horn et al. 2014).

Temperature also affects the developmental possibilities, directly interfering in population dynamics. A certain temperature threshold must be exceeded for the development to occur and, above this threshold each species requires a certain thermal sum to complete its development. The duration of the development from eggs to adults thus decreases when temperature increases, resulting in an increase of the number of annual generations for the multivoltine species, with positive consequence for annual productivity. Knowing both temperature thresholds and degree-days sums for a complete development allows predicting the number of annual generations in a given locality. If fecundity is also known, the theoretical rate of annual population increase can also be predicted. However, it does not seem that the thermal parameters are known for any of the Mediterranean bark beetle species, although the duration of the development of *O. erosus* has been quantified under various rearing temperatures (Mendel and Halperin 1982).

Flight also depends on temperature, which thus conditions the possibilities of dispersal. Minimum temperatures for flight are for example 17–18 °C for *O. erosus*, 16–17 °C for *P. calcaratus*, 13–14 °C for *H. micklitzi*, and 12 °C for *T. destruens* (Ghaioule et al. 1998; Faccoli et al. 2005). In order to avoid flight during unfavorable high temperature, *O. erosus* and *P. calcaratus* similarly change their diurnal flight patterns according to the season. By using funnel traps baited synthetic aggregation pheromone, it was found that in winter, flight occurred only during daylight and peaked at noon (18 °C). In spring, flight started when the temperature reached 15 °C with two peaks, one in the late morning (20 °C) and the other in the early evening (22–23 °C). In summer, two distinct daily flight periods were recorded: the first peaked in the early morning and the second soon after dusk. The bimodal flight pattern of both species in the warm season reflects hours of optimal flight conditions (Mendel et al. 1991).

Quantity of Breeding Material and Tree Weakness

As for all bark beetles, the most important factor of population increase of Mediterranean bark beetles is the quantity of suitable breeding material. By providing large quantities of highly suitable breeding material, storms, sudden severe droughts, extensive thinning operations, fire, application of herbicides, may become major abiotic factors of bark beetle population dynamics, often responsible for the initiation of outbreaks. Availability of such breeding material may in turn allow the population to increase during one or two generations. Furthermore, at the latent phase, the natural enemy populations often kept at extremely low levels as well. This rapid increase will make the beetle populations able to reach the critical attack density threshold and possibly the colonization of healthy trees. The effect of the above mentioned forces on tree resistance is however an extreme scenario of a general phenomenon. In fact, any abiotic or biotic factor susceptible to weaken trees, *i.e.* to lower their critical attack density threshold, is favorable to bark beetle population increase. The available breeding material for bark beetles indeed consists in trees of which the critical threshold of attack density is sufficiently low to allow establishment of the local beetle populations.

Factors of Tree Weakness

Water Stress Causes for trees weakness are very diverse. Even when trees are adapted to the local climatic conditions, intense water stress is an important weakness factor which can condition the success of reproductive attacks in stem or branches of living trees in the Mediterranean basin, and several papers have reported bark beetle damage as consequences of droughts. In Greece, the severe 1988 drought was followed in 1989 by considerable bark beetle damage in fir forests (Markalas 1992). In Croatia, the extreme droughts of the 2001–2003 period favored mass reproduction of several bark beetles species, among which *P. curvidens*, *P. spinidens*, *P. vorontzowi*, and *C. piceae*, which reached very high population levels and caused considerable damage in fir forests in 2005 (Matosevic et al. 2007). Possibly the repeated summer droughts of the Mediterranean climate may explain the heavy damages caused by *T. destruens* in the Mediterranean basin, whereas the temperate European *Tomicus* species never cause extended damage.

Drought however does not necessarily induce bark beetle damage. Indeed, water stress can have opposite effect on tree resistance depending on its intensity. Experimental isolated and mass inoculations of bark beetle associated fungi to potted *P. sylvestris* have indeed demonstrated that tree's defense mechanisms were more efficient and tree resistance higher in trees submitted to mild water stress (predawn needle water potential Ψ_{wp} above – 1.8 MPa at its minimum) than in unstressed trees (Croisé and Lieutier 1993; Dreyer et al. 2002). However, young *P. sylvestris* submitted to several cycles of intense stress (Ψ_{wp} below – 2 MPa) were less resistant to mass inoculations than control trees (Croisé et al. 2001). In the field, *Pinus yunnanensis* was also more resistant to mass inoculations in plots naturally experiencing mild water stress (Ψ_{wp} above – 1 MPa) than in unstressed plots (Sallé et al. 2008). Concerning *T. destruens*, water stress can also affect beetle choice and performances during shoot feeding, young unstressed *P. pinaster* being preferred and allowing better survival than stressed ones (Branco et al. 2010). However, literature most often report on drought followed by bark beetle damage rather than on drought without damage, which explains the lack of natural field observations on the role of water stress level. Nevertheless, Kailides (1985) for the period 1960–1983, mentioned that in Greek forests three drought episodes were followed by bark beetle outbreaks, which were not observed in four other similar cases.

Fires They are also an important tree weakening factor in the Mediterranean basin which, by altering tree defenses mechanisms, favors rapid beetle establishment and population increase on still alive (even severely) scorched trees. Such events are rather common after fire and several examples have already been given for Portugal, Spain and Greece (Sect. 6.3). However, population increase on fire scorched trees does not necessarily lead to an outbreak situation. For population to increase to an outbreak situation, three conditions seem needing to be filled jointly: attack initiation before trees defense recover to allow easy and rapid attack success, presence of enough still undamaged phloem for larval development, rarity of natural enemies for not compromising high brood productivity (Lombardero and Ayres 2011).

Fig. 6.5 (**a**) Attack of *Pinus brutia* by *Orthotomicus erosus* after a thinning operation; (**b**) *Pinus halepensis* killed by *Orthotomicus erosus*; (**c**) *Abies alba* killed by *Pityokteines vorontzowi*; (**d**) Gallery systems of *P. calcaratus* in the bark of a killed pine; (**e**) Heavy maturation feeding of *Phloeosinus armatus* on shoots of *Cupressus sempervirens* (**a**, **b**, **d**, **e**: photos Z. Mendel; **c**: photo F. Lieutier)

Silvicultural Methods They may also in some condition favor bark beetle population increase. This is especially the case of thinning. Thinning is normally performed to increase the economic value of the residual crop and, if performed properly, makes the stand more vigorous and less susceptible to insect pests (Nebeker and Hodges 1983). However, the stand soon after the thinning may undergo “thinning stress” (Harrington and Heukema 1983). In Israel, 10–30-year-old *P. halepensis* and *P. brutia* experienced severe outbreaks of *O. erosus* and *P. calcaratus* in the end of the summer and of *T. destruens* in early winter after thinning operation (Mendel et al. 1992 and Fig. 6.5a). Tree mortality was much greater when thinning was performed in the warm season (April–September) than in the cool season (October–March). However, this possible consequence of thinning can be modulated by natural enemies. Studies carried out in Israeli pine forests showed that the number of insect predators was higher in thinned stands than in the non-thinned ones and parasitoids experienced a quick recovering after an immediate mortality (Mendel and Opatowski 1997). In areas with continuous thinning activity, the density of the natural enemies in the adjacent plots would be high and they would quickly move into the new thinned plots, a situation which in turn could create high natural enemies/prey ratios and cause the extinguishing of the outbreak in an early stage. However, while adult predators may find refuge inside in the bark beetle colonized bark, the adult parasitoids usually emerged from trees as soon as they complete their development, making necessary for them to find food in order to exploit their full potential reproduction (Mendel and Opatowski 1997).

Biotic Aggressions Trees weakening leading to bark beetle infestations can be caused by biotic aggressions on initially healthy trees. In the Mediterranean basin, a famous example is that of *P. pinaster* succumbing to *T. destruens* and *O. erosus* attacks after invasion by the pine bast scale *Matsucoccus feytaudi* Duc. in southeastern France in the 1970s (Carle 1974a). A similar scenario has occurred in Israel since the 1940s, with deadly attacks of *P. calcaratus* in *P. halepensis* following outbreak of *Matsucoccus josephi* Bod. & Harpaz (Bodenheimer and Neumark 1955; Mendel 1988). Infestations of *C. sempervirens* by the phytopathogenic fungus *S. cardinale* have been reported to favor attacks by *P. armatus* and *P. bicolor* (Mendel et al. 1983).

6.7 Ecological and Economic Importance

6.7.1 Tree Colonisation and Mortality

Bark beetles usually infest the host plants by a sudden and massive attack, having devastating effects on tree vitality. Although, the attacked plants may initially show no specific symptoms, within a few weeks the canopy of the trees infested in spring and early summer turn yellow, then reddish and finally dries up completely (Fig. 6.5b, c). In conifers, a considerable fall of green needles can also be observed. With attacks carried out in late summer by second or third generations (e.g., *O. erosus* or *Pityogenes calcaratus*) or in autumn by winter developing species (e.g., *T. destruens*), the infested trees often keep green foliage throughout the autumn and winter, making the canopy symptoms to start only from the following spring. In these cases, the attack is often discovered months later because absence of symptoms on the canopy does not allow a prompt identification of the infested trees. However, infested plants die within a few months. The excavation of egg and larval galleries irreparably compromises the functionality of the bark tissues (cambium and phloem), which dry out and die in a few months. Large bark portions detach from the stem and fall down on the litter, because engraved internally by a complex set of galleries of various types (Fig. 6.5d), and punctuated externally by thousands of small circular holes bored by adults during bark colonization and then emergence. With infestations still in progress, tree debarking allows to check for the presence of larvae and adults boring in the phloem. While with completed infestation, i.e. after the emergence of adults of the new generation, only the tunnels bored during the previous months by adults and larvae of bark beetle species will remain visible under the bark. In this case, the subcortical symptoms can be however difficult to analyse due to the high colonization density, the confused net of maternal and larval galleries, the significant amount of sawdust present under the bark and the progressive bark decay. In many bark beetle species, nevertheless, the maternal galleries can remain visible and recognizable for years because partly engraved on the sapwood (Faccoli 2015). Mortality of the infested trees follows exhaustion of tree defenses by associated ophiostomatoid fungal species (Table 6.3) and beetle boring activity, and is probably caused by the conjunction of several factors involving various fungal species (Lieutier et al. 2009, and Sect. 6.6.1.2).

6.7.2 Ecological and Economic Consequence of Bark Beetle Infestations

Bark beetles differ in their ecological and economic importance. Scolytids are continuously killing a large number of trees which become available to a rich fauna of saproxylic organisms that live in dead wood. From an ecological point of view, bark beetles are therefore a crucial component of the forest ecosystems: they begin and speed up wood degradation – tissue otherwise difficult to decompose – making accessible substances not easily reached by other arthropod guilds. They infest and kill weakened trees, selecting genotypes not adapted to that specific site or stressed individual trees; they initiate long and complex food chains reaching also vertebrates; they create favorable microenvironments for a rich saproxylic fauna, contributing significantly to increase the biodiversity and, hence, the forest stability. Nevertheless, although relatively few in number, tree-killing bark beetles can have profound ecological effects, including impacts on species composition, tree age and stand structure, forest density, and woody debris inputs (Lindgren and Raffa 2013).

As the majority of bark beetle species breed in dead or dying tissues, they are not always considered of economic importance. Nevertheless, bark beetles are among the most important forest pests causing serious economic damage to forests and wood. Bark beetles are often responsible for extensive damage both directly, through death of plants, and indirectly through the economic reduction of timber quality as a result of wood discoloration due to symbiotic *blue*-staining fungi. Moreover, some species can become economically important when they transport pathogenic fungi to living trees, during feedings periods that young adults of some species carry out in shoots and twigs to mature their gonads. This is the case for instance for *Phloeosinus* spp. on cypress (Tiberi and Battisti 1998; Pennacchio et al. 2013). The adults of a relatively small number of species also feed on saplings or seedlings to reach sexual maturity (e.g., *Hylastes* and *Hylurgus*). Thus, scolytids may be responsible for major economic losses, causing damage estimated in millions of euros (Knížek and Beaver 2004). Such losses may occur in Mediterranean zones especially in conifer monocultures and plantations. A peculiar type of damage is the plant growth loss due to shoot damage caused by the maturation feeding of monogamous species, such as *Ph. armatus* on Cypress (Fig. 6.5e) or *T. destruens* on Mediterranean pines. Immature adults remain in the pine crowns for many months, feeding on shoots to reach sexual maturation. Shoot feeding may affect 13–16 % of the most vigorous shoots (Sabbatini-Peverieri et al. 2008; Lieutier et al. 2015). Finally, in case of trees suffering from adverse abiotic conditions (fire, drought, heat-wave) or weakened by non-lethal colonization of secondary pests (mainly defoliators), the most aggressive species (e.g., *Tomicus destruens*, *Orthotomicus erosus*, *Cryphalus* spp.) may show a rapid population increase which can bring to large outbreaks (Sect. 6.6). The sudden death of hundreds of trees may occur within a few weeks. In case of large infestations, the production of a huge number of new adults and simultaneous scarcity of susceptible trees – since all have been infested by previous generations – also determine the colonization of healthy and vigorous trees that would normally not be attacked. By this mechanism, the outbreaks – which always begin with plant-weakening events – may self-sustain and last for several years.

Besides the more strictly technological damage caused to wood and timber, the death and destruction of vast forested areas following bark beetle outbreaks have serious repercussions on forest characteristics and landscape and their management. For instance, high tree mortality could result in increased soil erosion, especially in sand dunes exposed to sea winds along the Mediterranean coasts, as observed in Cyprus following tree mortality caused by *T. destruens* on steep slopes with highly erosive soils (Ciesla 2004). Bark beetle infestations may also increase the costs for public safety in forested touristic areas, especially pine forests used for camping, extremely common along the Mediterranean coasts. Landscape of whole territories may also be altered following extended outbreaks killing thousands of trees and inducing a change in the forest presence and composition. Moreover, large tree mortality may affect the environment, with the early release of sequestered carbon from attacked trees, affecting even the global carbon balance (Kurz et al. 2008). Finally, since wildfire occurrence is high in Mediterranean pine forests, tree mortality caused by bark beetles creates higher fuel levels resulting in fires of greater intensity and frequency. Surprisingly very few attempts have been made to quantify the direct or indirect economic damage caused by these beetles in the Mediterranean basin. More specific information about damage caused by the various common species is given in Sect. 6.4.

6.8 Management of Bark Beetle Populations

The management of the bark beetle populations is based on two main approaches, which include forest survey and early detection of new infestations and their control.

6.8.1 Detection and Survey

The prompt identification of currently infested trees is a critical aspect to maximizing the effectiveness of direct control strategies. In this respect, a phytosanitary survey carried out every year assessing the general forest health conditions and the population density or damage caused by the main bark beetle species is of crucial importance to decide about management strategies and action priorities. Actually, a very few Mediterranean countries have a specific program of forest monitoring, and often the monitoring services are active only at local or regional scale. The available detection methods range from ground-based survey and trapping or sampling programs to monitor population densities, to aerial survey using simple methods such as sketch mapping, and to more sophisticated and expensive methods using remotely sensed data obtained from satellites (Wulder et al. 2006a, b; Meigs et al. 2011).

6.8.1.1 Ground-Based Survey

To date, methods for identifying currently infested trees depend primarily on ground-based survey. Forest health and the occurrence of bark beetle infestations should be monitored by a group of trained field operators supervised by a team of entomologists in collaboration with scientific institutes. In well-organized management units, where each operator may cover about 1000 ha, the effectiveness of infested tree detection is close to 100 % (Fettig and Hilszczanski 2015). Ground-based survey using trained dogs to detect infested trees has been demonstrated to be effective (Feicht 2006). Once infested trees are identified, field operators verify the degree of infestation, after which the priorities for action are established. During the visit, operators usually fill up specific reports, which include information concerning both the pest infesting the stand (species, development instar, density of population) and the total amount of damage (number of killed trees or volume of wood lost). Moreover, climate conditions (temperature and rain) and silvicultural characteristics (forest composition, tree age, stand origin, etc.) of the attacked stand are also reported. After validation, any information is finally recorded and stored in a database, integrated with mapping through a geographic information system. Data analysis allows establishing the areas the most susceptible to infestations and, consequently, those concerned with specific control measures, the data becoming thus a useful decision support of environmental management. Continuous survey and early detection are aimed at controlling the initial infestations to prevent more serious damage. In addition, specific special survey may be performed in case of prompt increase in population density of certain aggressive species, or after climatic events known to elicit outbreaks.

6.8.1.2 Trapping and Sampling Programs

Another way of monitoring the occurrence of bark beetles and the density of their populations is the use of traps baited with attractive lures. The trap technique can give information about the presence and the flight activity of the beetles, which allows knowing about phenology and voltinism of the species, and hence deciding about the best period of the year for the application of control measures. Trap catches can give also relative estimates of the beetle abundance, *i.e.* population density and its variation in space and time. Comparing trap catches in different sites but under similar conditions is possible to have information about population levels. In addition, permanent monitoring performed by traps may give indications regarding between-year population trends. Moreover, for those bark beetle species where mean catches per trap are someway correlated with damage – in terms of infested cubic meters or killed trees – monitoring by traps may be extremely useful in determining risk thresholds, thus becoming a making decision tool. The specific aggregation pheromones of the most common or the most damaging bark beetle species are already well known (see for instance the site www.pherobase.com) and available commercially. For instance, similar survey protocols were applied against *T. destruens* (Lieutier et al. 2015). However, despite the large number of investigations (Carle 1974b, 1978; Carle et al. 1978; Hamza and Chararas 1981), an aggregation pheromone specific for *T. destruens* has never been identified. To compensate that lack of pheromonal compounds, the use of host volatiles (mainly a-pinene and ethanol) emitted by trees suitable for *T. destruens* has been tested in forest (Sabbatini-Peverieri et al. 2004; Faccoli et al. 2008; Gallego et al. 2008), with promising results (a few hundreds of beetles per trap). These generic host volatiles might thus be useful for population monitoring of *T. destruens* (Lieutier et al. 2015).

Population density may be monitored also by specific sampling programs carried out periodically and focused on the assessment of the abundance of a bark beetle species in relation to presence of symptoms. This is the case, for instance, for *T. destruens* of which the presence and density in the forest can be revealed by the number of fallen and tunnelled pine shoots on the litter. Shoot survey represents one of the possibilities to estimate population levels both locally and on a landscape level. Although the number of damaged shoots per beetle may vary with local conditions, for instance depending on the occurrence of local strong winds, the number of fallen pine shoots is often well correlated with the estimated beetle population (Lieutier et al. 2015).

6.8.1.3 Aerial Survey

The application of remote sensing methods for detection and survey has been frequently used since the 1970s, especially in North America (Puritch 1981; Gimbarzevsky 1984). Usually, this survey is limited to detection of large infestations followed by more detailed surveys to identify currently infested trees, their characteristics and the pest species (Fettig and Hilszczanski 2015). Recently, more sophisticated methods have been applied. For example, surveys using helicopters with global positioning systems (GPS) and digital sketch-mapping equipment is one of the most precise and widely used methods (Wulder et al. 2005). Accurate survey methods have to provide spatially distinct data. In that respect, Landsat data are usually sufficient to detect large groups of trees, but not small or low-density infestations (Skakun et al. 2003). However, it is hard to achieve sufficient accuracy within large areas, especially when infested trees are scattered across a heterogeneous landscape (Wulder et al. 2006a, b). Some methods may provide quite precise data on individual trees through high spatial resolution, but are expensive (Bone et al. 2005). During aerial surveys, a common method of estimating tree infestation uses needle color and retention. During the later stages of infestation, trees lose their foliage and their canopies exhibit different colors from healthy to previously killed trees (Fettig and Hilszczanski 2015). Detection of currently infested trees is possible also with the use of thermal scanners (Heller 1968), and with the use of color-infrared film to improve contrasts between infested and uninfested trees (Arnberg and Wastenson 1973). Detection and survey of bark beetle infested trees by procedures of remote monitoring were experimentally performed also in Mediterranean forests of southern Europe (Lieutier et al. 2015). Aerial black and white, color, and infrared photographs of stone pine stands in central Italy were compared with tree ground survey. Photographs allowed the identification of trees suffering for climatic stress (water stress, wind damage) or attacked by bark beetles, mainly *T. destruens*. False color infrared images gave the best results (Tinelli and Catena 1992). Similar results were found also with aerial image acquisition using a lidar fluorosensor, an instrument that is mainly composed of a frequency-tripled laser and a telescope that detects Raman scattering by water and laser-induced fluorescence by chromophoric dissolved organic matter (Barbini et al. 1995). Infested or stressed trees have different concentrations of plant pigments inducing an altered light reflection of the canopies, which is detected by the fluorosensor.

6.8.2 Population Management

The general strategies available to control bark beetle populations in the Mediterranean countries are very similar to those applied in central-northern Europe. They include both direct and indirect control procedures, which can be summarized in the main following types.

6.8.2.1 Indirect Control

Silvicultural Methods

A sound silvicultural management of the conifer forests is probably the most feasible approach to prevent infestations. This category includes some of the most used methods for the integrated management against bark beetles. Clearing, thinning and pruning may help the maintenance of forests in healthy conditions and, hence, increasing the resiliency of forests to bark beetle infestations and other disturbances. Moreover, all cultural practices that reduce excessive tree density also reduce the susceptibility of individual trees, stands, and forests by strengthening insect resistance mechanisms (Fettig et al. 2007). Tree felling and harvesting should be carried out in winter or early spring before the spring-summer flight of the most species, reducing risk of attacks. Otherwise, when harvested logs are left in the forest for long periods (several months), bark beetle colonization may be prevented by log debarking or exposure to solar radiation, as suggested by Abgrall and Soutrenon (1991) for southern France. In return, the implementation of these measures requires human resources, is time-consuming and quite expensive.

Forest Biodiversity

Large and homogeneous forests are often highly susceptible to disturbances, including bark beetle infestations (Fettig et al. 2007). Instead, forests characterized by higher levels of biodiversity, in term of tree age and species composition, suffer lower damage caused by herbivories (Jactel and Brockerhoff 2007). In this respect, efforts to prevent or reduce tree mortality induced by bark beetles must also account for the spatial heterogeneity of the forests, reported in terms of extension and composition.

6.8.2.2 Direct Control

Cultural Methods

Cultural methods are mainly concerned with sanitation felling, *i.e.* the felling and removal or treatment of trees infested by bark beetles in order to destroy their brood before adult emergence. Where it is economically feasible, trees must be harvested and transported to mills where brood will be killed during timber processing. Otherwise, felled trees should be burned, chipped, or debarked (Fettig and Hilszczanski 2015). To be effective, sanitation felling must be carried out while carefully considering phenology and biology of the target species. Debarking carried out after adult emergence is useless or even negatively affecting bark beetle predators which usually emerge later than their prey. The best period is during the full larval development, when females have already laid all their eggs, but before pupation which usually occurs within bark thickness and which would thus not be affected by debarking. Lastly, some dead or dying trees should remain in the forest to maintain breeding substrate for the beetle natural enemies.

Use of Semiochemicals

Semiochemicals are volatile compounds used to modify the behavior of the flying beetles and reduce their possibility of reproduction. The most common type of semiochemicals used in bark beetle management are the attractants, which include both aggregation pheromones and host-volatiles (such as monoterpenes), employed to attract and concentrate the population in a trapping device (mass-trapping). Specific pheromones and lures are commercially available for many of the most damaging bark beetle species, and these compounds are usually used to bait traps. Mass-trapping, in which traps should be checked and emptied periodically (every 7–10 days), can affect population density only if a specific and effective aggregation pheromone is available, thus assuring high capture levels (several thousands of insects per trap and season). Attractants may also be used to induce attacks on individual trees or small groups of trees or logs (called trap-trees) to induce colonization prior to sanitation. Semiochemicals enhance the attractiveness of trap-trees, which are thus densely infested by bark beetles. Trap trees are then debarked before the emergence of the new brood. When specific pheromones are not available, trap-trees can be baited with attractive host-volatiles. However, host volatiles are not indicated for mass-trapping but only for population monitoring, as described in Sect. 6.8.1.2 for *T. destruens*. Although baited only with generic host-volatiles, these trees are attractive for bark beetle adults. In Mediterranean pine forests, trap-trees and trap-logs have been reported to be the most effective control methods against *T. destruens* and other pine bark beetles (Braquehais 1973; Triggiani 1984). Trap-trees are set up vertically in September or October in pine stand clear-cuts and removed or debarked in February, when pupae are still inside. When log debarking is not possible or too expensive, emerging insects can be killed by spraying trap-trees with synthetic pyrethroids (Abgrall and Soutrenon 1991). Although trapping efficiency varies with bait composition, release rate, trap design and placement, stand structure and composition, and abiotic factors (Fettig and Hilszczanski 2015), the use of traps and trap-trees baited with specific lures, when carefully planned, can reduce the bark beetle population density (Faccoli and Stergulc 2008).

Semiochemicals can be use not only to reduce population density by mass-trapping but also to reduce direct damage using colonisation inhibitors. Inhibitors are volatile compounds, such as anti-aggregation pheromones and non-host volatiles (NHV), repellent to bark beetle adults. They are being used to protect individual trees, forest hedges and trunk piles. Fresh timber and logs may be effectively protected from *T. destruens* bark colonization by the application of dispensers releasing NHV or green-leaf volatiles (GLV), causing inhibition of adult attack behavior (Guerrero et al. 1997). The most common method of applying inhibitors includes release devices stapled to individual trees or trunk piles prior to beetle flight, or applied in a gridded pattern to achieve uniform coverage and assure protection of the whole stand (Fettig and Hilszczanski 2015). To increase levels of inhibition and disrupt bark beetle searching more effectively, repellent blends are often composed of mixtures of diverse chemical cues from conspecifics, heterospecifics and non-hosts. Repellents against Mediterranean bark beetles are still poorly used. Nevertheless, for species without specific aggregation pheromones they may represent the main or the only effective tool to reduce insect damage. Recent applications of NHV, GLV and angiosperm bark volatiles gave positive results against *T. destruens* both in Spain (Guerrero et al. 1997) and Italy (Sabbatini-Peverieri et al. 2004). Trap-logs treated with various blends of repellents (octanol, verbenone, limonene, hexenol, hexanol) in some cases exhibited a colonization density lower than control (untreated logs) (Sabbatini-Peverieri et al. 2004).

Natural Enemies

Predators, parasitoids and entomopathogenic microorganisms, are important in regulating bark beetle populations at endemic levels, and have potential utility in biological control programs (Fettig and Hilszczanski 2015). Unfortunately, there are only very few cases where the mass release of natural enemies in forest have been reported to allow effective control of bark beetle outbreaks. No one has referred to the Mediterranean environment, although in Israel natural enemies are reported to be able to control *T. destruens* populations when appropriate silvicultural measures are applied (Mendel et al. 1986; Mendel 1987).

Chemical Control

Insecticides usage is highly regulated by the local governments, and therefore their integration in bark beetles management varies accordingly. Generally, trees growing in forests are not treated by insecticides due to practical and economic reasons, and because of their negative effects on the environment. Only high-value, individual trees growing in specific sites are treated (e.g., monumental trees, urban environments). In these cases, the routine approach is injection of systemic insecticides into the tree stem with pressurized systems. The major products used for stem injection are transported through the water system reaching different tissues according to the typical flow (the phloem where bark beetle feeding occurs, is not a strong sink). Injections can be applied at any time of year when the tree is actively translocating. Complete distribution of the active components within the tree may take several weeks (Fettig et al. 2014). Tree injections represent the more suitable system to minimize contamination of the environment and reduce non-target effects. The use of this technique was tested also in forests related to the chemical protection of live trees. Effectiveness, phytotoxicity, and residues of different insecticides were evaluated against *T. destruens* in a field experiment conducted in central Italy. The trial consisted of a stem infusion of insecticides with pressured equipment through holes bored at the base of stone pine trees. Phytotoxicity was assessed based on the degree of closing of the holes used for the stem infusion, and presence of residues in pine needles, shoots, and seeds (Paparatti et al. 2000). Although effective, this procedure is very economically expensive and usually being implement for protection of trees of relevant economic, cultural, or historical value, alone.

Insecticide treatments involving typical bark spray cover may be instead applied outside the forest to prevent bark colonisation of trunks piled in the sawmill paddocks. Sprays are usually applied in late spring prior to initiation of the adult flight period of the target bark beetle species. Length of residual activity varies according to active ingredient, formulation, bark beetle species, tree species, and location. In most cases the treatment is expected to last for 1 year, but 2 year duration is common in some bark beetle–host systems (Fettig et al. 2013). Corrective applications to kill adults and brood already occurring beneath the bark of infested trees are rarely used (Fettig et al. 2013). Another chemical-based control protocol concerns the treatment of trap-trees baited with aggregation lures and sprayed with contact insecticides. While the bait allows a strong population concentration on the trap-trees, their chemical protection allows the prompt death of all the insects landing on the sprayed barks, and treated trap-trees do not require debarking at the end of season.

Finally, integrated application of different control technics is probably the best strategy to reduce the risk of bark beetle infestations and manage the outbreaks ongoing in Mediterranean conifer forests (Lopez Pantoja et al. 2000).

6.9 Observed and Anticipated Effects of Climate Change

As all ectothermic organisms, bark beetles are particularly susceptible to temperature variations. Dramatic changes in bark beetle population have been already observed on the background of the climate change. Moreover, simulations of future climate predict that the Mediterranean basin is more vulnerable to global change than temperate and boreal regions, making its flora and fauna particularly concerned with future temperature increase (Chap. 28, Sect. 28.4). It is therefore expected that bark beetle development will be affected directly, whereas major impact on their population dynamic will be indirectly influenced through the effect of the climate change on their host trees and associates. Moreover, changes in the abundance and distribution of the local populations are expected, including major shifts in their geographic ranges. There are several examples in Mediterranean forest insect species proving that such changes are already operating and that they will certainly extend during the twenty-first century. All those possible effects are discussed in details in Chap. 28, Sect. 28.6, with many examples dealing with bark beetle populations. We thus only present below the main types of effects and mechanisms.

Direct effects on bark beetle life cycle will be mainly related to temperature increase. Higher temperatures will allow earlier spring flight and accelerated larval development of local populations, leading to increased voltinism and possibly higher annual brood productivity. This could facilitate reaching the tree's critical attack density threshold more easily, finally resulting in more frequent and extended outbreaks and damage on tree species on site. Temperature may however also drastically affect the relationships between bark beetles and their associated organisms, be they mutualistic or natural enemies. The consequences which may result from temperature effects on symbiotic fungi involved in beetle establishment on trees are not all clear. There are large among species variations in response of these fungi to temperature (Lieutier and Yart 1989; Hofstetter et al. 2007; Six and Bentz 2007), which may affect positively or negatively their relationships with bark beetle hosts and thus in turn on the attack success. In addition, the new climatic conditions and relationships with associated organisms may turn naïve bark beetle species into pests. Increase in the frequency and intensity of storms will inevitably create more available food for bark beetles, together with more fuel for fires which could become more frequent and extended, thus favoring in turn bark beetle population increase.

Considering only the role of direct effects on the beetle populations already allows predicting drastic changes in tree-bark beetle relationships, and thus in ecosystem functioning. However, indirect effects through modifications of trees characteristics will simultaneously interfere, exacerbating the changes in those relationships and making predictions even more complicated. Considering bark beetle communities, climate induced changes in trees will mainly result from effects of increased frequency and intensity of droughts. They can concern modifications of tree's quality, as well as resistance and attractiveness, which will affect beetles in various ways depending on stress intensity, feeding habits and modalities of tree choice by beetles and their natural enemies (Koricheva et al. 1998; Zverera and Kozlov 2006; Rouault et al. 2006; Jactel et al. 2012). In case of intense water stress, trees defenses could be less efficient, resulting in lowering of the critical threshold of attack density, a situation which, if combined with population increase resulting from temperature of storm effects, could lead to dramatic outbreaks. Drought-induced modifications in emissions of volatile organic compounds by trees could have consequences at all levels of tritrophic interactions.

Insect dispersion can be directly favored by temperature increase through reaching the temperature threshold for flight earlier in spring and flying during a longer period. In these conditions, species range extends in both latitude and altitude on its leading edge, while it may contract on its trailing edge (Netherer and Schopf 2010). However, each living species disperse at its own rate. Especially, phytophagous insects in general disperse much farther than their host plants and trees are particularly slow dispersal (Kinlan and Gaines 2003; Berg et al. 2010; Settele et al. 2014). Bark beetles will thus be able to colonize new areas if their usual host tree has a large geographic distribution (naturally or introduced) or if they can shift on new host trees. Polyphagous species will be thus favored, and *T. destruens* with its predicted northward extension constitutes an excellent example of such a possibility (Horn et al. 2012 and Chap. 28, Sect. 28.6.4). All species dispersing independently of each other's, new communities will be constructed, with large variations in species abundance, possibly thus including bark beetle outbreaks, especially if they escape natural enemies.

6.10 Conclusions and Research Needs

A significant amount of knowledge has been accumulated on bark beetles of the Mediterranean basin, giving biological bases for the most important species. However, the basic biology of many species and their relations with associated organisms still stays unknown. Even for the economically important species, some fundamental biological traits are still missing. For example, data on fecundity exist only for *T. destruens* and data on productivity expressed in number of daughter females per parent female for each generation do not exist for any species. If the number of sister broods is often known, their relative importance is unknown. Temperature and thermal sum requirements are also completely unknown for all species. These gaps in knowledge are particularly missing in the present context of facing climate change. There is thus an urgent need for studies on all basic parameters of most species and on how they may change under global warming.

Serious gaps also concern population dynamics. The critical attack density thresholds of the most damaging species need to be estimated for their various host conifers, as well as the threshold of stress corresponding to the passage from stimulation to inhibition of tree defenses. This represents a difficult task as this threshold is species specific but knowing such data would greatly help in anticipating bark beetle damage during drought periods, an important challenge in the Mediterranean areas. The role of the factors involved in population dynamics is also very poorly known. Attack density effects on all basic biological parameters should be investigated, as well as the exact role of natural enemies in the different phases of an outbreak and especially during the latent period of the populations. More generally, the role of all kinds of associates in the tree-bark beetle relationships should be specified in relation with changing climate, to open on multitrophic interactions and studies at the community level. In addition, reliable sampling methods should be built for the most damaging species, to make quantification and detailed survey easier. In order to supply valuable conclusions on the background of the heterogeneity and diversity in the situations in the Mediterranean basin, all these research fields need to be addressed in concert between countries of the Southern, Eastern and Northern rim of the Mediterranean Sea.

References

Abgrall JF, Soutrenon A (1991) La forêt et ses ennemis. CEMAGREF, Paris

Adams AS, Six DL (2007) Temporal variation in mycophagy and prevalence of fungi associated with developmental stages of *Dendroctonus ponderosae* (Coleoptera: Curculionidae). Environ Entomol 36:64–72

Amezaga I, Rodríguez MÁ (1998) Resource partitioning of four sympatric bark beetles depending on swarming dates and tree species. For Ecol Manage 109:127–135

Arnberg W, Wastenson L (1973) Use of aerial photographs for early detection of bark beetle infestations of spruce. Ambio 2:77–83

Aspöck H (2002) The biology of raphidioptera: a review of present knowledge. Acta Zool Acad Sci Hung 48(2):35–50

Avci M, Sarikaya O (2009) *Orthotomicus tridentatus* Eggers: distribution and biology in cedar forests of Turkey. Turk J Agric For Sci 33:277–283

Balachowsky AS (1949) Coléoptères Scolytides. Faune de France No 50. Fédération Française des Sociétés de Sciences Naturelles, Paris

Balachowsky AS (1969) Les scolytes du cèdre dans le Nord de l'Afrique. Ann Soc Ent Fr (N S) 5:647–655

Balachowsky AS, Chararas C (1961) Contribution à l'étude de *Phloeosinus armatus* Reitter (Coleoptera Scolytidae) nuisible au cypres dans le bassin oriental de la Méditeranée. Rev Pathol Vég Entomol Agric Fr 39:245–257

Ball J, Dahlsten D (1973) Hymeropterous parasites of *Ips paraconfusus* (Coleoptera: Scolytidae) larvae and their contribution to mortality. I. Influence of host tree and tree diameter on parasitization. Can Entomol 105:1453–1464

Barbey A (1925) Traité d'entomologie forestière. B Levrault, Paris

Barbini R, Colao F, Fantoni R et al (1995) Monitoraggio mediante lidar fluorosensore di piante di pino domestico attaccate dal Coleottero Scolitide Blastofago distruttore (*Blastophagus destruens* Woll.) al centro ENEA di Frascati. Atti ENEA, Dipartimento Innovazione, RT/INN/95/27, Frascati

Baruch O, Harari A, Mendel Z (2005) The mating behavior of the cypress bark beetles (*Phloeosinus* spp.). In: Abstracts of the conference on forest insect epidemics: population dynamics, dispersal and ecosystem impacts, University of Northern British Columbia, Prince George, 11–14 July 2005

Belhabib R, BenJamâa ML, Nouira S (2007) Biological characteristics of the cypress bark beetle *Phloeosinus aubei* in the Kessra forest, Center of Tunisia. Tunis J Plant Prot 2:99–108

Belhabib R, Lieutier F, BenJamâa ML et al (2009) Host selection and reproductive performances of *Phloeosinus bicolor* (Coleoptera: Curculionidae: Scolytinae) in indigenous and exotic *Cupressus* in Tunisia. Can Entomol 141:595–603

Ben Jamâa ML, Lieutier F, Jerraya A (2000) Les Scolytids ravageurs des pins en Tunisie. Annales de l'INGREF 4:27–39

Ben Jamâa ML, Lieutier F, Yart A et al (2007) The virulence of phytopathogenic fungi associated with the bark beetles *Tomicus piniperda* and *Orthotomicus erosus* in Tunisia. For Pathol 37:51–63

Berg MP, Kiers ET, Driessen G et al (2010) Adapt or disperse: understanding species persistence in a changing world. Glob Chang Biol 16:587–598

Berryman AA (1972) Resistance of conifers to invasion by bark beetle fungus associations. BioScience 22:598–602

Berryman AA (1976) Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. Environ Entomol 5:1225–1233

Berryman AA (1982) Population dynamics of bark beetles. In: Mitton JB, Sturgeon KB (eds) Bark beetles in North American conifers. University of Texas, Austin, pp 264–314

Bickel D (1985) A revision of the Nearctic *Medetera* (Diptera: Dolichopodidae). Technical bulletin no 1692. USDA, FS, Science, Education & Administration, Beltsville, p 109

Bickel DJ (1987) A revision of the Oriental and Australasian *Medetera* (Diptera: Dolichopodidae). Rec South Aust Mus 39:195–259

Bleiker KP, Six DL (2007) Dietary benefits of fungal associates to an eruptive herbivore: potential implications of multiple associates on host population dynamics. Environ Entomol 36:1384–1396

Blomquist GJ, Figueroa-Teran R, Aw M et al (2010) Pheromone production in bark beetles. Insect Biochem Mol Biol 40:699–712

Bodenheimer FS, Neumark S (1955) The Israel pine *Matsucoccus*. Kiryat Sepher, Jerusalem

Bone C, Dragicevic S, Roberts A (2005) Integrating high resolution remote sensing, GIS and fuzzy set theory for identifying susceptibility areas of forest insect infestations. Int J Remote Sens 26:4809–4828

Braasch H, Schmutzenhofer H (2000) *Bursaphelenchus abietinus* sp. n. (Nematoda: Parasitaphelenchidae), associated with the fir bark beetles (*Pityokteines* spp.) from declining trees in Austria. Russ J Nematol 8:1–16

Braasch H, Metge K, Burgermeister W (1999) *Bursaphelenchus*-Arten (Nematoda, Parasitaphelenchidae) in Nadelgeholzen in Deutschland und ihre ITS-RFLP-Muster. Nachrichtenbl Dtsch Pflanzenschutzdienst 51:312–320

Braasch H, Burgermeister W, Harmey MA et al (2000) Pest risk analysis of pinewood nematode related *Bursaphelenchus* species in view of South European pine wilt and wood imports from Asia. Final report of EU research project fair CT 95–0083

Branco M, Pereira JS, Mateus E et al (2010) Water stress affects *Tomicus destruens* host pine preference and performance during the shoot feeding phase. Ann For Sci 67:608

Braquehais F (1973) Trap trees as an integral part of the control of beetle pests. Boletin Estacion Central Ecologia 2:65–70

Bright D (1993) Systematics of bark beetles. In: Schowalter T, Philip G (eds) Beetle-pathogen interactions in conifer forests. Academic Press, New York, pp 23–33

Bueno A, Diez JJ, Fernandez MF (2010) Ophiostomatoid fungi transported by *Ips sexdentatus* (Coleoptera; Scolytinae) in *Pinus pinaster* in NW Spain. Silva Fenn 44:387–397

Bushing R (1965) A synoptic list of the parasites of Scolytidae (Coleoptera) in North America north of Mexico. Can Entomol 97:449–492

Byers J (1992) Attraction of bark beetles, *Tomicus piniperda*, *Hylurgops palliatus*, and *Trypodendron domesticum* and other insects to short-chain alcohols and monoterpenes. J Chem Ecol 18:2385–2402

Carle P (1974a) Le dépérissement du Pin mésogéen en Provence. Rôle des insectes dans les modifications d'équilibre biologique des forêts envahies par *Matsucoccus feytaudi* Duc. (Coccoidea Margarodidae). Ann Sci For 31:1–26

Carle P (1974b) Mise en e´vidence d'une attraction secondaire d'origine sexuelle chez *Blastophagus destruens* Woll. (Col. Scolytidae). Ann Sci Nat Zool Ecol Anim 6:539–550

Carle P (1975) Problèmes posés par les ravageurs xylophages des conifères en forêt méditerranéenne. Rev For Fr 27:283–296

Carle P (1978) Essais d'attraction en laboratoire et en forêt de *Blastophagus* (*piniperda* L. et *destruens* Woll.). Les colloques de l'INRA 38:92–101

Carle P, Descoins C, Gallois M (1978) Pheromones des *Blastophagus* (*piniperda* L. et *destruens* Woll.). Les colloques de l'INRA 38:87–91

Chakali G (2003) Influence climatique sur les populations de scolytes dans les peuplements de pin d'Alep en zone semi-aride (Djelfa). In: Séminaire impact des changements climatiques sur l'écologie des espèces animales, la santé et la population humaine Maghrébine, Gredur, p 10

Chakali G (2005) L'Hylésine des Pins, *Tomicus destruens* Wollaston 1865 (Coleoptera-Scolytidae) en Zone Semi-Aride (Algérie). Silva Lusitana 13:113–124

Chakali G (2007) Stratégie d'attaque de l'hylésine *Tomicus destruens* (Wollaston 1865) (Coleoptera: Scolytidae) sur le pin d'Alep en zone semi-aride (Algérie, Djelfa). Ann Soc Entomol Fr 43:129–137

Chararas C (1962) Scolytides des conifères. Lechevalier, Paris

Chararas C (1974) Recherches écophysiologiques sur certains Scolytidae spécifiques de *Cedrus atlantica* du Moyen Atlas, Travaux de la RC P 249. CNRS, Paris, pp 231–255

Chararas C (1978) Etude de la nutrition et de l'attraction chimique et sexuelle chez *Scolytus numidicus* Bris. (Coléoptère Scolytidae). Etude de certains milieux du Maroc et leur évolution récente, Travaux de la RCP 249. CNRS, Paris, pp 217–260

Christiansen E, Waring RH, Berryman AA (1987) Resistance of conifers to bark beetle attack: searching for general relationships. For Ecol Manage 22:89–106

Ciesla WM (1988) Pine bark beetles: a new pest management challenge for Chilean foresters. J For 86:27–31

Ciesla WM (2004) Forests and forest protection in Cyprus. For Chron 80:1–7

Colineau B, Lieutier F (1994) Production of *Ophiostoma*-free adults of *Ips sexdentatus* Boern. (Coleoptera: Scolytidae) and comparison with naturally contaminated adults. Can Entomol 126:103–110

Covassi M (1991) Il *Phloeosinus armatus* Reitter, Coleottero Scolitide del Cipresso, nuovo per l'Italia. In: Proceedings of Congress Il Cipresso. Proposte di valorizzazione ambientale e produttiva nei paesi mediterranei della Comunità Economica Europea, Firenze, 12–13 dicembre 1991

Croisé L, Lieutier F (1993) Effect of drought on the induced defence reaction of Scots pine to bark beetle-associated fungi. Ann For Sci 50:91–97

Croisé L, Lieutier F, Dreyer E (1998) Scots pine responses to number and density of inoculation points with *Leptographium wingfieldii* Morelet, a bark beetle associated fungus. Ann For Sci 55:497–506

Croisé L, Lieutier F, Cochard H et al (2001) Effect of drought and high density stem inoculations with *Leptographium wingfieldii* on hydraulic properties of young Scots pine trees. Tree Physiol 21:427–436

Dahlsten D (1982) Relationships between bark beetles and their natural enemies. In: Mitton J, Sturgeon K (eds) Bark beetles in North American conifers: a system for the study of evolutionary biology. University of Texas, Austin, pp 140–182

De Beer ZW, Seifert KA, Wingfield MJ (2013) A nomenclator for Ophiostomatoid genera and species in the Ophiostomatales and Microascales. In: Seifert KA, de Beer ZW, Wingfield MG (eds) Ophiostomatoid fungi: expanding frontiers, vol 12, CBS biodiversity series. CBS-KNAW Fungal Biodiversity Centre, Utrecht, pp 245–322

Dippel C (1996) Investigations on the life history of *Nemosoma elongatum* L. (Coleoptera: Ostomidae), a bark beetle predator. J Appl Entomol 120:391–395

Dippel C, Heidger C, Nicolai V et al (1997) The influence of four different predators on bark beetles in European forest ecosystems (Coleoptera: Scolytidae). Entomol Gener 21:161–175

Dori-Bachash M, Avrahami-Moyal L, Protasov A et al (2015) The occurrence and pathogenicity of *Geosmithia* spp. and common blue-stain fungi associated with pine bark beetles in planted forests in Israel. Eur J Plant Pathol 143:627–639

Dreyer E, Guérard N, Lieutier F et al (2002) Interactions between nutrient and water supply to potted *Pinus sylvestris* trees and their susceptibility to several pests and pathogens. In: Lieutier F (ed) Effects of water and nutrient stress on pine susceptibility to various pest and disease guilds, Final scientific report EU project FAIR 3 CT96-1854, pp 63–81

Durand-Gillmann M (2014) Interactions plantes-insectes dans deux écosystèmes forestiers méditerranéens contrastés: le cas des scolytes (Coleoptera : Curculionidae : Scolytinae) en région méditerranéenne. Dissertation, Université d'Aix-Marseille

Escherich K (1923) Forstinsekten Mitteleuropas. Band II. Paul Parey, Berlin

Fabre JP, Mouna M, Du Merle P et al (1999) Le point sur certains ravageurs du cèdre de l'Atlas en Afrique du Nord, en France et en Europe. For Méditerr 20:203–218

Faccoli M (2007) Breeding performances and longevity of *Tomicus destruens* on Mediterranean and continental pine species. Entomol Exp Appl 123:263–269

Faccoli M (2009) Breeding performance of *Tomicus destruens* at different densities: the effect of intraspecific competition. Entomol Exp Appl 132:191–199

Faccoli M (2015) European bark and ambrosia beetles: types, characteristics and identification of the mating systems. WBA Edition, Verona

Faccoli M, Stergulc F (2008) Damage reduction and performance of mass trapping devices for forest protection against the spruce bark beetle, *Ips typographus* (Coleoptera Curculionidae Scolytinae). Ann For Sci 65:309–317

Faccoli M, Battisti A, Masutti L (2005) Phenology of *Tomicus destruens* (Wollaston) in Northern Italian pine stands. In: Lieutier F, Ghaioule D (eds) Entomological research in Mediterranean forest ecosystems. INRA Editions, Paris, pp 185–193

Faccoli M, Anfora G, Tasin M (2008) Responses of the Mediterranean pine shoot beetle *Tomicus destruens* (Wollaston) (Coleoptera Curculionidae Scolytinae) to pine shoot and bark volatiles. J Chem Ecol 34:1162–1169

Feicht E (2006) Bark beetle hunting dogs. The suitability of dogs to find bark beetle infestations. Forst Holz 61:70–71

Fernández MM (1997) Los Hylesininae (Coleoptera: Scolytidae) parásitos de los pinos en la provincia de León. Boletin Asociación Española Entomología 21:195–209

Fernandez MM (2006) Colonization of fire-damaged trees by *Ips sexdentatus* (Boerner) as related to the percentage of burnt crown. Entomol Fennica 17:381–386

Fernandez MM, Salgado J (1999) Susceptibility of fire-damaged pine trees (*Pinus pinaster* and *Pinus nigra*) to attacks by *Ips sexdentatus* and *Tomicus piniperda*. Entomol Gen 24:105–114

Fernandez MM, Garcia J, Lieutier F (2004) Effects of various densities of *Ophiostoma ips* inoculations on *Pinus sylvestris* in North-Western Spain. For Pathol 34:213–223

Fernandez MM, Diez J, Moraza ML (2013) Acarofauna associated with *Ips sexdentatus* in Northwest Spain. Scand J For Res 28:352–358

Ferreira MC (1985) Impacte dos predators da classe insecta nos escolitideos do Pinheiro Bravo. Actas do II Congresso Iberico de Entomologia. Boletino da Sociedade Portuguesa de Entomologia 1:107–114

Ferreira MC, Ferreira GS (1987) Impacte de fogo nos escolitídeos associados com Pinheiro Bravo. Floresta 4–5:12–14

Fettig CJ, Hilszczanski J (2015) Management strategies for bark beetles in conifer forests. In: Vega FE, Hofstetter RW (eds) Bark beetles: biology and ecology of native and invasive species. Elsevier Academic Press, London, pp 555–584

Fettig CJ, Klepzig KD, Billings RF et al (2007) The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the Western and Southern United States. For Ecol Manag 238:24–53

Fettig CJ, Grosman DM, Munson AS (2013) Advances in insecticide tools and tactics for protecting conifers from bark beetle attack in the Western United States. In: Trdan S (ed) Insecticides – development of safer and more effective technologies. InTech, Croatia, pp 472–492

Fettig CJ, Munson AS, Grosman DM et al (2014) Evaluations of emamectin benzoate and propiconazole for protecting individual *Pinus contorta* from mortality attributed to colonization by *Dendroctonus ponderosae* and associated fungi. Pest Manag Sci 70:771–778

Francke-Grosmann H (1952) Über die Ambrosiazucht der beiden Kieferborkenkäfer *Myelophilus minor* Htg. und *Ips acuminatus* Gyll. Meddel Från Stat Skogsforsk 41:1–52

Francke-Grosmann H (1963) Zur Übertragung der Pilzflora bei dem Borkenkäfer *Ips acuminatus*. Z Angew Entomol 52:355–361

Francke-Grosmann H (1966) Über Symbiosen von xylo-mycetophagen und phloeophagen Scolytoidea mit holzbewohnenden Pilzen. In: Proceedings of international symposium on Holz und Organismen, Berlin-Dahlen, pp 503–522

Francke-Grosmann H (1967) Ectosymbiosis in wood-inhabiting insects. In: Henry SM (ed) Symbiosis, vol 2. Academic Press, New York, pp 141–205

Fuchs G (1930) Neue an Borkenkäfer und Rüsselkäfer gebundene Nematoden, halbparasitische und Wohnungseinmieter. Zoologische Jahrblatt, Jena, Abteil Systematik 59:505–646

Fuchs G (1937) Neue parasitische und halbparasitische Nematoden bei borkenkäfern und einige andere Nematoden. Zoologische Jahrblatt, Jena, Abteil Systematik 70:291–380

Gallego D, Canovas F, Esteve MA et al (2004) Descriptive biogeography of *Tomicus* (Coleoptera: Scolytidae) species in Spain. J Biogeogr 31:2011–2024

Gallego D, Galian J, Diez JJ et al (2008) Kairomonal responses of *Tomicus destruens* (Col., Scolytidae) to host volatiles alpha-pinene and ethanol. J Appl Entomol 132:654–662

Ghaioule D, Abourouh M, Bakry M et al (1998) Insectes ravageurs des forêts au Maroc. Ann Rech For Maroc 31:129–156

Gil LA, Pajares JA (1986) Los escolítidos de las coníferas en la Península Ibérica. Monografías INIA 53, Ministerio de Agricultura, Pesca y Alimentación, Instituto Nacional de Investigaciones Agrarias

Gimbarzevsky P (1984) Remote sensing in forest damage detection and appraisal-selected annotated bibliography. Information report, BC-X-253. Canadian Forestry Service, Victoria

Graf P, Mzibri M (1994) Les Scolytes des pins. In: El Hassani A, Graf P, Hamdaoui M et al (eds) Ravageurs et maladies des forêts au Maroc. DPVCRTF, Morocco, pp 33–47

Grüne S (1979) Handbuch zur bestimmung der europaischen Borkenkäfer (Brief illustrated key to European bark beetles). M. & H. Schaper, Hannover

Guérard N, Dreyer E, Lieutier F (2000) Interactions between Scots pine, *Ips acuminatus* (Gyll.) and *Ophiostoma brunneo-ciliatum* (Math.): estimation of critical thresholds of attack and inoculation densities and effect on hydraulic properties of the stem. Ann For Sci 57:681–690

Guerrero A, Feixas J, Pajares J et al (1997) Semiochemically induced inhibition of behaviour of *Tomicus destruens* (Woll.) (Coleoptera: Scolytidae). Naturwissenschaften 84:155–157

Haack RA (2004) *Orthotomicus erosus*: a new pine-infesting bark beetle in the United States. Newsl Michigan Entomol Soc 49:3–4

Halevy M (1995) The Israeli pine bast scale, *Matsucoccus josephi*, and its natural enemies in the pine forest of Israel (Hebrew, with English summary). Dissertation, The Hebrew University of Jerusalem

Halperin J (1966) Forest insects in Israel. Proc 6th World For Congr, Madrid 2:2100–2102

Halperin J, Holzchuh C (1984) Contribution to the knowledge of bark beetles (Col., Scolytoidea) and associated organisms in Israel. Isr J Entomol 18:21–37

Hamza MH, Chararas C (1981) Etude de l'attraction primaire et de la nutrition chez *Blastophagus piniperda* L. Ann INRF 6:1–30

Harrington TC (1993) Biology and taxonomy of fungi associated with bark beetles. In: Schowalter TD, Filip GM (eds) Beetle-pathogen interactions in conifer forests. Academic Press, New York, pp 37–58

Harrington TC (2005) Ecology and evolution of mycetophagous bark beetles and their fungal partners. In: Vega FE, Blackwell M (eds) Insect-fungal associations: ecology and evolution. Oxford University Press, New York, pp 257–289

Harrington CA, Heukema DL (1983) Initial shock and long-term stand development following thinning in a Douglas-fir plantation. For Sci 29:33–46

Hedgren P, Schroeder RL (2004) Reproductive success of the spruce bark beetle *Ips typographus* (L.) and occurrence of associated species: a comparison between standing beetle killed trees and cut trees. For Ecol Manage 203:241–250

Hedqvist K (1998) Bark beetle enemies in Sweden II. Braconidae (Hymenoptera). Entomol Scand Suppl 52:87

Heller RC (1968) Previsual detection of ponderosa pine trees dying from bark beetle attack. In: Proceedings of the fifth symposium on remote sensing of environment, University of Michigan, Ann Arbor, pp 387–434

Herting B (1973) Coleoptera to Strepsiptera. A catalogue of parasites and predators of terrestrial arthropods. Section A. Host or Prey/Enemy. 3:9 Commonwealth Agricultural Bureaux, Institute of Biological Control

Hofstetter RW, Moser JC (2014) Role of mites in insect-fungus associations. Annu Rev Entomol 59:537–557

Hofstetter RW, Cronin JT, Klepzig KD et al (2006a) Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. Oecologia 147:679–691

Hofstetter RW, Klepzig KD, Moser JC et al (2006b) Seasonal dynamics of mites and fungi and their interactions with southern pine beetle. Environ Entomol 35:22–30

Hofstetter RW, Dempsey TD, Klepzig KD et al (2007) Temperature-dependent effects on mutualistic, antagonistic, and commensalistic interactions among insects, fungi and mites. Community Ecol 8:47–56

Hofstetter RW, Moser JC, Blomquist SR (2013) Mites associated with bark beetles and their hyperphoretic ophiostomatoid fungi. Biodiv Ser 12:165–176

Hofstetter RW, Dinkins-Bookwalter J, Davis TS et al (2015) Symbiotic associations with bark beetles. In: Vega FE, Hofstetter FW (eds) Bark beetles: biology and ecology of native and invasive species. Elsevier, Oxford, pp 209–245

Horn A, Kerdelhué C, Lieutier F et al (2012) Predicting the distribution of the two bark beetles *Tomicus destruens* and *Tomicus piniperda* in Europe and the Mediterranean region. Agric For Entomol 14:358–366

Horn A, Kerdelhué C, Lieutier F et al (2014) Modelling the geographic distributions of the two bark beetles *Tomicus destruens* and *Tomicus piniperda* in Europe and in the Mediterranean region. Ann INRGREF 17:157–171

Hulcr J, Pollet M, Ubik K et al (2005) Exploitation of kairomones and synomones by *Medetera* spp. (Diptera: Dolichopodidae), predators of spruce bark beetles. Eur J Entomol 102:655–662

Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. Ecol Lett 10:835–848

Jactel H, Petit J, Desprez-Loustau ML et al (2012) Drought effects on damage by forest insects and pathogens: a meta-analysis. Glob Chang Biol 18:267–276

JeLínek J, Audisio P (2004) Family Monotomidae. Fauna Europaea version 2.4. http://www.faunaeur.org. Accessed Mar 2013

Kailides DS (1985) Dry periods and secondary dying and bark beetle epidemics in forests of Greece. Publication – Ergasterio Ulorikes, Tmema Dasologias kai Fusikou Periballontos – Aristoteleio Panepistemio Thessalonikes, 2, pp 1–16

Kakulia GA, Shalibashvili G (1976a) The nematode fauna of *Hylastes ater* in the pine forests of the Pitsundskii and Ritsinskii reserves. Zapovedniki Gruzii Sbornik Trudov 4:259–262

Kakulia GA, Shalibashvili G (1976b) The nematode fauna of *Pityokteines curvidens* Germ. in the conifer forests of Abkhaziya. Zapovedniki Gruzii Sbornik Trudov 4:317–320

Karaman S, Tezcan S (2006) A review of natural enemies of bark beetles (Coleoptera: Scolytidae) (in Turkish). Ege Ormancilik Arastirma Müdürlügü Dergisi 42:78–102

Kaya HK (1984) Nematodes parasites of bark beetles. In: Nickle WR (ed) Plant and insect nematodes. Marcel Dekker, New York, pp 727–754

Kenis M, Wermelinger B, Grégoire JC (2004) Research on parasitoids and predators of Scolytidae – a review. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer, Dordrecht, pp 237–290

Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007–2020

Kirisits T (2004) Fungal associates of European bark beetles with special emphasis on the ophiostomatoid fungi. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer, Dordrecht, pp 181–235

Kirisits T, Grubelnik R, Führer E (2000) Die ökologische Bedeutung von Bläuepilzen für rindenbrütende Borkenkäfer. In: Müller F (ed) Mariabrunner Waldbautage 1999 – Umbau sekundärer Nadelwälder. Schriftenreihe der Forstlichen Bundesversuchsanstalt, Wien, FBVA-Berichte 111:117–137

Kirisits T, Diminić D, Hrašovec B et al (2009) First reports of silver fir blue staining ophiostomatoid fungi associated with *Pityokteines spinidens*. Croat J For Eng 30:51–57

Kirschner R, Oberwinkler F (1999) A new *Ophiostoma* species associated with bark beetles infesting Norway spruce. Can J Bot 77:247–252

Klepzig KD, Six DL (2004) Bark beetle-fungal symbiosis: context dependency in complex associations. Symbiosis 37:189–205

Klepzig KD, Moser JC, Lombardero MJ et al (2001a) Mutualism and antagonism: ecological interactions among bark beetles, mites and fungi. In: Jeger MJ, Spence NJ (eds) Biotic interactions in plant-pathogen associations. CAB International, Wallingford, pp 237–267

Klepzig KD, Moser JC, Lombardero MJ et al (2001b) Symbiosis and competition: complex interactions among beetles, fungi and mites. Symbiosis 30:83–96

Knížek M (2011) Scolytinae. In: Löbl I, Smetana A (eds) Catalogue of palaearctic coleoptera, vol 7. Apollo Books, Stenstrup, pp 204–251

Knížek M, Beaver R (2004) Taxonomy and systematics of bark and ambrosia beetles. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer, Dordrecht, pp 41–54

Kolarik M, Kubatova A, Hulcr J et al (2008) *Geosmithia* fungi are highly diverse and consistent bark beetle associates: evidence from their community structure in temperate Europe. Microb Ecol 55:65–80

Koricheva J, Larsson S, Haukioja E (1998) Insect performance on experimentally stressed woody plants: a meta-analysis. A Rev Entomol 43:195–216

Kovarik P, Caterino M (2000) Histeridae. In: Junior A, Thomas M (eds) American beetles, vol 1. CRC Press, Boca Raton, pp 212–227

Kozak V (1976) The importance of naturel enemies introducing the numbers of bark-beetles in coniferous trees. Zakhist Roslin 23:7–10

Krivosheina NP, Rozkosny R (1985) Additional notes on Palaearctic Pachychasterinae (Diptera, Stratiomyidae). Acta Entomol Bohemoslov 82:143–149

Krokene P (2015) Conifer defenses and resistance to bark beetles. In: Vega FE, Hofstetter RW (eds) Bark beetles: biology and ecology of native and invasive species. Elsevier, Oxford, pp 177–207

Kruger K, Mills NJ (1990) Observations on the biology of three parasitoids of the spruce bark beetle, *Ips typographus* (Col., Scolytidae): *Coeloides bostrychorum*, *Dendrosoter middendorffi* (Hym., Braconidae) and *Rhopalicus tutela* (Hym., Pteromalidae). J Appl Entomol 110:281–291

Kurawhvili BE, Kakulia GA, Devdariani TG (1980) Parasitic nematodes of bark beetles in Georgia. Matsniereba, Tbilisi

Kurz WA, Dymond CC, Stinson G et al (2008) Mountain pine beetle and forest carbon: feedback to climate change. Nature 454:987–990

Langewald J (1989) Studies on the habitat selection of the bark beetle predator *Thanasimus formicarius* l. Coleoptera Cleridae. Anz Schaedlingskd Pflanzenschutz Umweltschutz 62:88–90

Långström B (1983) Life cycles and shoot-feeding of the pine shoot beetles. Stud For Suec 163:1–29

Långström B, Hellqvist C (1990) Spatial distribution of crown damage and growth losses caused by recurrent attacks of pine shoot beetles in pine stands surrounding a pulp mill in southern Sweden. J Appl Entomol 110:261–269

Långström B, Solheim H, Hellqvist C et al (1993) Effects of pruning young Scots pines on host vigour and susceptibility to *Leptographium wingfieldii* and *Ophiostoma minus*, two blue-stain fungi associated with *Tomicus piniperda*. Eur J For Pathol 23:400–415

Långström B, Hellqvist C, Ehnström B (1999) Susceptibility of fire damaged Scots pine (*Pinus sylvestris* L.) to attack by *Tomicus piniperda* L. In: Lieutier F, Mattson WJ, Wagner MR (eds) Physiology and genetics of tree-phytophage interactions. INRA Editions, Versailles, pp 299–311

Lattin JD (1999) Bionomics of the Anthocoridae. A Rev Entomol 44:207–231

Laumond C, Carle P (1971) Nématodes associés et parasites de *Blastophagus destruens* Woll. (Col. Scolytidae). Entomophaga 16:51–66

Lee JC, Smith SL, Seybold SJ (2005) Mediterranean Pine Engraver. Pest Alert, R5-PR-016. USDA Forest Service, State and Private Forestry Pacific Southwest Region, Berkeley

Lévieux J, Lieutier F, Moser JC et al (1989) Transportation of phytopathogenic fungi by the bark beetle *Ips sexdentatus* Boerner and associated mites. Z Angew Entomol 108:1–11

Lieutier F (1980) Le parasitisme d'*Ips sexdentatus* (Boern.) (Coleoptera: Scolytidae) par les nematodes du genre *Parasitaphelenchus* Fuchs. Relations avec le parasitisme par *Contortylenchus diplogaster* (v. Lins.). Rev Nematol 3:271–281

Lieutier F (1984a) Les perturbations induites par *Parasitorhabditis ipsophila* (Nematoda : Rhabditidae) dans le tube digestif d'*Ips sexdentatus* (Insecta : Scolytidae). Ann Parasitol Hum Comp 59:597–605

Lieutier F (1984b) Observations histologiques sur les capsules induites par *Contortylenchus diplogaster* v. Lins. (Nematoda: Allantonematidae) dans le tissu adipeux d'*Ips sexdentatus* (Coleoptera: Scolytidae). Ann Parasitol Hum Comp 59:245–251

Lieutier F (1985) Influence des nematodes parasites sur l'hémolymphe des adultes d'*Ips sexdentatus* Boern. (Coleoptera: Scolytidae). Ann Parasitol Hum Comp 60:195–204

Lieutier F (1992) Les réactions de défense des conifères et stratégies d'attaque de quelques Scolytides européens. Mém Soc R Belge Entomol 35:529–539

Lieutier F (2002) Mechanisms of resistance in conifers and bark beetle attack strategies. In: Wagner MR, Clancy KM, Lieutier F et al (eds) Mechanisms and deployment of resistance in trees to insects. Kluwer, Dordrecht, pp 31–75

Lieutier F (2004) Host resistance to bark beetles and its variations. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer, Dordrecht, pp 135–180

Lieutier F, Laumond C (1978) Nématodes parasites et associés à *Ips sexdentatus* et *Ips typographus* (Coleoptera: Scolytidae) en region parisienne. Nematologica 24:187–200

Lieutier F, Seureau C (1981) Encapsulement cellulaire de *Contortylenchus diplogaster* v. Lins. (Nematoda : Allantonematidae) dans le tissu adipeux d'*Ips sexdentatus* Boern. (Coleoptera : Scolytidae). Ann Parasitol 56:607–612

Lieutier F, Vallet E (1982) Observations sur les nématodes parasites et associés aux principaux Scolytidae ravageurs du pin sylvestre en forêts d'Orléans et de Sologne. Acta Oecol, Oecol Appl 3:131–148

Lieutier F, Yart A (1989) Preferenda thermiques des champignons associés à *Ips sexdentatus* Boern. et *Tomicus piniperda* L. (Coleoptera; Scolytidae). Ann For Sci 46:411–415

Lieutier F, Jastrabsky M, Bonnafé P (1985) Modifications du spectre protéique de l'hémolymphe et des ovaires d'*Ips sexdentatus* (Coleoptera: Scolytidae) sous l'action des nematodes parasites. Ann Parasitol Hum Comp 60:715–725

Lieutier F, Cheniclet C, Garcia J (1989a) Comparison of the defense reactions of *Pinus pinaster* and *Pinus sylvestris* to attacks by two bark beetles (Coleoptera: Scolytidae) and their associated fungi. Environ Entomol 18:228–234

Lieutier F, Yart A, Garcia J et al (1989b) Champignons phytopathogènes associés à deux coléoptères scolytidae du pin sylvestre (*Pinus sylvestris* L.) et étude préliminaire de leur agressivité envers l'hôte. Ann For Sci 46:201–216

Lieutier F, Garcia J, Yart A et al (1991) Ophiostomatales (Ascomycetes) associées à *Ips acuminatus* (Coleoptera: Scolytidae) sur le pin sylvestre (*Pinus sylvestris*) dans le Sud-Est de la France, et comparaison avec *Ips sexdentatus* Boern. Agronomie 11:807–817

Lieutier F, Garcia J, Yart A et al (1995) Wound reaction of Scots pine (*Pinus sylvestris* L.) to attacks by *Tomicus piniperda* L. and *Ips sexdentatus* Boern. (Coleoptera: Scolytidae). J Appl Entomol 119:591–600

Lieutier F, Ghaioule D, Yart A et al (2002) Attack behavior of pine bark beetles in Morocco and association with phytopathogenic fungi. Ann Rech For Maroc 35:96–109

Lieutier F, Day KR, Battisti A et al (2004a) Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer, Dordrecht

Lieutier F, Yart A, Ye H et al (2004b) Between-isolate variations in the preformances of *Leptographium wingfieldii* Morelet, a fungus associated with the bark beetle *Tomicus piniperda* L. Ann For Sci 61:45–53

Lieutier F, Ghaioule D, Yart A (2005) Virulence and possible role of fungi associated with the bark beetles *Tomicus piniperda* L. and *Orthotomicus erosus* Woll. In Morocco. In: Lieutier F, Ghaioule D (eds) Entomological research in Mediterranean forest ecosystems. INRA, Paris, pp 195–208

Lieutier F, Yart A, Sallé A (2009) Stimulation of tree defenses by ophiostomatoid fungi can explain attack success of bark beetles on conifers. Ann For Sci 66:801

Lieutier F, Långström B, Faccoli M (2015) The genus *Tomicus*. In: Vega FE, Hofstetter FW (eds) Bark beetles: biology and ecology of native and invasive species. Elsevier, Oxford, pp 371–426

Lindgren BS, Raffa KF (2013) The evolution of tree-killing by bark beetles: trade-offs between the maddening crowds and a sticky situation. Can Entomol 145:471–495

Lindquist EE (1985) Discovery of sporothecae in adult female *Trochometridium* Cross, with notes on analogous structures in *Siteroptes* Amerling (Acari: Heterostigmata). Exp Appl Acarol 1:73–85

Lombardero MJ, Ayres MP (2011) Factors influencing bark beetle outbreaks after forest fires on the Iberian Peninsula. Environ Entomol 40:1007–1018

Lombardero MJ, Klepzig KD, Moser JC et al (2003) Biology, demography and community interactions of *Tarsonemus* (Acarina: Tarsonemidae) mites phoretic on *Dendroctonus frontalis* (Coleoptera: Scolytidae). Agric For Entomol 2:193–202

Lopez Pantoja G, Sanchez Callado FM, Gomez de Dios MA et al (2000) Prototipo de control integrado para *Tomicus piniperda* ecotipo *destruens* (Woll.) y *Orthotomicus erosus* (Woll.) en los pinares litorales de la provincia de Huelva. In: Proceedings of the 1st symposium on stone pine (*Pinus pinea* L.), Valladolid, pp 319–326

Mackenzie M, Dick M (1984) *Verticicladiella* root disease. For Pathol New Zeal 8:1–4

Markalas S (1992) Site and stand factors related to mortality rate in a fir forest after a combined incidence of drought and insect attack. For Ecol Manage 47:367–374

Markalas S (1997) Frequency and distribution of insect species on trunks in burnt pine forests of Greece. Mitteil Schweizerischen Entomol Gesell 70:57–61

Mathiesen A (1950) Über einige mit Borkenkäfern assoziierte Bläuepilze in Schweden. Oikos 2:275–308

Mathiesen A (1951) Einige neue *Ophiostoma*-Arten in Schweden. Sven Bot Tidskr 45:203–232

Mathiesen-Käarik A (1953) Eine Übersicht über die gewöhnlichsten mit Borkenkäfern assoziierten Bläuepilze in Schweden und einige für Schweden neue Bläuepilze. Meddel frän Stat Skogforsk 43:1–74

Mathiesen-Käarik A (1960) Studies on the ecology, taxonomy and physiology of Swedish insect-associated blue stain fungi, especially the genus *Ceratocystis*. Oikos 11:1–24

Matosevic D, Pernek M, Zupanic M (2007) Diagnosis and prognosis of harmful biotic and abiotic factors in Croatian forests during the period 2001 to 2005. Glasilo Biljne Zastite 7:387–393

Médail F, Diadema K (2009) Glacial refugia influence plant diversity patterns in the Mediterranean basin. J Biogeogr 36:1333–1345

Meigs GW, Kennedy RE, Cohen WB (2011) A Landsat time series approach to characterize bark beetle and defoliator impacts on tree mortality and surface fuels in conifer forests. Remote Sens Environ 115:3707–3718

Mendel Z (1984) Life history of *Phloeosinus armatus* Reitter and *P. aubei* Perris (Coleoptera: Scolytidae) in Israel. Phys Chem Chem Phys 12:89–97

Mendel Z (1985a) Predation on *Orthotomicus erosus* (Col., Scolytidae) by the Syrian woodpecker (*Picoides syriacus*, Aves, Picidae). J Appl Entomol 100:355–360

Mendel Z (1985b) Mortality rates inflicted by Hymenopteran parasitoids on Orthotomicus erosus in Israeli pine forest. Unpublished report (in Hebrew), submitted to KKL forest stirring committee, Forests Department, KKL, Eshtaol, pp 1–9

Mendel Z (1986a) Hymenopterous parasitoids of bark beetles [Scolytidae] in Israel: host relation, host plant, abundance and seasonal history. Entomophaga 31:113–125

Mendel Z (1986b) Hymenopterous parasitoids of bark beetles [Scolytidae] in Israel: relationships between host and parasitoid size, and sex ratio. Entomophaga 31:127–137

Mendel Z (1987) Major pests of man-made forests in Israel: origin, biology, damage and control. Phys Chem Chem Phys 15:131–137

Mendel Z (1988) The relation of bast scale and bark beetle outbreaks to management of pine plantations in Israel. In: Payne TL, Saarenmaa H (eds) Proceedings of the IUFRO working party, XVII international Congress of entomology. Vancouver, pp 329–335

Mendel Z, Halperin J (1981) Parasites of bark beetles (Coleoptera: Scolytidae) on pine and cypress in Israel. Entomophaga 26:375–379

Mendel Z, Halperin J (1982) The biology and behavior of *Orthotomicus erosus* in Israel. Phytoparasitica 10:169–181

Mendel Z, Opatowski D (1997) Effect of pine stand thinning on bark beetle and natural enemy population dynamics in Israel. Unpublished report, Forests Department, KKL, Eshtaol, pp 1–76

Mendel Z, Golan Y, Madar Z et al (1983) Insect pests and diseases of cypress in Israel. La-Yaaran 33:37–41

Mendel Z, Madar Z, Golan Y (1985) Comparison of the seasonal occurrence and behavior of seven pine bark beetles (Coleoptera: Scolytidae) in Israel. Phys Chem Chem Phys 13:21–32

Mendel Z, Madar Z, Golan Y (1986) Hymenopterous parasitoids of pine bark beetles in Israel. Hassadeh 66:1899–1901

Mendel Z, Podoler H, Livne H (1990) Interactions between *Aulonium ruficorne* (Coleoptera; Colydiidae) and other natural enemies of bark beetles (Coleoptera: Scolytidae). Entomophaga 35:99–105

Mendel Z, Boneh O, Shenhar Y et al (1991) Diurnal flight patterns of *Orthotomicus erosus* and *Pityogenes calcaratus* in Israel. Phytoparasitica 19:23–31

Mendel Z, Boneh O, Riov J (1992) Some foundations for application of aggregation pheromone to control pine bark beetles in Israel. J Appl Entomol 114:217–227

Mignot E, Anderson R (1970) Bionomics of the bark beetle predator *Temnochila virescens* Coleoptera: Ostomidae. Entomol News 81:85–91

Milligan RH (1978) *Hylastes ater* (Paykull), black pine bark beetle. Forest and Timber Insects in New Zealand, no 29. New Zealand Forest Service, Forest Research Institute, Rotorua, pp 1–7

Mills NJ, Schlup J (1989) The natural enemies of *Ips typographus* in Central Europe: impact and potential use in biological control. In: Kulhavy DL, Miller MC (eds) Potential for biological control of *Dendroctonus* and *Ips* bark beetles. University of Texas Press, Austin, pp 131–146

Mills NJ, Krüger K, Schlup J (1991) Short-range host location mechanisms of bark beetle parasitoids. J Appl Entomol 111:33–43

Monleón A, Blas M, Riba JM (1996) Biologia de *Tomicus destruens* (Wollaston, 1865) (Coleoptera; Scolytidae) en los bosques mediterraneos. Elytron 10:161–167

Moraza ML, Fernandez MM, Jurc M (2013) Phoretic mites on the six-spinned engraver beetle, *Ips sexdentatus* (Boerner, 1776) (Coleoptera, Scolytinae), on *Pinus halepensis* in Slovenia. Intern J Acarol 39:597–599

Moser JC (1985) Use of sporothecae by phoretic *Tarsonemus* mites to transport ascospores of coniferous bluestain fungi. Trans Br Mycol Soc 84:750–753

Moser J, Thatcher R, Pickard L (1971) Relative abundance of the southern pine beetle associates in East Texas. Ann Entomol Soc Am 64:72–77

Mulock P, Christiansen E (1986) The threshold of successful attack by *Ips typographus* on *Picea abies*: a field experiment. For Ecol Manage 14:125–132

Nageleisen LM (2004) Les insectes sous-corticaux des résineux en 2002: diminution inattendue des dommages dus aux scolytes. In: Les Cahiers du DSF 1-2003/2004 (La santé des forêts [France] en 2002), pp 29–31

Nebeker TE, Hodges JD (1983) Influence of forestry practices on host-susceptibiliry to bark beetles. J Appl Entomol 96:194–208

Nedelchev S, Takov D, Pilarska D (2011) *Prothallonema tomici* n. sp. (Tylenchida: Sphaerulariidae) parasitizing *Tomicus piniperda* (Coleoptera: Curculionidae: Scolytinae) in Bulgaria. Nematology 13:741–746

Netherer S, Schopf A (2010) Potential effects of climate change on insect herbivores in European forests – general aspects and the pine processionary moth as specific example. For Ecol Manage 259:831–838

Noyes JS (2015) Universal Chalcidoidea database. World Wide Web electronic publication. http://www.nhm.ac.uk/chalcidoids

Nuorteva M (1971) The bark beetles (Coleoptera: Scolytidae) and their insect enemieses in Kuusamo commune, northern Finland. Ann Entomol Fennici 37:65–72

Overgaard N (1968) Insects associated with the southern pine beetle in Texas, Louisiana and Mississippi. J Econ Entomol 61:1197–1201

Özkazanç O, Iktüeren S, Yücel M (1985) Studies on the biology and control of *Orthotomicus erosus* (Woll.) in Mediterranean and Aegean regions. Ormancilik Arastirma Enstitüsü Yayinnlari 152:1–56

Paine TD, Raffa KF, Harrington TC (1997) Interactions among scolytids bark beetles, their associated fungi, and live host conifers. A Rev Entomol 42:179–206

Paparatti B, Cinti S, Leandri A et al (2000) Esperienze sul controllo di *Tomicus destruens* (Wollaston) (Coleoptera, Scolytidae). Atti Giornate Fitopatologiche 1:433–440

Penas AC, Bravo MA, Naves P et al (2006) Species of *Bursaphelenchus* Fuchs, 1937 (Nematoda: Parasitaphelenchidae) and other nematode genera associated with insects from *Pinus pinaster* in Portugal. Ann Appl Biol 148:121–131

Pennacchio F, Danti R, Benassai D et al (2013) A new additional record of *Phloeosinus armatus* Reitter from Italy (Coleoptera Curculionidae Scolytinae). Redia 96:45–50

Péricart J (1996) Family Anthocoridae Fieber, 1836 – flower bugs, minute pirate bugs. In: Aukema B, Rieger C (eds) Catalogue of the Heteroptera of the Palaearctic region, vol 2, Cimicomorpha I. The Netherlands Entomological Society, Amsterdam, pp 108–140

Pernek M (2007) Influence of the entomopathogenic fungi *Beauveria bassiana* on the mortality of fir bark beetles *Pityokteines spinidens* and *Pityokteines curvidens* (In Croatian). Radovi – Sumarski Institut Jastrebarsko 42:143–153

Pernek M, Hrašovec B, Matošević D et al (2008) Phoretic mites of three bark beetles (*Pityokteines* spp.) on silver fir. J Pest Sci 81:35–42

Pernek M, Matošević D, Hrašovec B et al (2009) Occurrence of pathogens in outbreak populations of *Pityokteines* spp. (Coleoptera, Curculionidae, Scolytinae) in silver fir forests. J Pest Sci 82:343–349

Pernek M, Wirth S, Blomquist SR et al (2012) New associations of phoretic mites on *Pityokteines curvidens* (Coleoptera, Curculionidae, Scolytinae). Cent Eur J Biol 7:63–68

Peyerimhoff P (1919) Notes sur la biologie de quelques Coléoptères phytophages du Nord africain (3ème série). Ann Soc Entomol Fr 88:169–258

Pfeffer A (1995) Zentral und westpaläarktische Borken und Kernkäfer. Naturhistorisches Museum, Basel

Podoler H, Mendel Z, Livne H (1990) Studies on the biology of a bark beetle predator, *Aulonium ruficorne* (Coleoptera: Colydiidae). Environ Entomol 19:1010–1016

Poinar GO Jr (1972) Nematodes as facultative parasites of insects. A Rev Entomol 17:103–122

Puritch GS (1981) Nonvisual remote sensing of trees affected by stress: a review. Forestry technical report BC-X- 30. Natural Resources Canada, Canadian Forestry Service, Victoria

Purrini K, Halperin J (1982) *Nosema calcarati* n. sp. (Microsporidia), a new parasite of *Pityogenes calcaratus* Eichhoff (Col., Scolytidae). Z Angew Entomol 94:87–92

Purrini K, Halperin J (1983) Studies of some protozoan parasites of the bark beetles (Scolytidae, Coleoptera) in Israel. Boll Lab Entomol Agraria 'Filippo Silvestri' 40:61–68

Raffa KF, Berryman AA (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecol Monogr 53:27–49

Rennerfelt E (1950) Über den Zusammenhang zwischen dem Verblauen des Holzes und den Insekten. Oikos 2:120–137

Romón P, Zhou X, Iturrondobeitia JC et al (2007) *Ophiostoma* species (Ascomycetes: Ophiostomatales) associated with bark beetles (Coleoptera: Scolytinae) colonizing *Pinus radiata* in Northern Spain. Can J Microbiol 53:756–767

Ross H (1965) A textbook of entomology. Wiley, New York

Rouault G, Candau JN, Lieutier F et al (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. Ann For Sci 63:613–624

Rühm W (1956) Die nematoden der Ipiden. Parasitol Schrift 6:1–437

Rühm W (1960) Ein Beitrag zur Nomenklatur und Systematik einiger mit Scolytiden vergesellschafteter Nematodenarten. Zool Anz 164:201–213

Rungs CEE (1940) Les ennemis du cèdre au Maroc. C R Soc Sc Nat Maroc 5(3):14–16

Sabbatini-Peverieri F (2010) First record of Cercoleipus Coelonotus Kinn (Acari Mesostigmata Cercomegistidae) from Italy. Redia 93:79–81

Sabbatini-Peverieri G, Faggi M, Marziali L et al (2004) Use of attractant and repellent substances to control *Tomicus destruens* (Coleoptera: Scolytidae) in *Pinus pinea* and *P. pinaster* pine forests of Tuscany. Entomologica 38:91–102

Sabbatini-Peverieri G, Capretti P, Tiberi R (2006) Associations between *Tomicus destruens* and *Leptographium* spp. in *Pinus pinea* and *P. pinaster* stands in Tuscany, Central Italy. For Pathol 36:14–20

Sabbatini-Peverieri G, Faggi M, Marziali L et al (2008) Life cycle of *Tomicus destruens* in a pine forest of central Italy. Bull Insectol 61:337–342

Safranyik L, Shrimpton DM, Whitney HS (1975) An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Cabada. In: Baumgartner D (ed) Management of lodgepole pine ecosystems. Whashington State University Cooperative Extension Service, Pullman

Sallé A, Ye H, Yart A et al (2008) Seasonal water stress and the resistance of *Pinus yunnanensis* to a bark beetle associated fungus. Tree Physiol 28:679–687

Santolamazza Carbone S, Pestaña M, Vega JA (2011) Post-fire attractiveness of maritime pine (*Pinus pinaster* Ait.) to xylophagous insects. J Pest Sci 84:343–353

Santoro AE, Lombardero MJ, Ayres MP et al (2001) Interactions between fire and bark beetles in an old grown pine forest. For Ecol Manage 144:245–254

Sarikaya O, Avci M (2010) Distribution and biology of the Mediterranean pine shoot beetle *Tomicus destruens* (Wollaston, 1865) in the western Mediterranean region of Turkey. Türkiye Entomoloji Dergisi 34:289–298

Sauvard D (1989) Capacités de multiplication de *Tomicus piniperda* L. (Col., Scolytidae). 1. Effets de la densité d'attaque. J Appl Entomol 108:164–181

Schimitschek E (1944) Forstinsekten der Türkei und ihre Umweh. Volk und Reich Verlag, Prag/Amsterdam/Berlin/Wien

Schmitt J, Goyer R (1983a) Consumption rates and predatory habits of *Scoloposcelis mississippensis* and *Lyctocoris elongatus* (Hemiptera: Anthocoridae) on pine bark beetles. Environ Entomol 12:363–367

Schmitt J, Goyer R (1983b) Laboratory development and description of immature stages of *Scoloposcelis mississippensis* Drake abd Harris and *Lyctocoris elongatus* (Reuter) (Hemiptera: Anthocoridae) predators of southern pine bark beetles (coleopteran:Scolytidae). Environ Entomol 76:868–872

Schmutzenhofer H (1981) A nematode involved in the silver for decline in Austria. In: Proceedings of the 17th IUFRO Congress, Kyoto

Schroeder L (1996) Interactions between the predators *Thanasimus formicarius* (Col.: Cleridae) and *Rhizophagus depressus* (Col.: Rhizophagidae), and the bark beetle *Tomicus piniperda* (Coleoptera: Scolytidae). Entomophaga 41:63–75

Selmi E (1989) Türkiye Ipinae (Coleoptera, Scolytidae) Türleri. İ.Ü. Orman Fakültesi, İstanbul

Settele J, Scholes R, Betts R et al (2014) Terrestrial and inland water systems. In: Field CB, Barros VR, Dokken DJ et al (eds) Climate change 2014. Impacts, adaptation and vulnerability. Part A: global and sectorial aspects. Contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge/New York, pp 271–359

Shepherd W, Goyer R (2003) Seasonal abundance, arrival and emergence patterns of predaceous hister beetles (Coleoptera: Histeridae) associated with *Ips engraver* beetles (Coleoptera: Scolytidae) in Louisiana. J Entomol Sci 38:444–452

Shepherd W, Goyer R (2005) Impact of *Platysoma parallelum* and *Plegaderus transversus* (Coleoptera: Histeridae) predation on developing *Ips calligraphus* and *Ips grandicollis* (Coleoptera: Scolytidae) brood. J Entomol Sci 40:80–87

Siemaszko W (1939) Fungi associated with bark beetles in Poland. Planta Polonica 7:1–54

Six DL (2003) Bark beetle fungal symbiosis. In: Miller T, Kourtzis K (eds) Insect symbiosis. CRC Presa, Boca Raton, pp 97–114

Six DL, Bentz BJ (2007) Temperature determines symbiont abundance in a multipartite bark beetle-fungus ectosymbiosis. Microbiol Ecol 54:112–118

Six DL, Klepzig KD (2004) *Dendroctonus* bark beetles as model systems for studies on symbiosis. Symbiosis 37:207–232

Skakun RS, Wulder MA, Franklin SE (2003) Sensitivity of the thematic mapper enhanced wetness difference index to detect mountain pine beetle red-attack damage. Remote Sens Environ 86:433–443

Skarmoutsos G, Braasch H, Michalopoulou H (1998) *Bursaphelenchus hellenicus* sp. n. (Nematoda, Aphalenchoididae) from Greek pine wood. Nematologica 44:623–629

Slobodyanyuk OV (1973) On the biology of the nematode *Parasitaphelenchus papillatus* (Aphelenchoididae) from the beetle *Blastophagus piniperda*. Trudy Gel'mintol Lab 23:155–159

Slobodyanyuk OV (1974) Biological features of the genus *Parasitorhabditis* (Rhabditidae). Trudy Gel'mintol Lab 24:160–168

Solheim H, Långström B, Hellqvist C (1993) Pathogenicity of the blue stain fungi *Leptographium wingfieldii* and *Ophiostoma minus* to Scots pine: effect of tree pruning and attack density. Can J For Res 23:1438–1443

Solheim H, Krokene P, Långström B (2001) Effects of growth and virulence of associated blue-stain fungi on host colonization behaviour of the pine shoot beetles *Tomicus piniperda* and *T. minor*. Plant Pathol 50:111–116

Stergulc F (2002) Studio sulle condizioni fitosanitarie della pineta di Valle Vecchia (Caorle, VE). Proposte per interventi di controllo del blastofago dei pini (*Tomicus destruens* Wollaston) e del marciume radicale da *Heterobasidion annosum* (Fr.). Bref Veneto Agricoltura, Settore Ricerca e Sperimentazione Forestale e Fuori Foresta, Padova

Tenkáková I, Mituch J (1987) Nematodes new for the fauna of Czechoslovak Socialist Republic with the affinity to scolytids (Coleoptera: Scolytidae). Helminthologia 24:281–291

Tenkáková I, Mituch J (1988) Nematofauna of the Scolytidae on silver fir (*Abies alba* Mill.) from the Polana region. For J Bratislava 34:125–131

Thalenhorst W (1958) Grundzüge der populationsdynamik des grössen Fichten-borkenkäfer *Ips typographus* L. Shrift Forst Fakültat Univität Göttingen 21:1–126

Tiberi R, Battisti A (1998) Relationships between phytophagous insects and cypress canker. Annali, Accademia Italiana di Scienze Forestali 47:35–44

Tinelli A, Catena G (1992) Applicazione della fotografia aerea per indagini fitosanitarie della pineta. Monti e Boschi 43:26–29

Tomalak M, Michalski J, Grocholski J (1984) The influence of nematodes on the structure of genitalia of *Tomicus piniperda* (Coleoptera: Scolytidae). J Invertebr Pathol 43:352–358

Tomiczek C (2000) A survey of *Bursaphelenchus* spp. In conifers in Austria and implications to Austria forests. In: Abstracts of the XXI IUFRO World Congress Kuala Lumpur, 6–12 Aug 2000

Triggiani O (1984) *Tomicus* (*Blastophagus*) *piniperda* (Coleoptera, Scolytidae Hylesininae): biologia, Danni e controllo nel litorale ionico. Entomologica 19:5–21

Upadhyay HP (1981) A monograph of *Ceratocystis* and *Ceratocystiopsis*. University of Georgia Press, Athens

Vega FE, Hofstetter RW (2015) Bark beetles, biology and ecology of native and invasive species. Elsevier, Oxford

Viedma MG (1964) *Hylurgus ligniperda* F., plaga de las repoblaciones de pino: sintomas de su ataque. Bol Serv Plag For 7:61–63

Vosilite BS (1990) A new nematode species, *Diplogasteroides sexdentati* sp. n. and some biological data on the ectonematodes of stenograph bark beetle. In: Sonin MD (ed) Helminths of insects. E.J. Brill, Leiden, pp 27–36

Waring RH, Pitman GB (1980) A simple model of host resistance to bark beetles, Res note 65. Oregon State University, School of Forestry, Corvallis

Wegensteiner R (2004) Pathogens in bark beetles. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer, Dordrecht, pp 291–313

Wegensteiner R, Wermelinger B, Herrmann M (2015) Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes. In: Vega FE, Hofstetter RW (eds) Bark beetles: biology and ecology of native and invasive species. Elsevier, Oxford, pp 247–304

Whitney HS (1982) Relationships between bark beetles and symbiotic organisms. In: Mitton JB, Sturgeon KB (eds) Bark beetles in North American conifers. University of Texas Press, Austin, pp 183–211

Wingfield MJ, Gibbs JN (1991) *Leptographium* and *Graphium* species associated with pine-infesting bark beetles in England. Mycol Res 95:1257–1260

Wingfield MJ, Knox-Davies PS (1980) Root-disease, associated with *Verticicladiella alacris*, of pines in South Africa. Plant Dis 64:569–571

Wingfield MJ, Marasas WFO (1983) Some *Verticicladiella* species, including *V. truncata* sp. nov., associated with root diseases of pine in New Zealand and South Africa. Trans Br Mycol Soc 80:231–236

Wingfield MJ, Capretti P, Mackenzie M (1988) *Leptographium* spp. As roots pathogens on conifers. An international perspective. In: Harrington TC, Cobb FW Jr (eds) *Leptographium* diseases on conifers. American Phytopathological Society, St. Paul, pp 113–128

Wood DL (1982) The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. A Rev Entomol 27:411–446

Wulder MA, Skakun RS, Dymond CC et al (2005) Characterization of the diminishing accuracy in detecting forest insect damage over time. Can J Rem Sens 31:421–431

Wulder MA, Dymond CC, White JC et al (2006a) Detection, mapping, and monitoring of the mountain pine beetle. In: Safranyik L, Wilson B (eds) The mountain pine beetle – a synthesis of biology, management, and impacts on lodgepole pine. Natural Resources Canada, Canadian Forestry Service, Victoria, pp 123–154

Wulder MA, Dymond CC, White JC et al (2006b) Surveying mountain pine beetle damage of forests: a review of remote sensing opportunities. For Ecol Manage 221:27–41

Zocchi R (1956) Insetti del cipresso Il Gen. *Phloeosinus* Chap. in Italia. Redia 41:129–225

Zverera E, Kozlov V (2006) Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a metaanalysis. Glob Chang Biol 12:27–41

Chapter 7
Native Buprestid and Longhorn Beetles in the Mediterranean Basin

Aurélien Sallé

7.1 Introduction

Several species of Cerambycidae and Buprestidae have been reported as tree pests in the Mediterranean Basin. They are mostly considered as secondary pests, which preferentially colonize trees injured by inappropriate silvicultural practices or weakened by biotic or abiotic stresses, like a water deficit for instance (Schaefer 1949; Bouhraoua et al. 2002; Naveiro et al. 1999; Sallé et al. 2014). Therefore, these beetles can play a prominent role as inciting factors during forest declines (Sallé et al. 2014). In this regard, it is not surprising that most of the species reported here particularly affect *Quercus suber* L. and *Q. ilex* L. since both oak species are experiencing a widespread dieback since the 1980s in the Mediterranean Basin (Brasier 1992; Costa et al. 2010). The frequency and extent of forest declines will probably increase in the future and, in southern Europe, recent forest declines have already been attributed to the climate change (Allen et al. 2010; Carnicer et al. 2011). Consequently, both the ecological and economical importance of the longhorn and buprestid beetles presented in this chapter is likely to grow in the next decades (Sallé et al. 2014).

Some of these species can be considered also as primary pests, infesting apparently healthy trees, like the buprestids *Coraebus florentinus* Herbst and *C. undatus* F. (Evans et al. 2004). The longhorn *Cerambyx welensii* Küster has also become more aggressive recently, apparently as a consequence of changes in silvicultural practices (Naveiro et al. 1999; Torres-Vila et al. 2012).

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7.2 Longhorns

7.2.1 *General Presentation*

In the Mediterranean Basin, three species of longhorns may cause significant damage on broadleaved forest trees, especially on oaks: *C. welensii*, *Prinobius myardi* Mulsant and *Cerambyx cerdo* L. In the Iberian Peninsula, two species dominate: *C. welensii* and, to a lesser extent, *P. myardi* (Lopez et al. 2004; Naveiro et al. 1999), while *C. cerdo* is the prominent species in Northern Africa, and several European countries (Bouhraoua et al. 2002; Gonzalez et al. 2010; Kenis and Hilszczanski 2004; Villemant and Fraval 1993). The tunneling activity of these xylemophagous species result in significant physiological and mechanical damage. Galleries bored in the inner bark and the sapwood, together with the induced compartmentalization of host tissues in response to attack (Shigo 1984), can affect sap conduction, and therefore the crown condition. Infestation can increase leaves fall and induce visible drying of branches, sometimes over a significant part of the crown (Bouhraoua et al. 2002; Gonzalez et al. 2010). In addition to this direct damage, the wide emergence holes of these beetles, up to 2 cm diameter for *C. cerdo*, may act as entryways to inner tree tissues for plant pathogens (Martin et al. 2005; Villemant and Fraval 1993). For instance, in Spain, the density of *Cerambyx* spp. emergence holes on infested *Q. suber* correlated with subsequent infection by the fungal pathogen *Biscogniauxia mediterranea* (De Not) Kunze (Martin et al. 2005). Regarding the interactions with microorganisms it should be mentioned that longhorn beetles might also serve as vectors of tree pathogens. One the best example is the vection by *Monochamus* species of the invasive pine wood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle, responsible of the pine wilt disease (Sousa et al. 2001). These longhorns are generally considered of low, or occasionally medium, aggressiveness in southern Europe (Evans et al. 2004), but the vection of *B. xylophilus* by *Monochamus galloprovincialis* (Olivier) could dramatically change the extent and composition of the pine stands in southern Europe (see Chap. 12).

Finally, the activity of these big longhorn species also creates an extended network of galleries and an accumulation of dead wood on decaying trees, thereby generating particular habitats colonized by specific microbiota and fauna, including rare saproxylic species (Buse et al. 2008; Villemant and Fraval 1993). In this context, *C. cerdo* can be regarded as an ecosystem engineer, which activity promotes biodiversity (Buse et al. 2008).

7.2.2 *The Species*

Cerambyx welensii Küster. It is a 25–60 mm-long longhorn, blackish-brown. *Cerambyx velutinus* Brullé is a synonym of *C. welensii* (Sama 2013). This species can be encountered in Europe, mostly in the Mediterranean countries and warm regions of central Europe, and in the Middle East (Berger 2012; Sama et al. 2010). The host range includes oaks, especially *Q. suber* and *Q. ilex*, but this insect can also develop in willow, poplars and carob trees (Berger 2012; Vives 2000).

Adults are crepuscular or nocturnal and mainly feed on tree exudates or ripe fruits. They are rather sedentary and may feed, mate and lay eggs on the same tree (Lopez-Pantoja et al. 2008; Torres-Vila et al. 2012, 2013). The propensity to dispersal might be density-dependant however, and stimulated by intraspecific competition when population density is high (Torres-Vila et al. 2012). The beetles can fly over several hundreds of meters, but the estimated average dispersion ranges from 20 to 100 m for both males and females (Torres-Vila et al. 2012, 2013). Males are territorial and can fight for a tree, trees being both a mating area and a food resource (Lopez-Pantoja et al. 2008; Torres-Vila et al. 2012). This is a univoltine insect. Larval development can last for 2 to 3 years. Larvae start their development in the inner bark and then tunnel into the sapwood and the heartwood. The galleries can extend from the collar to the main branches (Torres-Vila et al. 2012). Pupation occurs in a pupal cell in the sapwood, where adults overwinter. Following the emergence from their host tree, the adults are active from spring until the end of summer (Berger 2012; Torres-Vila et al. 2013). They probably have a short life span, ranging from a few weeks to a month (Torres-Vila et al. 2012). Electroantennography investigations indicated that *C. welensii* can perceive monoterpenes emitted by evergreen oaks leaves (Sanchez-Osorio et al. 2009), and was attracted by synthetic blends mimicking fermentation-related volatile compounds (Torres-Vila et al. 2012, 2013; Sanchez-Osorio et al. 2015). Both stimuli probably help the adults to find suitable hosts and food sources.

Among the bark and wood boring species acting as inciting factors during oak declines, this longhorn is considered as the most damaging insect in the Iberian Peninsula (Carrasco 2009; Torres-Vila et al. 2012). In this area, damage has increased since the last decades. Previously restricted to decaying trees, the beetles are now frequently encountered on healthy trees (Torres-Vila et al. 2012, 2013). This is apparently linked with changes in silvicultural practices and mismanagement of dehesa ecosystems (Naveiro et al. 1999; Torres-Vila et al. 2012).

No biological control is currently used to manage this longhorn. Except raptors such as the tawny owl, *Strix aluco* L. (Fattorini et al. 2001), predators or parasitoids of this longhorn or not known (Kenis and Hilszczanski 2004). *Cerambyx welensii* can be infected by the entomopathogenic fungus *Beauveria bassiana* (Bals.-Criv.) Vuill., which could potentially be used as a control agent (Morales-Rodriguez et al. 2015). Chemical control is seldom applied because of practical and environmental issues (Torres-Vila et al. 2012). Mass trapping might be interesting and efficient to manage this insect, especially considering that population densities, even in damaged areas, are generally low (Lopez-Pantoja et al. 2008; Torres-Vila et al. 2012). Yet it is not currently operational (Torres-Vila et al. 2013; Sanchez-Osorio et al. 2015).

Prinobius myardi Mulsant. It is a 30–50 mm long, blackish-brown longhorn. *Prionius germari* Dejean, *P. scutellaris* Germar, *Macrotoma germari* Chevrolat, *Prinobius proksi* Slama, *P. atropos* Chevrolat, *P. cedri* Marseul, *P. gaubili* Chevrolat, *P. goudoti* Chevrolat, *P. lethifer* Fairmaire are synonyms of *P. myardi* (Berger 2012; Sama 2013). This species is distributed throughout the Mediterranean Basin, Caucasus and the Near East (Sama et al. 2010; Lopez-Pantoja et al. 2011; Berger 2012). It develops preferentially in evergreen oaks, especially *Q. ilex* and *Q. suber*. It has also been reported in several other broadleaved trees including ash, maple, poplar, willow, alder, olive tree, white mulberry, eucalyptus, plane tree and fruit trees (Navarro et al. 2008; Berger 2012).

Adults have nocturnal habits and apparently do not feed. In the daytime they rest in larval galleries or under dehiscent bark fragments. Larval development takes several years. Larvae bore galleries in the sapwood of trunks or main branches of their host tree. Pupation occurs in spring. Adults emerge through typical elliptical exit holes and are active in summer, generally later than *C. welensii* (Lopez-Pantoja et al. 2011; Berger 2012).

To our knowledge, there is no known natural enemy of this longhorn. This species is frequently observed in decaying cork and holm oaks in the Iberian Peninsula and is therefore considered as an aggravating factor of oak declines in this area (Lopez-Pantoja et al. 2011). It is often associated with *C. welensii* in decaying oaks (Naveiro et al. 1999; Sanchez-Osorio 2005; Lopez-Pantoja et al. 2011; Torres-Vila et al. 2013). However, it seems to be a more secondary pest than *C. welensii*, and rather preferentially colonizes trees previously damaged by this latter species (Torres-Vila et al. 2013).

Cerambyx cerdo L. The great capricorn beetle is 24–62 mm long, blackish-brown. *Cerambyx acuminatus* Motschulsky, *C. heros* Scopoli, *C. luguber* Voet, and *Hammaticherus pfisteri* Stierlin are synonyms of *C. cerdo* (Berger 2012; Sama 2013). There are two subspecies, *C. cerdo mirbeckii* Lucas, and *C. cerdo cerdo* L. (Sama 2013). *Cerambyx cerdo mirbeckii* is encountered mostly in the southern rim of Mediterranean Sea, but has also been reported from the Iberian Peninsula (Peris-Felipo et al. 2008; Sama 2013). *Cerambyx cerdo cerdo* has a western Palaearctic distribution, and is present throughout Europe, Northern Africa and Asia Minor (Sama et al. 2010). *Cerambyx cerdo* is a red-listed species in Europe, very rare or extinct in the northern margin of its range, but it can be abundant in some areas, especially in the Mediterranean Basin (Evans et al. 2004; Berger 2012). It develops in various oak species, including *Quercus petraea* (Matt.) Liebl., *Q. robur* L., *Q. pubescens* Willd., *Q. ilex* and *Q. suber*. It has also been mentioned in ash, elm, alder and chestnut trees (Berger 2012).

The adults are active at dusk, and live from 2 weeks to 2 months, feeding on bark exudates or on ripe fruits (Neumann 1985; El Antry 1999). These insects preferentially colonize sun-exposed, large trees (Buse et al. 2007). They are attracted by fermentation-related compounds and can probably detect suitable host-trees on a long-range (Dajoz 2007). This longhorn species lacks prothoracic glands frequently involved in sex pheromones emission (Ray et al. 2006), and consequently probably relies on antennal contact to detect females walking on the bark of their host tree, where mating occur (Hanks 1999). Females can lay up to 300 eggs. They are laid separately in bark cracks, in the lower portion of the trunk. Larval development starts in the inner bark but continue in the sapwood and the heartwood. Depending on climatic conditions, it can last from 2 to 5 years. Pupation occurs in a pupal cell, where adults overwinter before emergence. Adults emerge in spring and summer making exit holes that can be up to 2 cm diameter. These exit holes are located mainly in sun-exposed parts of the trunk, nearby the ground (Neumann 1985; El Antry 1999; Albert et al. 2012; Berger 2012).

Few natural enemies have been described, the most common being the egg parasitoid *Oobius rudnevi* (Novicki). Several ichneumonids, namely *Dolichomitus imperator* (Kriechbaumer), *D. tuberculatus* (Geoffroy), *Ephialtes manifestor* (L.) and *Ontsira longicaudis* (Giraud) can also attack this species (Kenis and Hilszczanski 2004). Raptors such as the eagle owl, *Bubo bubo* (L.), can also prey on *C. cerdo* (Papageorgiou et al. 1993).

Cerambyx cerdo develops preferentially in weakened or senescent veteran oaks. Occasionally recorded as a pest in Europe, it is more commonly involved in severe oak declines in the southern rim of the Mediterranean Sea (Villemant and Fraval 1993; Bouhraoua et al. 2002; Kenis and Hilszczanski 2004; Gonzalez et al. 2010). In particular, the subspecies *C. cerdo mirbeckii* is frequently involved in extensive damage on cork oaks (Villemant and Fraval 1993; Bouhraoua et al. 2002).

7.3 Buprestids

Three species of buprestid beetles can be considered as Mediterranean pests: *C. florentinus*, *C. undatus* and *Trachypteris picta* (Pallas). These three species develop in broadleaved trees. They are not geographically restricted to the Mediterranean Basin but their damage incidence is more pronounced in this area (Evans et al. 2004). On conifers, *Phaenops cyanea* (F.) can also cause, on occasion, extensive damage to pine stands in the Mediterranean area (Pozo et al. 1995), but this species is more frequently reported as a pest in western and central Europe, and Scandinavia (Evans et al. 2004).

Coraebus florentinus Herbst. This is a borer developing in oak branches. *Buprestis florentinus* Herbst, *B. fasciatus* Villers, *B. bifasciatus* Olivier, *Agrilus semiviolaceus* Pic, *Coraebus mequignoni* Obenberger, *C. obscuricolor* Pic, *C. obscurior* Pic, *C. trifasciatus* Regimbeau, *C. aethiops* Obenberger, *C. obscuricollis* Pic are synonyms of *C. florentinus* (Théry 1942; Kuban and Bily 2013). This buprestid occurs in western and central Europe, and has been mentioned in Northern Africa (Cardenas and Gallardo 2012; Kuban and Bily 2013). It is more frequent in southern Europe, where most damage occur, but recently its geographical range has increased northwardly, together with damage records, as a consequence of global warming (Buse et al. 2013; Sallé et al. 2014). *Coraebus florentinus* colonizes the branches of various oak species, including *Quercus robur*, *Q. ilex*, *Q. suber*, *Q. pubescens*, *Q.*

faginea Lam., *Q. canariensis* Willd., *Q. cerris* L., *Q. coccifera* L., *Q. pyrenaica* Willd. and *Q. petraea*. It can also be found in the branches of chestnut, *Castanea sativa* Mill. (Schaefer 1949; Cardenas and Gallardo 2012).

Adults are 12–16 mm long, shiny green with an alternation of transverse lines, blackish or bluish and whitish, on the last third of the elytra. In summer, females lay eggs on the branches, preferentially close to the tip of 1- or 2-year old shoots (Schaefer 1949; Cardenas and Gallardo 2012). This buprestid is heliophilous and thermophilous and consequently preferentially lays its eggs on sun-exposed branches (Cardenas and Gallardo 2013). The larval development can last from 2 to 4 years. The development is shortened when temperature rise, at least, up to 28 °C suggesting a high thermal optimum (Cardenas and Gallardo 2012). Larvae start tunneling in the inner bark but last instars dig into the sapwood. Galleries are orientated from the tip to the base of the branch and can be up to 1.5 m long (Schaefer 1949). Before the last molt, the fifth instar larva digs a circular gallery in the inner bark, interrupting sap flow. Finally, the larva moves upwards and excavates a pupal cell in the sapwood of the dry branch (Schaefer 1949; Cardenas and Gallardo 2012). Pupation occurs in spring and the emergence of adults from trees spans from spring to summer. It results in typical D-shaped holes in the bark (Schaefer 1949). Following emergence from their host, adults perform a maturation feeding on leaves, where they mate. Several compounds have been collected from males and females, and three of them elicited antennal response in males (Fürstenau et al. 2012). In addition, behavioral assays have indicated that some of these compounds were attractive for females (geranylacetone) or males (decanal). This suggests a production of sex pheromones by the females (Fürstenau et al. 2012). Green leaf volatiles from *Q. suber* also elicited responses from both males and females of *C. florentinus* during electroantennography assays. Some of these compounds were also attractive for females and might therefore play a role in host selection for maturation feeding and/or oviposition (Fürstenau et al. 2012).

This buprestid can colonize the crowns of apparently healthy trees. Damage, until recently, mostly occurred in the Mediterranean area (Schaefer 1949; Evans et al. 2004; Dajoz 2007; Sallé et al. 2014). For evergreen oaks leaves of colonized branches turn red, while they fall prematurely for deciduous tree species (Schaefer 1949). Ultimately, larval activity results in the drying and death of branches, sometimes over a significant part of the crown. This leads to significant aesthetic impacts and contributes to further weaken the host-tree. In addition, as for other bark and wood boring insects, emergence holes might serve as entry holes for plant pathogens. In this regard, it has been suggested that the plant pathogenic fungus *Diplodia mutila* Fr. Apud Mont. could be vectored by *C. florentinus*, from infested, decaying, larval host to novel host-trees (Tiberi and Ragazzi 1998). However, transmission of fungal pathogens to host plants by *C. florentinus* has never been reported and since oviposition occurs outside host tissues, it is unsure that they could be efficient vectors of pathogenic fungi.

Solinas (1974) has described several species of parasitoids for *C. florentinus* in Italy. Parasitoids were different according to larval instars. Second and third instars were attacked by *Spathius radjabii* Fisher, fourth and fifth instars by two braconid species, and the last instar by an ichneumonid wasp, named *Cryptus maculipennis* Dufour, which unfortunately cannot be currently found in ichneumonid nomenclature (Schaefer 1949; Kenis and Hilszczanski 2004). This parasitoid is considered as an important regulation factor for the populations of *C. florentinus* (Solinas 1974). In addition the ichneumonid wasps *Rimphoctona megacephalus* (Gravenhorst), *Echthrus reluctator* L. and *Xylophrurus coraebi* Thomson, the braconid *Polystenus rugosus* (Foester) and the eupelmid *Eusandalum ibericum* (Bolivar and Pieltrain) have been recorded as parasitoids of this buprestid (Schaefer 1949; Kenis and Hilszczanski 2004). The buprestid larvae and adults can also be preyed on by woodpeckers and the wasp *Cerceris bupresticida* Dufour, and the larvae only can be attacked by the Bothrideridae *Ogmoderes angusticollis* Bris. and the clerid *Denops albofasciatus* Charp. (Théry 1942; Schaefer 1949; Kenis and Hilszczanski 2004). Current management strategies rely mostly on curative control, through the cutting and destruction of infested branches before the emergence of adults (Schaefer 1949; Evans et al. 2004).

Coraebus undatus Fabricius. This is a borer colonizing the bark of oaks, and a significant pest of cork production. *Buprestis undatus* Fabricius, *B. pruni* Panzer, *Coraebus coeruleotinctus* Obenberger are synonyms of *C. undatus* (Kuban and Bily 2013). This is a Palaeartic species occurring in western and central Europe, and North Africa (Schaefer 1949; Kuban and Bily 2013). This buprestid colonizes preferentially oaks like *Q. suber*, *Q. robur*, *Q. pubescens*, *Q. ilex* and *Q. pyrenaica* (Schaefer 1949). It is also mentioned on chestnut trees, poplar, beech, hazel, Japanese persimmon and pine (Théry 1942; Schaefer 1949; Jimenez et al. 2012).

Adults are 10–14 mm long, bronzed and bluish or greenish with sinuous lines, whitish or grayish, on the elytra. Females lay their eggs in bark crevices of the trunk or main branches, preferentially on the sun-exposed sides (Du Merle and Attié 1992). Two to three weeks later, eggs hatch and the larvae dig into the cork, down to the upper layer of the inner bark, the phellogen and the phelloderm (Evans et al. 2004). The larval development lasts from 1 to 3 years during which larvae tunnel in the phelloderm, but may also excavate superficial galleries in the rhytidome or in the sapwood (Du Merle and Attié 1992, Romanyk and Cadahia in Evans et al 2004; Jimenez et al. 2012). Galleries can be up to 2 m long. After five larval instars, larvae excavate a pupal cell in the cork. Adults emerge at the end of spring, leaving their host tree through typical D-shaped holes. They perform a maturation feeding on leaves, where they mate. Field trapping has demonstrated that females were attracted by green leaf volatiles emitted by *Q. suber*, but also by visual cues, suggesting that both stimuli could be involved in host and/or mate detection (Fürstenau et al. 2015).

In spite of its economic importance, the natural enemies of *C. undatus* have not been investigated (Kenis and Hilszczanski 2004). To our knowledge, only the eulophid wasp *Cirrospilus acasta* Walker has been mentioned as a parasitoid of this buprestid (Gonzalez and Matthews 2005).

Coraebus undatus is considered a significant pest of cork oaks throughout the Mediterranean Basin, where cork is harvested (Du Merle and Attié 1992; Jimenez et al. 2012). Larval galleries in the inner bark affect the cork generating tissues and the formation of the new cork layer. They also induce the formation of adherences between the cork and the phellogen layer, impeding cork harvest and production (Gallardo et al. 2012). In addition, the pupal cells in the cork decrease its economic value (Evans et al. 2004). For this, this insect is considered as one of the major pests of cork production (Du Merle and Attié 1992; Soria et al. 1992; Gallardo et al. 2012). Repeated attacks by *C. undatus* may also weaken the host-tree, favor its infection by parasites and pathogens, and ultimately lead to tree death (Evans et al. 2004; Gallardo et al. 2012). During a survey in southern Spain, *C. undatus* was found in most of the cork oaks forests investigated and 28–99 % of trees were infested (Jimenez et al. 2012). Most of the infested forests exhibited low damage levels, but almost a third of them medium to high damage levels (Jimenez et al. 2012). In Extremadura (Spain), it is estimated that this pest causes an average annual economic loss of five million euros (Gallardo et al. 2012). This buprestid is frequently involved in cork and holm oaks declines in the Iberian Peninsula, but has been also reported in other oak declines in European countries (Evans et al. 2004; Sallé et al. 2014). Stand conditions like tree density, understory type, altitude and orientation can modulate the level of damage undergone by the cork oak forests (Du Merle and Attié 1992; Jimenez et al. 2012).

Trachypteris picta (Pallas). This insect is a borer colonizing poplars. There are three subspecies, *T. picta picta* (Pallas) with an oriental distribution, *T. picta indica* (Théry) occurring in India, and *T. picta decostigma* F. with an occidental distribution, the latter subspecies is apparently the only one occurring in the Mediterranean Basin. *Melanophila picta* (Pallas), *M. silphoides* (Schrank), *M. chrysostigma* F., *M. quatuordecimpunctata* (Olivier), *M. anatolica* Pic, *M. henoni* Bedel are synonyms of *T. picta decostigma* (Kuban and Bily 2013). *Trachypteris picta decostigma* F. is distributed throughout southern, central and eastern Europe, Near East and North Africa (Schaefer 1949). It has also been introduced in South America (Moore 1986). This insect develops in poplars like *Populus nigra* L., *P. alba* L. and *P. x canadensis* Moench., and willows like *Salix alba* L. It may also develop in ash (Théry 1942; Schaefer 1949; Georgiev and Doychev 2010).

The adults are 9–14 mm long, bronzed with yellow spots on the elytra. This is a monovoltine species. The females lay their eggs in spring or beginning of summer, in bark crevices or around buds in the lower part of the trunk. A female can lay on average 100 eggs. The larvae dig galleries that can be up to 10 cm long, firstly in the inner bark then into the sapwood. The last larval instar overwinters in the sapwood. In spring larvae molt into a pre-pupa, followed by a pupa. The last molt occurs in a pupal cell located in the bark or in the superficial layers of sapwood. The adults emerge in spring and summer (Schaefer 1949; Kailidis 1966; Babmorad et al. 2008).

A few parasitoid species have been recorded for *T. picta*. The records comprise ichneumonid wasps like *Dolichomitus* sp. and *Atractogaster semisculptus* Kriechbaumer, which is probably a hyperparasitoid, the braconids *Iphiaulax impostor* (Scopoli), *Spathius curvicaudis* Ratzeburg, *S. melanophilae* Fisher and *Atanycolus ivanowi* (Kokujev), and the chalcid *Cratocentrus fastuosus* Masi (Kenis and Hilszczanski 2004). The buprestid can also be preyed on by the green woodpecker, *Picus viridis* L. (Kenis and Hilszczanski 2004).

Trachypteris picta mostly colonizes freshly killed or felled trees but can also infest weakened hosts, especially trees experiencing a water deficit (Schaefer 1949). This buprestid is also considered a major pest of young poplars in plantations or nurseries in the Mediterranean area, especially in Greece and the Iberian Peninsula, but also in central Europe and Middle East (Schaefer 1949; Kailidis 1966, 1970; Evans et al. 2004; Babmorad et al. 2008; Georgiev and Doychev 2010). The galleries weaken the infested trees and make them prone to windbreak. An infestation can rapidly lead to dieback of young trees (Schaefer 1949).

Chemical control has been used to manage this buprestid in young poplar plantations. A good control of pest population was achieved, but the efficiency varied according to the application mode and period (Kailidis 1966; Gul and Chaudhry 1980; Avtzis 2001). Susceptibility varies among poplar genotypes suggesting that host resistance could also be used to control this pest (Kailidis 1966; Adabi et al. 2013). Finally inappropriate silvicultural practices may favor this pest as damage is higher on trees growing on dry soils or with low irrigation levels (Kailidis 1966; Lapietra and Allegro 1990; Adabi et al. 2013).

References

Adabi ST, Sadeghi SE, Bagheri R (2013) Effect of irrigation intervals and poplar clones on density of *Chrysomela populi* (Col. Chrysomelidae) and *Melanophila picta* (Col. Buprestidae) in Karaj area. Iran J For Range Prot Res 10:120–129

Albert J, Platek M, Cizek L (2012) Vertical stratification and microhabitat selection by the great capricorn beetle (*Cerambyx cerdo*) (Coleoptera: Cerambycidae) in open-grown, veteran oaks. Eur J Entomol 109:553–559

Allen CD, Macalady AK, Chenchouni H et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259:660–684

Avtzis DN (2001) Control of the most dangerous insects of Greek forests and plantations. In: Liebhold AM, Mcmanus ML, Otvos IS, Fosbroke SLC (eds) Proceedings of integrated management and dynamics of forest defoliating insects, Victoria, pp 1–5

Babmorad M, Abaei M, Zeynali S (2008) Biological study of *Melanophila* (= *Trachypteris*) *picta* (Col.: Buprestidae) in Karaj. Appl Entomol Phytopathol 75:55–71

Berger P (2012) Coléoptères Cerambycidae de la faune de France continentale et de Corse: actualisation de l’ouvrage d’André Villiers, 1978. A.R.E, Perpignan

Bouhraoua RT, Villemant C, Khelil MA et al (2002) Situation sanitaire de quelques subéraies de l’ouest algérien: impact des xylophages. IOBC/WPRS Bull 25:85–92

Brasier CM (1992) Oak tree mortality in Iberia. Nature 360:539

Buse J, Schröder B, Assmann T (2007) Modelling habitat and spatial distribution of an endangered longhorn beetle – a case study for saproxylic insect conservation. Biol Conserv 137:372–381

Buse J, Ranius T, Assmann T (2008) An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. Conserv Biol 22:329–337

Buse J, Griebeler EM, Niehuis M (2013) Rising temperatures explain past immigration of the thermophilic oak-inhabiting beetle *Coroebus florentinus* (Coleoptera: Buprestidae) in south-west Germany. Biodivers Conserv 22:1115–1131

Cardenas AM, Gallardo P (2012) The effect of temperature on the preimaginal development of the jewel beetle, *Coroebus florentinus* (Coleoptera: Buprestidae). Eur J Entomol 109:21–28

Cardenas AM, Gallardo P (2013) The effects of oviposition site on the development of the wood borer *Coroebus florentinus* (Coleoptera: Buprestidae). Eur J Entomol 110:135–144

Carnicer J, Coll M, Ninyerola M et al (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proc Natl Acad Sci 108:1474–1478

Carrasco A (2009) Procesos de decaimiento forestal (la Seca): situacion del conocimiento. Consejeria de Medio Ambiente, Junta de Andalucia, Cordoba

Costa A, Pereira H, Madeira M (2010) Analysis of spatial patterns of oak decline in cork oak woodlands in Mediterranean conditions. Ann For Sci 67:204–214

Dajoz R (2007) Les insectes des forêts. Rôle et diversité des insectes dans le milieu forestier. Lavoisier Tec & Doc, Paris

Du Merle P, Attié M (1992) *Coroebus undatus* (Coleoptera: Buprestidae) sur chêne liège dans le Sud-Est de la France: estimation des dégâts, relations entre ceux-ci et certains facteurs du milieu. Ann Sci For 49:571–588

El Antry S (1999) Biologie et dégâts de *Cerambyx cerdo mirbecki* Lucas (Coleoptera: Cerambycidae) en suberaie de la Mamora (Maroc). IOBC/WPRS Bull 22:59–67

Evans HF, Moraal LG, Pajares JA (2004) Biology, ecology and economic importance of Buprestidae and Cerambycidae. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Berlin, pp 447–474

Fattorini S, Manganaro A, Salvati L (2001) Insect identification in pellet analysis: implications for the foraging behaviour of raptors. Buteo 12:61–66

Fürstenau B, Rosell G, Guerrero A et al (2012) Electrophysiological and behavioral responses of the black-banded oak borer, *Coroebus florentinus*, to conspecific and host-plant volatiles. J Chem Ecol 38:378–388

Fürstenau B, Quero C, Riba JM et al (2015) Field trapping of the flathead oak borer *Coroebus undatus* (Coleoptera: Buprestidae) with different traps and volatile lures. Insect Sci 22:139–149

Gallardo A, Jimenez A, Antonietty CA et al (2012) Forecasting infestation by *Coroebus undatus* (Coleoptera, Buprestidae) in cork oak forests. Int J Pest Manag 58:275–280

Georgiev GT, Doychev D (2010) New xylophagous beetles (Insecta: Coleoptera) on poplars in Bulgaria. Acta Zool Bulg 62:175–179

Gonzalez JM, Matthews RW (2005) An annotated bibliography of *Melittobia* (Hymenoptera: Eulophidae). Caribb J Sci 8:1–41

Gonzalez E, Gallego D, Gutierrez JLL et al (2010) Propuesta de una metodología para la determinación de los niveles de infestación por *Cerambyx cerdo* (Linnaeus 1758)(Coleoptera: Cerambycidae). Evaluación de los niveles de infestación en Malllorca, año 2009. Bol Sanid Veg Plag 36:157–164

Gul H, Chaudhry MI (1980) Efficacy of granular insecticides against flat-headed poplar borer *Melanophila picta* Pall (Buprestidae, Coleoptera). Pak J For 30:81–87

Hanks LM (1999) Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annu Rev Entomol 44:483–505

Jimenez A, Gallardo A, Antonietty CA et al (2012) Distribution of *Coroebus undatus* (Coleoptera: Buprestidae) in cork oak forests of southern Spain. Int J Pest Manag 58:281–288

Kailidis DS (1966) *Melanophila picta* Pall. (= *decastigma* F.) a dangerous insect on our new poplar plantations. Delt Ereun Stath Dasik Ereun Makedon Thrakes, Thessalonika

Kailidis DS (1970) The poplar insect problem in Greece. Anz Schädlingskd Pfl 43:167–171

Kenis M, Hilszczanski J (2004) Natural enemies of Cerambycidae and Buprestidae infesting living trees. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer Academic Press, Dordrecht, pp 475–498

Kuban V, Bily S (2013) Fauna Europaea: Buprestidae. In: Alonso-Zarazaga MA Fauna Europaea: Coleoptera 1. Fauna Europaea version 2.6.2. http://www.faunaeur.org

Lapietra G, Allegro G (1990) Insects damaging poplars in Italy during 1987–89, control strategies and future perspectives. In: Proceedings-Working Party on insects and other animal pests, FAO International Poplar Commission, Rome, pp 31–36

Lopez G, Dominguez L, Sanchez I et al (2004) Population ecology of xylophagous beetles (Coleoptera: Cerambycidae) in mediterranean *Quercus* forest (southwest of Iberian Peninsule). Incidencie on oak trees health (*Quercus ilex* L. spp *ballota* and *Quercus suber* L.). In: Arianoutsou M, Papanastasis VP (eds) Ecology, conservation and management of Mediterranean climate ecosystems. Proceedings of the 10th MEDECOS conference, Rhodes, pp 66–74

Lopez-Pantoja G, Nevado L, Sanchez-Osorio I (2008) Mark-recapture estimates of the survival and recapture rates of *Cerambyx welensii* Küster (Coleoptera cerambycidae) in A cork oak dehesa in Huelva (Spain). Cent Eur J Biol 3:431–441

Lopez-Pantoja G, Dominguez L, Sanchez-Osorio I (2011) Analysis of *Prinobius myardi* Mulsant population dynamics in a Mediterranean cork oak stand. Ann Soc Entomol Fr 47:260–268

Martin J, Cabezas J, Buyolo T et al (2005) The relationship between *Cerambyx* spp. damage and subsequent *Biscogniauxia mediterranum* infection on *Quercus suber* forests. For Ecol Manag 216:166–174

Moore T (1986) Aporte al conocimiento de los bupréstidos de Chile (Coleoptera: Buprestidae). Tercera contribución. Rev Chil Entomol 13:37–46

Morales-Rodriguez C, Sanchez-Gonzalez A, Conejo-Rodriguez Y et al (2015) First record of *Beauveria bassiana* (Ascomycota: Clavicipitaceae) infecting *Cerambyx welensii* (Coleoptera: Cerambycidae) and pathogenicity tests using a new bioassay method. Biocontrol Sci Technol (in press)

Navarro J, Urbano JM, Llinares A (2008) Especímenes vivos y muertos de *Prinobius myardi* Mulsant, 1842 (Coleoptera, Cerambycidae, Prioninae, Prinobiini) bajo cortezas de eucalipto en Cádiz (Andalucía, España). Bol Soc Andal Entomol 15:44–49

Naveiro F, Pulido F, Gonzalez MA et al (1999) Situación fitosanitaria del arbolado de las dehesas en Extremadura: influencia de las labores selvicolas. Bol Sanid Veg Plag 25:425–433

Neumann V (1985) Der Heldbock: Cerambyx cerdo, Die Neue Brehm-Bücherei. Ziemsen Verlag, Wittenberg

Papageorgiou NK, Vlachos CG, Bakaloudis DE (1993) Diet and nest site characteristics of eagle owl (*Bubo bubo*) breeding in two different habitats in north-eastern Greece. Avocetta 17:49–54

Peris-Felipo FJ, Moreno-Mari J, Oltra-Moscardo MT et al (2008) Cerambícidos (Coleoptera: Cerambycidae) capturados en el Parque Natural de La Tinença de Benifassà (Castellón, España). Bol Aso Esp Entomol 32:95–116

Pozo ED, Garcia F, Monreal JA (1995) Note on A severe attack by the buprestid *Phaenops cyanea* (F.) on a grove of *Pinus nigra* Arnold in Sierra del Segura. Albacete. Bol Sanid Veg Plag 21:475–479

Ray AM, Lacey ES, Hanks LM (2006) Predicted taxonomic patterns in pheromone production by longhorned beetles. Naturwissenschaften 93:543–550

Sallé A, Nageleisen LM, Lieutier F (2014) Bark and wood boring insects involved in oak declines in Europe: current knowledge and future prospects in a context of climate change. For Ecol Manag 328:79–93

Sama G (2013) Fauna Europaea: Cerambycidae. In: Audisio P (ed) Fauna Europaea: Coleoptera 2. Fauna Europaea version 2.6.2. http://www.faunaeur.org

Sama G, Buse J, Orbach E et al (2010) A new catalogue of the Cerambycidae (Coleoptera) of Israel with notes on their distribution and host plants. Munis Entomol Zool 5:1–55

Sanchez-Osorio I (2005) Orientación olfativa de *Cerambyx welensii* Küster y *Prinobius germari* Dejean, principales cerambícidos xilófagos de encina (*Quercus ilex* L. subsp. *ballota*) y alcornoque (*Quercus suber* L.), para la localización de hospedantes. Huelva University, Huelva

Sanchez-Osorio I, Tapias R, Dominguez L et al (2009) Intraspecific variability of olfactory responses in *Cerambyx welensii* Küster (Coleoptera, Cerambycidae). Influence of anatomical, physiological and experimental factors. For Syst 18:140–151

Sanchez-Osorio I, Lopez-Pantoja G, Paramio AM et al (2015) Field attraction of *Cerambyx welensii* to fermentation odors and host monoterpenes. J Pest Sci (in press)

Schaefer L (1949). Les Buprestides de France. Ed. Scientifiques du Cabinet Entomologique E Le Moult, Paris

Shigo AL (1984) Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. Annu Rev Phytopathol 22:189–214

Solinas M (1974) *Coroebus florentinus* (Herbst), (Coleoptera, Buprestidae). Biologia, danni, lotta. Entomologica 10:141–193

Soria FJ, Villagran M, Ocete ME (1992) Estudios poblacionales sobre *Coroebus undatus* (Fabr.) (Col.: Buprestidae) en alcornocales de Andalucia Occidental. II: Aspectos ecologicos de la larva. Bol Sanid Veg Plag 18:385–394

Sousa E, Bravo MA, Pires J et al (2001) *Bursaphelenchus xylophilus* (Nematoda; aphelenchoididae) associated with *Monochamus galloprovincialis* (Coleoptera; Cerambycidae) in Portugal. Nematology 3:89–91

Théry A (1942) Coléoptères Buprestides, Faune de France, vol 41. Paris

Tiberi R, Ragazzi A (1998) Association between fungi and xylophagous insects of declining oaks in Italy. Redia 81:83–91

Torres-Vila LM, Sanchez-Gonzalez A, Ponce-Escudero F et al (2012) Assessing mass trapping efficiency and population density of *Cerambyx welensii* Küster by mark-recapture in dehesa open woodlands. Eur J For Res 131:1103–1116

Torres-Vila LM, Sanchez-Gonzalez A, Merino-Martinez J et al (2013) Mark–recapture of *Cerambyx welensii* in dehesa woodlands: dispersal behaviour, population density, and mass trapping efficiency with low trap densities. Entomol Exp Appl 149:273–281

Villemant C, Fraval A (1993) La faune entomologique du chêne-liège en forêt de la Mamora (Maroc). Ecol Mediterr 19:89–98

Vives E (2000) Insecta Coleoptera Cerambycidae. Fauna Iberica, vol 12. Consejo Superior de Investigaciones Científicas. Museo Nacional de Ciencias Naturales, Madrid

Chapter 8
Foliage Feeding Invasive Insects: Defoliators and Gall Makers

Manuela Branco, Andrea Battisti, and Zvi Mendel

Abstract In this chapter we concentrate on the main invasive species which feed on the foliage, by consuming leaves or inducing galls, and which affect both native and non-native tree species. We provide details on their biology, invasion routes, host tree species, damage to native and non-native trees and control strategies.

8.1 Introduction

Mediterranean forests display high biological diversity, demonstrated by the great number of tree species richness as compared with that observed in the large bordering temperate areas in the north, Irano-Turanian in the east, and Saharo-Sindian in the south. Many of the Holarctic and Eurasian tree species survived the glacial ages in the Mediterranean (Huntley and Birkes 1989), among them pines and oaks which are the most successful trees in the Mediterranean basin in term of diversity and distribution area. Several non-indigenous tree species, with no congeners in Europe, such as the genera *Eucalyptus* (Myrtaceae), *Robinia pseudoacacia*, and *Acacia* (Fabaceae) as many others trees with European congeners, were further introduced to the Mediterranean basin for forest plantations, mainly during the twentieth century. Among exotic trees, eucalypts and acacia are dominant in the Mediterranean basin, especially *Eucalyptus camaldulensis* and *Eucalyptus globulus*, which are the most widespread. The black locust *R. pseudoacacia* native to North America was first planted in Europe in France at the beginning of the

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Table 8.1 List of insect species feeding on the foliage, defoliators and gall makers, invasive in the Mediterranean basin

Species	Host tree genus	Origin	Introduced range
Defoliators			
Aproceros leucopoda	*Ulmus*	East Asia	Europe
Cameraria ohridella	*Aesculus*	Macedonia	Europe
Cydalima perspectalis	*Buxus*	East Asia	Europe
Epinotia cedricida	*Cedrus*	North Africa	France
Gonipterus platensis	*Eucalyptus*	Australia	Spain, Portugal
Gonipterus sp.	*Eucalyptus*	Australia	France, Italy
Hyphantria cunea	Several broadleaves	North America	Europe
Parectopa robiniella	*Robinia pseudoacacia*	North America	Europe
Phyllonorycter robiniella	*Robinia pseudoacacia*	North America	Europe
Gall makers			
Dryocosmus kuriphilus	*Castanea*	Asia	Europe
Leptocybe invasa	*Eucalyptus*	Australia	Mediterranean
Ophelimus maskelli	*Eucalyptus*	Australia	Mediterranean
Ophelimus sp.	*Eucalyptus*	Australia	Southern Europe
Obolodiplosis robiniae	*Robinia pseudoacacia*	North America	Europe

seventeenth century and is largely planted in east central Europe. In the Mediterranean the black locust is mostly used as ornamental in urban parks.

Both native and non-native forest trees are currently exposed to an increase number of invasive defoliators and gall makers (Table 8.1). On its native range exotic tree species, particularly *Eucalyptus*, harbour rich arthropod fauna, many of which feed on the foliage (e.g. Abbott et al. 1992). Several of these insect species were introduced in the Mediterranean basin where they became invasive. But native trees are also exposed to invasive species, especially polyphagous ones as well as those with congener host tree species in their native range (Bertheau et al. 2010). Interestingly, there is no record of direct effect on native pines and oaks by alien insect defoliators or gall makers in the Mediterranean basin (see also Kenis et al. 2008). We may assume that the introduction frequency of oak and pine defoliators and gallers from East Palearctic and Nearctic would be similar to the frequency of those feeding on eucalyptus introduced from Australia. The fact that exotic species did not reach invasive pest status in the case of pine and oak could be explained by the higher diversity of fauna associated with these species. The question whether exotic species, plants or arthropods, might more easily invade areas of low species diversity than area of high species diversity was addressed by many ecologists (e.g. Stohlgren et al. 1999; Brockerhoff et al. 2006; Fridley et al. 2007). Still, the general conception is that high species richness alone cannot prevent the establishment of an exotic species which may reach a pest status and thus these native tree species may be at risk in receiving invasive species.

8.2 Defoliators

Several invasive insect defoliators are presented bellow. Most of them are polyphagous, especially those that affect native trees, while other are specific to some non-native tree species or genera, such as *Gonipterus* spp. that feed on *Eucalyptus* or *Parectopa robiniella* which feeds on *Robinia pseudoacacia*. Other species are highly polyphagous and may affect both native and non-native trees, such as *Hyphantria cunea* (Table 8.1).

8.2.1 Aproceros leucopoda

The elm sawfly *Aproceros leucopoda* Takeuchi (Hymenoptera Argidae) originates from East Asia and has invaded Europe at least 2003 (Blank et al. 2010). The larvae defoliate native and non-native elm trees (*Ulmus* spp.) with a typical zigzag feeding when they are young, then they consume the whole leaf blade (Fig. 8.1). Defoliation can be completed and continuous because of up to four generations can develop in a year. Reproduction is parthenogenetic. Defoliations can worse the health condition of elms which are continuously threatened by the Dutch elm disease (Zandigiacomo et al. 2011).

8.2.2 Cameraria ohridella

The horse-chestnut leaf miner *Cameraria ohridella* Deschka & Dimić (Lepidoptera Gracillariidae) is a typical example of an insect native to a small part of the native host range which has become invasive when taken outside. The native host in the Balkans is the horse-chestnut (*Aesculus hippocastanum*) (Sapindaceae), which is widely planted outside of its range especially in Europe. However, *C. ohridella* oviposits on all species of *Aesculus*, but shows preferences for *A. hippocastanum* and a few phylogenetically related horse-chestnut species, where it can complete the life cycle (D'Costa et al. 2014). Sometimes it can attack also maple (*Acer pseudoplatanus*), mainly when it grows close to infested horse-chestnuts. There are up to four generations per year depending on latitude and elevation, with the first one starting at bud break and originated by pupae which have spent the winter in the dead leaves on the ground. A female lays up to 40 eggs and the larvae dig mines in the mesophyll (Fig. 8.2). The leaves can be completely affected and turn brown quite early, with dramatic consequences on the ornamental value of the trees. Regrowth of the leaves may happen and the infestation can be sustained until leaf drop. Interestingly, outbreaks are known also in the native range (Lees et al. 2011)

Fig. 8.1 Typical zig-zag feeding of the young larva of *Aproceros leucopoda* (*above*), followed by feeding of mature larva, cocoon and adult female (Klaus Hellrigl)

and the expansion has not been regulated by the high number of natural enemies known to attack the larvae in the mines (Grabenweger et al. 2010). The pest represents a major limitation to the growth and ornamental function of horse chestnut trees in towns. A number of methods have been developed to limit the damage, including pheromone tools.

Fig. 8.2 Adult of *Cameraria ohridella* with details of larva, pupa and mine in the horse chestnut leaves (Klaus Hellrigl)

8.2.3 Cydalima perspectalis

The box-tree moth *Cydalima perspectalis* (Walker) (Lepidoptera: Crambidae) is a native pest of box trees (*Buxus* spp.) in Asia. It was introduced to Europe in 2006–2007 and rapidly spread on native (*Buxus sempervirens*) and ornamental box trees (Wan et al. 2014). The larvae overwinter mainly in the diapausing third instar in Europe and at least two generations have been observed. Female moths lay hundreds of eggs and the larvae destroy completely the leaves, tying them with silky threads (Fig. 8.3), and sometimes also the bark. It has become a nasty pest in every garden and it is currently threatening the valuable native stands of box tree in Southern Europe. Sustainable control strategies for *C. perspectalis* in Europe are lacking, primarily owing to the inadequate information regarding the biology and the ecology of this recent invader (Nacambo et al. 2014). Several studies conducted in Asia, however, may provide important information for the development of management strategies against *C. perspectalis*.

Fig. 8.3 Damage on *Buxus sempervirens*, matura larva and adult of *Cydalima perspectalis* (Evangelia Chazdimitriou)

8.2.4 Epinotia cedricida

The cedar tortricid *Epinotia cedricida* Diakonoff (Lepidoptera Tortricidae) is a significant pest affecting cedars (*Cedrus* spp.) in France, where it has been introduced from its native range either in the Middle East or in Northern Africa (Fabre 1997). The cedar tortricid has been reported so far only in France where it has colonized practically all the cedar stands. There is only one generation per year, starting with oviposition in the summer. The young larvae are needle miners and feed across the winter. When they reach the final instars they feed on the needles from outside, protected by silk threads. The development is over before the bud break in the spring, then the larvae drop to the ground and pupate in the soil. Outbreaks have been observed only in the introduction range and occurred about every 10 years, leading to total defoliation of the trees in early spring. The synthetic sex pheromone is available and can be used for monitoring. Other species of tortricids are known for cedars and are potential candidates for introduction (Mouna 2013).

8.2.5 **Gonipterus *spp.***

A few species of the Australasian genus *Gonipterus* (Coleoptera: Curculionidae), which feed on Eucalyptus leaves, established in several Mediterranean regions outside Australia. Until recently, most of these species were false mentioned in the literature as *G. scutellatus* Gyllenhal (Mapondera et al. 2012). The first report of "*G. scutellatus*" outside Australia is from New Zealand in 1890 (Withers 2001). In 1916 the weevil was reported in South Africa (Tooke 1955). South America was next to report the Eucalyptus weevil, in Argentina in 1925. In the Mediterranean basin, the Eucalyptus weevil was first recorded in Italy in 1975 and 2 year later in France (OEPP/EPPO 2005). Still, only in the nineties, "*G. scutellatus*" was first reported in the western Mediterranean, in Spain and Portugal (Mansilla Vazquez 1992). By that time, the species was also reported in North America (California) (Hanks et al. 2000). Island regions such as Canary Islands in 1997, were also colonized. Interestingly, there are no reports for the presence of the Eucalyptus weevil in the south rim of the Mediterranean Basin.

Besides *G. scutellatus*, two other species were reported in South America, *G. platensis* Marelli, which was described from specimens collected in Argentina and considered a distinguished species from *G. scutellatus* (Marelli 1927). In Brazil, two separate species, *G. gibberus* Boisduval and *G. scutellatus* were found to co-occur (Rosado-Neto and Marques 1996; Sanches 2000). Recent taxonomic study brought some clarification to the so called "*G. scutellatus*" complex comprising more than 10 species (Mapondera et al. 2012). This work also highlights that *G. platensis*, originate from Tasmania, is the most common species worldwide, established in New Zealand, South and North America and in Western Australia. *G. platensis* also correspond to the species present in the Iberian Peninsula in the western Mediterranean basin; whereas an undescribed *Gonipterus* sp. is present in France and Italy as well as in South Africa. Ironically, *G. scutellatus* never left its original distribution in New South Wales, Australia.

In the Mediterranean basin, *Gonipterus* spp. may present two or three overlapping generations per year depending on climate. Larvae feed on the young leaves, concomitantly young leaves are also the ones chosen by the females for oviposition. The adults, however, may be found on the entire tree crown. Adult feed mainly on the margins on the leaves leaving typical bit marks (Fig. 8.4). Egg masses are laid

Fig. 8.4 Adult of *Gonipterus platensis* on *Eucalyptus globulus* leaves; typical chewing bites made by adults are visible on the leaves margins (Ana Reis)

in clusters holding about 8–10 eggs, covered by hard capsules attached to leaves. Neonate larvae start to feed on the same leave where egg mass was laid and after moves to other leaves. At 27 °C, egg stage lasts about 1 week; larva develops through 2 weeks and pupae in about 1 month, thus complete development occurs in about 2 months (OEPP/EPPO 2005). Pupation occurs in the soil. Adults live on average 3 months and during its lifetime the females mate and lay eggs several times. During winter both adults and pupae may hibernate. During the summer the feeding and reproduction activity may be also reduced and, at minor extension, resumed during autumn. A direct effect of the high temperatures may affect the weevil's activity during summer. Yet, the more likely hypothesis would be an indirect effect of the host plant physiology, which, under water stress conditions, may hinder the production of sprouts and renewal of young leaves, and thus no foliage will be available for the young larvae development and oviposition substrate.

Many Eucalyptus species are reported as favourable hosts for "*G. scutellatus*". In Spain, Rivera and Carbone (2000) found that the weevil could feed on 14 species out of 20 species tested. *E. globulus*, *E. longifolia*, *E. grandis* and *E. propinqua* were preferred hosts, followed by *E. ovata*, *E. viminalis*, *E. citriodora* and *E. pauciflora. E. globulus*, which is the main eucalyptus species planted in the Iberian Peninsula, revealed to be also one of the most susceptible species to *G. platensis*. In Italy, heavy damage was registered on *E. globulus* by *Gonipterus* sp. whereas *E. camaldulensis* and *E. gunnii* were apparently unaffected (Inghilesi et al. 2013). Altogether we may infer a large array of host species used by *Gonipterus* spp. with no apparently striking differences among the two *Gonipterus* species established in the Mediterranean basin. In Eucalyptus species presenting leaf differentiation, i.e. variation in texture and size of the leaves from juvenile to mature leaves, as observed on *E. globulus*, juvenile leaves are typically immune to the weevil. Thus, trees are become susceptible to defoliation only when the mature foliage develops. In *E. globulus* plantations, this happens when trees are about 2-year old, becoming then highly susceptible to *Gonipterus* spp.

The weevil main damage results from the larval feeding activity, which preferentially mine the parenchyma of young leaves and sprouts, especially on the upper third of the tree crown (Mansilla Vazquez 1992). Damage caused by *Gonipterus* spp. may lead to high, even complete, defoliation and severe wood loss. In Portugal, by comparing inventory data previously to the establishment of *G. platensis* (1995–1998) with inventory data from the affected areas in 2004–2006, Reis et al. (2012) predicted a 51 % decrease in wood volume production. Estimated loss in wood volume increased exponentially with defoliation reaching 86 % for 100 % of tree defoliation.

The severity of damage caused by the weevil, early in the twenties, gave rise to several tentative of control by means of insecticides and cultural methods in South Africa (Tooke 1955). Still, chemical control rendered to be in great part ineffective due to the quick growth of the weevil population and the need for multiple applications of chemical treatments. Recently, in Spain and Portugal, the high damage led to test new chemical control strategies for the management of the Eucalyptus weevil (Santolamazza-Carbone and Fernandez 2004). In Portugal the use of Flufenoxuron to treat Eucalyptus plantations was authorized in 2007, but its use was abandoned as it compromised forest certification by the Forest Stewardship Council (FSC). In 2010 a new program was started for the homologation of the neonicotinoids Acetamiprid and Tiacloprid to treat Eucalyptus plantations.

In 1926 an egg parasitoid, *Anaphes nitens* Girault (Hymenoptera: Mymaridae), was brought from Australia to South Africa, 0.75 million individuals were released between 1927 and 1933. In the following years, *A. nitens* was found to have successfully controlled the weevil, with parasitism rates up to 98 %, except on very high mountain areas and sites with poor soil conditions (Tooke 1955). Subsequent introductions followed in other countries: *A. nitens* was released in Europe in Italy (1978), France (1986), Spain (1994) and Portugal (2000).

Since its first introduction, *A. nitens* has been the sole organism used for the control of *Gonipterus* spp. Despite the enormous success of *A. nitens* worldwide, in some particular areas, this biocontrol strategy was ineffective, such as in some regions in South Africa (Tribe 2005), southwestern Australia (Loch 2008), South America (Sanches 2000) and in cold regions in the Iberian Peninsula (Reis et al. 2012). In these areas parasitism rates are variable, usually below 40 % during late winter and early spring. Yet in late spring parasitism may reach more than 85 %. In Portugal, the efficacy of the parasitoid was found to decrease linearly with altitude and increase proportionally with the temperature on the coldest months (Reis et al. 2012). Since, the severity of defoliation was found to increase with the decrease on parasitism rates, concomitantly, higher damage was observed at higher altitude. Differences on climate niche between the parasitoid and the weevil, in particular regarding low-temperature thresholds for initiating reproduction, were proposed to explain the failure of *A. nitens* to achieve high parasitism rates in colder areas. In fact, in cold mountain areas parasitism by *A. nitens* is extremely low in late winter, early spring when *G. platensis* starts laying eggs and then mean air temperatures are below 10–12 °C.

Two other Australian species of *Anaphes* were recovered in Tasmania from *Gonipterus* spp. egg masses, described as *A. tasmaniae* and *A. inexpectatus* (Huber and Prinsloo 1990). Their release in southern Africa was impaired by bureaucratic procedure. In 2011, the two species were collected in Australia and brought to Portugal for laboratory studies. The laboratory rearing of *A. tasmaniae* could not be established for unknown reasons, still laboratory rearing of *A. inexpectatus* were successfully established. Field releases were done from 2012 to 2014, after a risk assessment report using EPPO Standard PM 6/1 procedure (Bigler et al. 2005). The successful establishment of the parasitoid in the field is not yet ascertained. In consequence of the still high economic costs suffered by the forestry in these regions research on alternative control strategies, such as through tree breeding programs and the search for new biocontrol agents, is in course.

8.2.6 Hyphantria cunea

The fall webworm *Hyphantria cunea* (Drury) (Lepidoptera Erebidae Arctiinae) is a polyphagous defoliator introduced in various parts of the world from N America in the twentieth century. In the Mediterranean Basin it is mainly associated with lowland plantations of poplars and mulberry, although it may become a nuisance in towns, especially on ornamental American maples. It may complete two generations in a year, overwintering as a pupa in bark crevices or at the base of the trees. Deployment of pupation traps such as wrapped cardboard along the stem can be an useful tool for monitoring and control on ornamental trees. Defoliations are always associated with occurrence of tents spun along the branches, which are a typical symptom (Fig. 8.5). Populations are regulated by a large number of natural enemies and pathogens, although *Btk* has been successfully applied locally.

8.2.7 Parectopa robiniella

The black locust leaf miner *Parectopa robiniella* Clemens (Lepidoptera Gracillariidae) is an invasive pest of the introduced American black locust *Robinia pseudoacacia*, which has been largely used for afforestation in several southern European countries. The mines are located in the upper part of the mesophyll and extend in many directions, causing the wilting and the early drop of the leaves at high level of infestation. There are several generations per year and the larvae overwinter. The damage can be conspicuous especially in towns, although control measures are generally not necessary as natural enemies keep the populations under acceptable levels.

Fig. 8.5 Defoliation by *Hyphantria cunea* with details of an ovipositing female moth and of larval feeding (Fabio Stergulc)

8.2.8 Phyllonorycter robiniella

The locust leaf miner *Phyllonorycter robiniella* (Clemens) (Lepidoptera Gracillariidae) is native to North America. This insect species was introduced in Europe in the eighties and its currently distributed west to east, from France to Serbia. In Europe *P. robiniella* affects *R. pseudoacacia*. The larvae mine the leaves producing galleries which causes premature leaf fall and affects negatively the trees aesthetic value in urban areas. Several natural enemies were reported in Europe, these are polyphagous parasitoids, dominantly of the family Eulophidae which also develop on other species of leaf miners affecting native plant species (Serini 1990; Stojanović and Marković 2005).

8.3 Gall Makers

Three *Eucalyptus* gall wasps, *Leptocybe invasa* Fisher & La Salle, *Ophelimus maskelli* (Ashmead), and *Ophelimus* sp. (Hymenoptera Eulophidae), the chestnut gall wasp *Dryocosmus kuriphilus* (Hymenoptera Cynipidae) and the gall midge *Obolodiplosis robiniae* (Haldeman) (Diptera Cecidomyiidae) were all recently established in the Mediterranean basin. Another invasive gall wasp species also distributed in the Mediterranean basin, *Quadrastichodella nova* Girault, feeds on the seeds of *E. camaldulensis*, and thus will not be addressed in this chapter. Considering *Eucalyptus*, many gall makers were established outside its native range in Australia. So far 12 species of gall wasps were established in the new areas where *Eucalyptus* was introduced and most of these invasive species present a worldwide distribution (Table 8.2). Only one among the 11 invasive species was recorded previously in Australia. There is thus a serious risk that other *Eucalyptus* gall makers may reach the Mediterranean in a near future increasing the present numbers of invasive galls wasps.

Larson (1998) suggested that sink competition for nutrients between developing leaves and growing gall tissue may account for the negative impacts of sink-inducing gall makers on photosynthesis. Gall wasps may be thus benefactors of a host plant's nutritive gains, and may target vigorous hosts (Price 1991). This seems to be the case with the herein examine gall wasps. They seem to differ from cynipids on roses and oak trees which perform best on plant tissue that is less vigorous as measured by nitrogen deficiency (Pike et al. 2006; Williams and Cronin 2004). The severe injury inflicted by these wasps with a strong impact on tree growth and even survival to host trees on its invaded range indicates that in their native areas these gall wasps are restrained by natural enemies.

We may safely assume that lack of pressure of their principal natural enemies and competitor allows these gall makers to become more aggressive and in some cases to widen their host range by including less susceptible hosts in the invaded range as demonstrated in the case of *O. maskelli* (Branco et al. 2014).

Table 8.2 Eucalyptus gall wasps established in areas outside Australia

Wasp species	Main host tree	Where first recorded	Year	Source
Eulophidae				
Aprostocetus sp.	*Corymbia citriodora*	Hawaii	1995	Beardsley and Perreira (2000)
Epichrysocharis burwelli (Schauff)	*C. citriodora*	California, Brazil	2000	Schauff (2000)
Leptocybe invasa (Fisher & La Salle)	*E. camaldulensis*, *E. tereticornis*	Israel	2001	Mendel et al. (2004)
Leprosa milga (Kim & La Salle)	*E. camaldulensis*	South Africa	2003	Kim and La Salle (2008)
Ophelimus eucalypti (Gahan)	*E. saligna*, *E. botryoides*	New Zealand	1921	Bain (1977), Withers et al. (2000)
Ophelimus maskelli (Ashmead)	*E. camaldulensis*, *E. tereticornis*	New Zealand	1900	Ashmead (1900)
Ophelimus nr. eucalypti	*E. saligna*, *E. botryoides*	New Zealand	1987	Walsh (1996)
Ophelimus sp. 1	*E. globulus*	Chile	2005	Anonymous (2006)
Ophelimus sp. 2	*E. globulus*	France	2011	Borowiec et al. (2012)
Quadrastichodella nova (Girault)	*E. camaldulensis*	Australia	1922	Girault (1922a)
Selitrichodes globulus (La Salle and Gates)	*E. globulus*	California	2009	La Salle et al. (2009)
Pteromalidae				
Nambouria xanthops (Berry and Withers)	*E. cinerea*	New Zealand	2002	Berry and Withers (2002)
Torymidae				
Megastigmus zebrinus (Grissell)	*E. camaldulensis*	South Africa	1998	Grissell (2006)

8.3.1 Leptocybe invasa

The red gum gall wasp, *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae: Tetrastichinae) naturally occurs in Australia was found so far in Queensland where its chalcid-associated parasitoids were also found (Kim et al. 2008; Kelly et al. 2012). It induces typical bump-shaped galls on the leaf midribs, petioles and stems of new growth. The wasp was first noticed in Israel, Algeria, Iraq and Iran in 2000 on twigs of river red gum *Eucalyptus camaldulensis*. The galler was determined as a new genus and species of Eulophidae (Mendel et al. 2004). During the 14 years after its detection at few spots in the Mediterranean basin and Middle East, the gall wasp spread over much the eucalyptus areas of the world

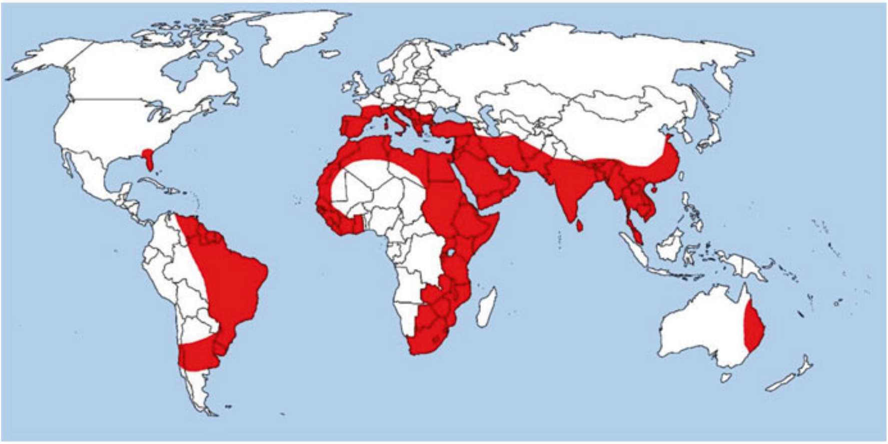

Fig. 8.6 World distribution of *Leptocybe invasa* in 2014

(Fig. 8.6). The incredible spread was noticed also within each infested regions (e.g. Mendel et al. 2004; Ramanagouda et al. 2010; Hassan 2012; Zheng et al. 2014a).

Reproduction of *L. invasa* displays thelytokous mode (Mendel et al. 2004; Doganlar 2005). However, male adults were also found in Turkey (Doganlar 2005), China (Chen et al. 2009) and India (Akhtar et al. 2012). Mating behavior was also observed (Chen et al. 2009). The sex ratio could be range between about 1:2–1:5 (Doganlar 2005; Luo et al. 2011; Liang et al. 2010). Zheng et al. (2014b) provides morphological characteristics for identification of both sexes. *L. invasa*, adults might prolong their activity by feeding on nectar of *E. camaldulensis*.

Attacks take place within 1–2 weeks of bud break. Eggs are laid in the epidermis of the upper sides of newly developed leaves, on both sides of the midrib, in the petioles and in very young stems. The larvae are greenish (young) and white (advanced stage) with spherical shape very thin. Each larva occurs in a separate gall chamber within the host plant. The first attack symptom is a pitchout of white gum, and then followed by development of a cork tissue appearing at the egg insertion spot 1–2 weeks after oviposition (Mendel et al. 2004) (Fig. 8.7a, b). In the following weeks the cork scar becomes bigger and the changes in the attacked tissue are evident. Typical bump shape of the galls develops and they reach their maximum size of about 2.5 mm wide in a rather early stage of the larva development (Fig. 8.7b). The galls tend to change from green to pink – reddish when reaching maximum size. This colour is typical to red gums, *E. camaldulensis* and *E. tereticornis* when exposed to the sun. However when the galled leaves are in the shade or induce on a blue gum, e.g. *E. globulus*, they stay green. The lengths of female and male adults are 1.1–1.4 mm and 0.9–1.2 mm, respectively (Mendel et al. 2004). Threshold minimum temperature for all development stages is around 0 °C and degree-days required for the development of the egg, larva, pupae and adults are 146.6, 1228.0, 161.7 and 205.2, respectively (Zheng et al. 2014a). In the Mediterranean region *L.*

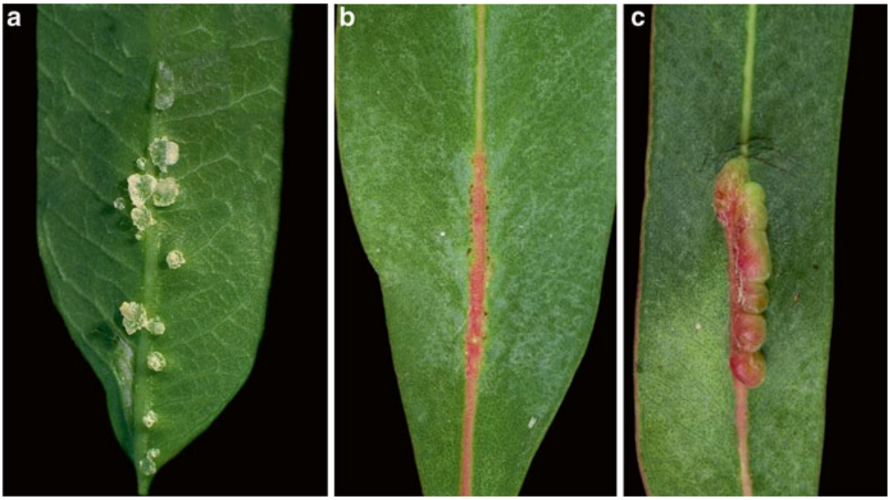

Fig. 8.7 *Leptocybe invasa* signs of attack: (**a**) first attack symptom, pitchout of white gum; (**b**) cork tissue at the egg insertion spots; (**c**) typical bump shape of the gall at the maximum size (Zvi Mendel)

invasa produces two or three overlapping generations annually, and overwinters as larvae or pupae (Mendel et al. 2004; Hesami et al. 2005).

About 21 species of eucalypts were so far recorded as suitable hosts of *L. invasa* (Mendel et al. 2004; Thu et al. 2009; Nyeko et al. 2010). Most of the host species were reported from the *Symphyomyrtus* subgenus; with the most susceptible species belong to the section Exsertaria (*E. camaldulensis*, *E. exserta rudis*. and *E. tereticornis*). Less susceptible are species of the section Latoangulata (*E. botryoides*, *E. grandis*, *E. pellita*, *E. saligna* and *E. robusta*) and even lesser are species of the section Maidenaria (*E. bridgesiana*, *E. cinerea*, *E. dunnii*, *E. globulus*, *E. gunii*, *E. nicholii*, *E. pulverulenta*, *E. smithii*, *E. urophylla* and *E. viminalis*). One species *E. microcorys* was reported from the subgenus *Minutifructus* (section Equatoria) and another one, *E. pilularis* from the subgenus *Eucalyptus* (section Pseudophloius). There is wide range of susceptibility among provenances and subspecies and between various hybrids (e.g. Luo et al. 2014).

About 20 species of parasitic wasps were recorded from *L. invasa* galls; most of them belong to two families, Eulophidae and Torymidae (Table 8.3). A reach species complex is associated with *L. invasa* in Australia, so far 3 eulophids and 5 torymids were found. These eulophids were released in Israel, Turkey and South Africa (Table 8.3). In East Mediterranean *Megastigmus zwimendeli* was established as well. In its new areas *L. invasa* is subjected to fortuitous biological control, mainly by *Megastigmus* spp. In India besides *Megastigmus viggiani* two local *Aprostocetus* spp., a mymarid and a scelionid were recovered from *L. invasa* galls. The native host of these fortuitous species are unknown. For example, *Aprostocetus gala* which was recorded from *L. invasa* in India, was also reared from various host species,

Table 8.3 Hymenopteran parasitoids develop in gall of *L. invasa* as related to the study area

Native area	Family	Species	Source
Australia	Eulophidae	*Quadrastichus mendeli* Kim & La Salle[a]	Kim et al. (2008)
		Selitrichodes kryceri Kim & La Salle[a]	Kim et al. (2008)
		Selitrichodes neseri Kelly & La Salle[b]	Hurley (2012), Kelly et al. (2012)
	Torymidae	*Megastigmus zwimendeli* Doganlar & Hassan[a]	Doganlar (2005), Doganlar and Hassan (2010)
		Megastigmus judikingae Doganlar & Hassan	Doganlar (2005), Doganlar and Hassan (2010)
		Megastigmus lawsoni Doganlar & Hassan	Doganlar (2005), Doganlar and Hassan (2010)
		Megastigmus flavivariegatus Girault	Doganlar (2005), Doganlar and Hassan (2010)
		Megastigmus erolhassani Doganlar & Hassan	Doganlar (2005), Doganlar and Hassan (2010)
Brazil	Torymidae	*Megastigmus brasiliensis* Doganlar, Zache & Wilcken	Doganlar (2005), Doganlar and Hassan (2010)
India	Eulophidae	*Aprostocetus gala* Walker	Kavitha (2009)
	Eulophidae	*Aprostocetus* sp.	Kavitha (2009)
	Mymaridae	*Parallelaptera* sp.	Kavitha (2009)
	Scelionidae	*Telenomus* sp.	Kavitha (2009)
	Torymidae	*Megastigmus viggiani* Narendran & Sureshan	Doganlar (2015), Doganlar and Hassan (2010)
Israel, Turkey, Italy	Torymidae	*Megastigmus leptocybus* Doganlar & Hassan	Doganlar (2015), Doganlar and Hassan (2010)
South Africa	Torymidae	*Megastigmus pretorianensis* nov. sp.	Doganlar (2015), Doganlar and Hassan (2010)
Sri Lanka	Scelionidae	*Telenomus* sp.1	Udagedara and Karunaratne (2014)
	Torymidae	*Telenomus* sp.2	Udagedara and Karunaratne (2014)
	Pteromalidae	*Megastigmus* sp. sp?	Udagedara and Karunaratne (2014)
Thailand	Torymidae	*Megastigmus thailandiensis* Doganlar & Hassan	Doganlar (2015), Doganlar and Hassan (2010)
		Megastigmus thitipornae Doganlar & Hassan	Doganlar (2015), Doganlar and Hassan (2010)

[a] Established in Israel and Turkey
[b] Established in South Africa

such as cecidomyiid *Erosomyia indica* on mango in India (Fasih and Srivastava 1990) or the curculionid *Diaprepes abbreviatus* in Puerto Rico (Hall et al. 2001). Some of these wasps may be inquilines rather than true parasitoids.

In Israel the activity of the native *Megastigmus leptocybus* alone did not display any significant role in the population of the gall wasp. However, release in 2005 of *Quadrastichus mendeli* (uniparental species), *Selitrichodes kryceri* and *Megastigmus zwimendeli* (both biparental species) led to efficient control of *L. invasa*.

8.3.2 Ophelimus maskelli

Ophelimus maskelli (Ashmead) (Eulophidae) was first collected in Wellington, New Zealand and described by Ashmead (1900) as *Pteroptrix maskelli* and was considered as a psyllid parasitoid. It appeared again in the Mediterranean in 1999 in Italy (Arzone and Alma 2000) and misidentified as *Ophelimus eucalypti* Gahan (Viggiani and Nicotina 2001). In the next years the wasp was reported as *O. eucalypti* from other area of the Mediterranean mainly on *E. camaldulensis*, e.g. by Pujade-Villar and Riba-Flinch (2004), and Kavallieratos et al. (2006) from Greece. *O. maskelli* was discovered in Israel in 2003 and in the same year it was found on *E. camaldulensis* at Wagga Wagga in New South Wales (Protasov et al. 2007b). The most distinctive characteristic of *O. maskelli* as compared with other congeners is the presence of only a single seta on the submarginal vein (Protasov et al. 2007b). The principle host plant species and gall design of *O. maskelli* much differ from those of *O. eucalypti* (see Raman and Withers 2003). *O. maskelli* is a uniparental species that develops most successfully on eucalyptus species of the Exsertaria section and induces galls on the leaf blade (Protasov et al. 2007b). *O. eucalypti* is a biparental species with clear sexual dimorphism, that develops on eucalyptus species of the section Latoangulatae and induce extensive galling on leaf midribs and branches (Raman and Withers 2003).

The current geographical distribution of *O. maskelli* is present in Fig. 8.8. The gall invaded from Australia to New Zealand more than 100 years ago. The galler began to spread in the Mediterranean during the first decade of the twenty-first century (Mendel et al. 2004; EPPO 2006; Branco et al. 2006). In North Africa it was discovered in 2006 (Dhahri et al. 2010). During last years the wasp found in Southern Asia, from Vietnam to Indonesia (Lawson et al. 2012) and in 2014 it has been collected in South Africa (Hurley 2014) and for the first time also from the Western Hemisphere, in California (Burks et al. 2015). The occurrence of *O. maskelli* outside Australia is probably a result of several introductions as noticed by the disconnected areas of spread.

Ophelimus maskelli develops in a single-cell-type gall. The galls are pimple-like, nearly round and occur only on the leaf blade; under epidemic conditions the entire leaf surfaces are usually densely covered with galls (Fig. 8.9). Only females emerged from galls collected in various areas. Aggregation tendency was observed within and among trees in recently colonized *E. camaldulensis* stands in Israel and in stands in Wagga Wagga (NSW, Australia) where *O. maskelli* occurs naturally. Maximum survival of the adult when fed with honey solution is about 6 days; feeding on *E. camaldulensis* flowers significantly improve their survival as compared

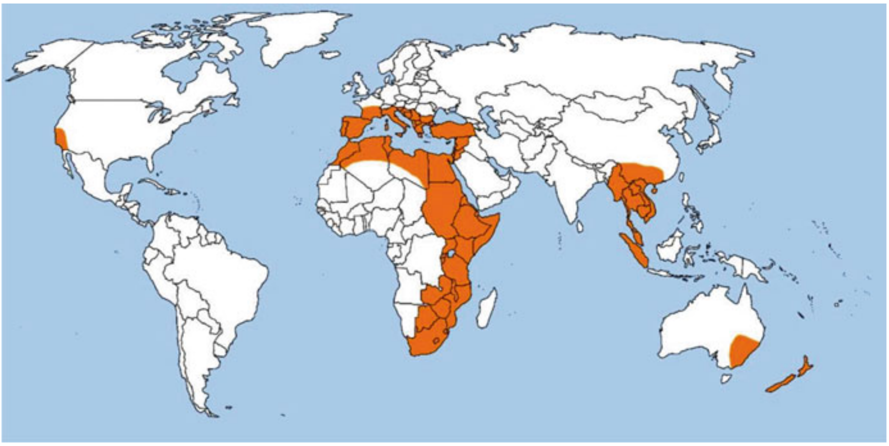

Fig. 8.8 World distribution of *Ophelimus maskelli* in 2014

Fig. 8.9 Leaf covered with galls induced by *Ophelimus maskelli* (Photo M. Branco)

with water alone. Oviposition was observed during daytime, mainly in the morning. Number of galls induced per individual ranged between 63 and 136. The preferred leaves of *E. camaldulensis* for oviposition are 30–45 days old after bud break. However, for full development leaves from 15 to 90 days after bud break are appropriate.

Visible signs of gall development appear about 30–35 days after oviposition. After additional 2–3 weeks, the galling tissue is slightly swollen and the typical green color of the leaf changed. After another 2–3 weeks the gall reaches it maximum size and after more 3–4 weeks gall contain the pupa. Two weeks later the emergence takes place. The gall color may be green, greenish-yellow, pink, or purple to dark purple depending on the level of exposure to the direct sunlight (Protasov et al. 2007b). Gall induced on different Eucalyptus species may vary in shape and color, such conspicuous differences were observed on leaves of host from different

Eucalyptus sections. The larvae develop through three instars, the first larvae occurs while the gall symptoms are hardly visible. *O. maskelli* has three generations per year in Israel, the summer generation, which starts in July, lasts about 3 months. More than one generation per year was also observed in Italy (Bagnoli and Roversi 2004; Lo Verde et al. 2009).

Protasov et al. (2007b) tested the susceptibility of 85 *Eucalyptus* spp. belonging to 6 subgenera, 15 sections and 52 series of eucalyptus. Fourteen species belonging to three sections of the genus: Exsertaria, Latoangulata and Maidenaria, were found to be suitable for the development of *O. maskelii* (*E. botryoides*, *E. bridgesiana*, *E. camaldulensis*, *E. cinerea*, *E. globulus*, *E. grandis*, *E. gunii*, *E. nicholii*, *E. pulverulenta*, *E. robusta*, *E. rudis*, *E. saligna*, *E. tereticornis*, and *E. viminalis*). Alike the case of *L. invasa*, species of the section Exsertaria are the most susceptible to *O. maskelii*. Heavy galling by *O. maskelli* results in premature shedding of the leaves. For *E. camaldulensis*, non-galled leaves survived approximately 243 days, whereas heavily galled leaves survived for only 70 days.

There is ample evidence that under outbreak situation adult wasps cause health problems to people near heavily infested trees during the mass emergence periods. In Israel such damage were reported from industrial areas, schools and recreation sites, but also in agriculture area due to the tendency of wasp to be attracted to green color.

Similar to the previous invasions of eucalypt pests, these gall wasps were not accompanied by their principal natural enemies, which occur in Australia, and therefore they quickly reached epidemic levels. In Israel prior to the acclimatization of natural enemies, sporadic occurrence unidentified *Megastigmus* sp. was obtain from galled leaves. All together six species were associated with *O. maskelli* in Australia (Table 8.4). The mean percentage of the four species collected in 2004 in Wagga Wagga were as follows: *C. chamaeleon* 33.7 %, *S. breviovipositor* 9.3 % *S. ophelimi* 50.5 % and Tetrastichinae sp 2. 6.3 %. Three species were released in Israel *C. chamaeleon* and two mymarid species, *S. ophelimi* and *S. breviovipositor*. The first releases were conducted during the winter of 2005–2006 in various sites in Israel. In samples conducted in 2010 and 2013 only two species were recovered

Table 8.4 Hymenopteran parasitoids develop in gall of *O. maskelli* as related to the study area

Native area	Family	Species	Source
Australia	Eulophidae	*Closterocerus chamaeleon* (Girault)	Girault (1922b)
		Ophelimus sp.[a,b]	La Salle (pers. comm.)
		Sp. 1 (Tetrastichinae, yellow)[b]	La Salle (pers. comm.)
		Sp. 2 (Tetrastichinae, black)[c]	La Salle (pers. comm.)
	Mymaridae	*Stethynium ophelimi* Huber	Huber et al. (2006)
		Stethynium breviovipositor Huber	Huber et al. (2006)
Israel	Torymidae	*Megastigmus* sp.	Protasov and Mendel (pers. comm.)
South Africa	Eulophidae	Sp. 3 (Tetrastichinae)	Hurley (2014)

[a] May be inquilines

[b] Collected in the botanical garden of Sydney

[c] Collected together with C. *chamaeleon* in Wagga Wagga

(among about 16,000 emerging parasitoids), *C. chamaeleon* and *S. ophelimi*, 85 % and 15 %, respectively Protasov et al. (2007a). Biological observation on *C. chamaeleon* were done in Italy by Viggiani et al. (2008). *Closterocerus chamaeleon* spread incredibly fast from points of releases in Israel and Italy and within 3 years its covered the Mediterranean area (Rizzo et al. 2006; Sasso et al. 2008; Branco et al. 2009, 2014; Caleca et al. 2011). In 2014 it appeared in South Africa accompanying its host (Hurley 2014).

Captures of *O. maskelli* as well as *C. chamaeleon* was by far greater on the green sticky plates as compared with on plates of the six other colors. Green sticky plates may serve for monitoring of both species (Mendel et al. 2007). Lo Verde et al. (2010) tested several compounds against *O. maskelli*; only application of imidacloprid gave some significant of galling densities.

8.3.3 **Ophelimus** ***sp.***

In 2010 a new species of *Ophelimus* (Hymenoptera: Eulophidae), still unidentified, was first found in the Mediterranean basin, in southern France (Borowiec et al. 2012). At the same time, the species was confirmed to be also present in the neighbor country Italy. Field surveys done in 2011 confirmed its presence in Portugal. The new *Ophelimus* sp. was separated from *Ophelimus maskelli* (the only other congener in the area) based on molecular and morphological criteria (Borowiec et al. in preparation). The adults are very similar, but can be distinguished by the number of setae present on the submarginal vein of the forewing. In *O. maskelli* a single setae is present, whereas in the new *Ophelimus* sp. 2, 3 or 4 setae may be found on the submarginal vein. The body length of the adults is slightly shorter for *Ophelimus* sp. in comparison with *O. maskelli* but the lengths overlap (Garcia et al. 2014). Molecular data show close proximity of the *Ophelimus* sp. individuals found in Europe (France, Portugal and Italy) with individuals collected in Australia from *E. globulus* (Borowiec et al. in preparation).

The galls are similar to those caused by *O. maskelli* but differ on color, shape, texture and size. The galls induced by *Ophelimus* sp. are slightly smaller and expand uniquely to the upper surface of the leaf, whereas *O. maskelli* galls expands to both sides of the leaf blade. Also, *Ophelimus* sp. galls have a brown-grey coloration and a rough aspect, unlike *O. maskelli* galls which are green or reddish and have a smooth texture (Fig. 8.10). One year survey of the gall development indicates that *Ophelimus* sp. is univoltine in the Mediterranean basin, unlike *O. maskelli* which is multivoltine. Adult emerge in April–May in Portugal, immediately followed by egg laying. Adults may live in the laboratory up to 2 weeks when fed with honey at low temperatures (5 °C) but survival sharply declines for 2–3 days at higher temperatures (25 °C). Larvae are found inside galls from October until March. Pupation takes place from March until April.

From surveys conducted in Portugal and France, the host range of *Ophelimus* sp. was found to be restricted to host species from the section Maidenaria: *E. cinerea*,

Fig. 8.10 Galls of *Ophelimus* sp. on *Eucalyptus globulus* in Portugal. Gall on the *right* was open to expose the larvae (Photo A. Garcia)

E. cypellocarpa, *E. globulus*, *E. gunni*, *E. parvula*, *E. bicostata* and *E. nitens* (Borowiec et al. 2012, unp. data). *E. globulus* is one of the most affected species whereas *O. maskelli* thrives on species of the section Exsertaria (Protasov et al. 2007b; Branco et al. 2014). Thus, host range major distinguishes the ecological niche of the two species. Since *E. globulus* is the most cultivated species in southern Europe, particularly in the Iberian Peninsula, there could be a potential high economic impact of the new *Ophelimus* sp. for the Eucalyptus industry. In a study conducted in Portugal, the attacks were found to be more intense in a colder region in the North where up to 70 % of juvenile leaves had galls, than in the South of the country. A preference for juvenile leaves, which are produced by young plants up to 3 years old, was determined in *E. globulus* (Branco, unpublished data) which may limit the damage inflicted by this gall wasp.

No parasitoids of this species were observed in France or Portugal, despite the presence in the same site of *C. chamaeleon*, parasitoid of the congener *O. maskelli*. It may be important to note that another *Ophelimus* sp. found in the recent years in Chile is parasitized by the above mentioned eulophid.

8.3.4 Dryocosmus kuriphilus

The chestnut gall wasp *Dryocosmus kuriphilus* (Yasumtsu) (Hymenoptera Cynipidae) is native to China. The galls interfere with normal shoot development, twig elongation, flowering, and nut production, and can lead to twig dieback and even tree death (Kato and Hijii 1997; Battisti et al. 2014). Apparently, *D. kuriphilus* can infest all species of chestnut (*Castanea* spp.). It was discovered in 1951 following its introduction to Japan in 1941, and later it was introduced in N America, Korea, Nepal, and finally in Europe (Italy) in 2002 (EFSA PLH 2010). *D. kuriphilus* is parthenogenetic (all adults are females) and has 1 year life cycle. Adults become active in early summer and lay eggs in the newly developed buds of chestnut trees.

Fig. 8.11 Different types of galls caused by *Dryocosmus kuriphilus* on a chestnut shoot (Klaus Hellrigl)

Larvae feed briefly after hatching and then enter diapause within the buds and overwinter. When bud break occurs the next spring, larvae initiate development and galls form on buds, leaves, male flowers, and shoots (Fig. 8.11). Each gall may contain one or more chambers with a single larva in each. Pupation occurs within the gall in early summer, after which the adult females emerge and seek out newly developed chestnut buds for oviposition. After adult emergence, the galls turn woody and can be retained for years. Various native parasitoids associated with gall wasps attack *D. kuriphilus* in the areas of introduction, and a few parasitoids from the area of origin were released as biocontrol agents. Among the latter only *Torymus sinensis* Kamijo (Hymenoptera Torymidae) has been successful and is now widely used (Quacchia et al. 2008)

8.3.5 Obolodiplosis robiniae

The locust gall midge *Obolodiplosis robiniae* (Haldeman) (Diptera Cecidomyiidae) induces galls on the leaves of the black locust *R. pseudoacacia* by rolling leaf margins. The gall midge, originate from North America, was first recorded in Europe in North Italy in 2003 from where it spread rapidly to other regions (Skuhravá et al. 2007). A few years before, the presence of this insect pest had been also recorded in South-Korea and Japan. In Europe the populations are partially controlled by polyphagous parasitoids and predators (Tettigonidae). Further, a specialized parasitoid *Platygaster robiniae* (Hymenoptera: Platygastridae) seems to be very effective in regulating midge population (Buhl and Duso 2008; Tóth et al. 2011).

References

Abbott I, Burbidge T, Williams M et al (1992) Arthropod fauna of jarrah (*Eucalyptus marginata*) foliage in Mediterranean forest of Western Australia: spatial and temporal variation in abundance, biomass, guild structure and species composition. Aust J Ecol 17:263–274

Akhtar M, Patankar N, Gaur A (2012) Observations on the biology and male of eucalyptus gall wasp *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae). Indian J Entomol 74:173–175

Anonymous (2006) Informativo Fitosanitario Forestal. Servicio Agricola y Ganadero, vol 3. Ministero de Agricultura, Santiago

Arzone A, Alma A (2000) Eulofide galligeno dell'Eucalipto in Italia. Inf Fitopatol 50:43–46

Ashmead WH (1900) Notes on some New Zealand and Australian parasitic Hymenoptera, with descriptions of new genera and species. Proc Linn Soc N S W 25:346

Bagnoli B, Roversi P (2004) Annotazioni morfologiche e biologiche su un Eulofide di recente introduzione in Italia galligeno fogliare su Eucalipto. In: Atti XIX Congresso Nazionale italiano di Entomologia, Catania 10–15 Giugno 2002, Sondrio, pp 955–960

Bain J (1977) *Megastigmus spermotrophus* Wachtl (Hymenoptera: Chalcidoidea: Torymidae); *Rhicnopeltella eucalypti* Gahan (Hymenoptera: Chalcidoidea: Eulophidae), blue-gum chalcid. For Timber Insects N Z, N Z For Serv 14–15, 4p

Battisti A, Benvegnù I, Colombari F et al (2014) Invasion by the chestnut gall wasp in Italy causes significant yield loss in *Castanea sativa* nut production. Agric For Entomol 16:75–79

Beardsley JW, Perreira WD (2000) *Aprostocetus* sp. (Hymenoptera: Eulophidae: Tetrastichinae), a gall wasp new to Hawaii. Proc Hawaii Entomol Soc 34:203

Berry JA, Withers TM (2002) New gall-inducing species of ormocerine pteromalid (Hymenoptera: Pteromalidae: Ormocerinae) described from New Zealand. Aust J Entomol 41:18–21

Bertheau C, Brockerhoff EG, Roux-Morabito G et al (2010) Novel insect-tree associations resulting from accidental and intentional biological 'invasions': a meta-analysis of effects on insect fitness. Ecol Lett 13:506–515

Bigler F, Bale JS, Cock MJW et al (2005) Guidelines on information requirements for import and release of invertebrate biological control agents in European countries. Biocontrol News Inf 26:115N–123N

Blank SM, Hara H, Mikulás J et al (2010) *Aproceros leucopoda* (Hymenoptera: Argidae): an East Asian pest of elms (Ulmus spp.) invading Europe. Eur J Entomol 107:357–367

Borowiec N, Thaon M, Brancaccio L et al (2012) L'eucalyptus menacé par une nouvelle espèce d'Ophelimus en France. Phytoma 656:42–44

Branco M, Franco J, Valente C et al (2006) Survey of Eucalyptus gall wasps in Portugal. Bol San Veg Plagas 32:199–202

Branco M, Boavida C, Durand N et al (2009) Presence of the Eucalyptus gall wasp *Ophelimus maskelli* and its parasitoid *Closterocerus chamaeleon* in Portugal: first record, geographic distribution and host preference. Phytoparasitica 37:51–54

Branco M, Dhahri S, Santos M et al (2014) Biological control reduces herbivore's host range. Biol Control 69:59–64

Brockerhoff EG, Liebhold AM, Jactel H (2006) The ecology of forest insect invasions and advances in their management. Can J For Res 36:263–268

Buhl PN, Duso C (2008) *Platygaster robiniae* n. sp. (Hymenoptera: Platygastridae) parasitoid of *Obolodiplosis robiniae* (Diptera: Cecidomyiidae) in Europe. Ann Entomol Soc Am 101:297–300

Burks R, Mottern J, Waterworth R et al (2015) First report of the Eucalyptus gall wasp, *Ophelimus maskelli* (Hymenoptera: Eulophidae), an invasive pest on Eucalyptus, from the Western Hemisphere. Zootaxa 3926:448–450

Caleca V, Lo Verde G, Rizzo M et al (2011) Dispersal rate and parasitism by *Closterocerus chamaeleon* (Girault) after its release in Sicily to control *Ophelimus maskelli* (Ashmead) (Hymenoptera, Eulophidae). Biol Control 57:66–73

Chen S, Qin Y, Liang Y (2009) The evolution of sexual reproduction and a preliminary description of the male adult. Study J Mod Educ Teach 7:47–48

D'Costa L, Simmonds MSJ, Straw N et al (2014) Leaf traits influencing oviposition preference and larval performance of *Cameraria ohridella* on native and novel host plants. Entomol Exp Appl 152:157–164

Dhahri S, Ben Jamaa M, Lo Verde G (2010) First record of *Leptocybe invasa* and *Ophelimus maskelli* eucalyptus gall wasps in Tunisia. Tunis J Plant Prot 5:229–234

Doganlar O (2005) Occurrence of *Leptocybe invasa* Fisher & La Salle, 2004 (Hymenoptera: Chalcidoidea: Eulophidae) on *Eucalyptus camaldulensis* in Turkey, with description of the male sex. Zool Middle East 35:112–114

Doganlar M (2015) Diagnosis of *Megastigmus* spp. (Hymenoptera: Torymidae) reared from galls of *Leptocybe invasa* Fisher & La Salle, 2004, (Hymenoptera: Eulophidae) on *Eucalyptus* spp. (Myrtaceae), with description of a new species from South Africa. Entomofauna 43:561–580

Doganlar M, Hassan E (2010) Review of Australian species of *Megastigmus* (Hymenoptera: Torymidae) associated with eucalyptus, with descriptions of new species. Aust J Basic Appl Sci 4:5059–5120

EFSA Panel on Plant Health (2010) Risk assessment of the oriental chestnut gall wasp, *Dryocosmus kuriphilus* for the EU territory and identification and evaluation of risk management options. EFSA J 8:1495

EPPO (2006) First report of two new eucalyptus pests in the South of France: *Ophelimus maskelli* and *Leptocybe invasa*. EPPO Rep Serv 2006:189

Fabre JP (1997) Geographical distribution of the tortricid moth *Epinotia cedricida* (Lepidoptera: Tortricidae) within the natural and artificial ranges of the cedar trees *Cedrus atlantica* and *C. LIBANI*. Eur J Entomol 94:485–494

Fasih M, Srivastava R (1990) Parasites and predators of insect pests of mango. Int Pest Control 32:39–41

Fridley JD, Stachowicz JJ, Naeem S et al (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17

Garcia A, Matos S, Borowiec N et al (2014) A new gall wasp *Ophelimus* sp. affecting Eucalyptus globulus in Southwestern Europe. Poster presentation at the Xth European Congress of Entomology, New York, 3–8 August 2014

Girault A (1922a) New chalcid flies from eastern Australia (Hymenoptera, Chalcididae). I. Insecutor Inscitiae Menstruus 10:40

Girault A (1922b) New chalcid flies from eastern Australia (Hymenoptera, Chalcididae). II. Insecutor Inscitiae Menstruus 10:102

Grabenweger G, Kehrli P, Zweimüller I et al (2010) Temporal and spatial variations in the parasitoid complex of the horse chestnut leafminer during its invasion of Europe. Biol Invasions 12:2797–2813

Grissell E (2006) A new species of *Megastigmus Dalman* (Hymenoptera: Torymidae), galling seed capsules of *Eucalyptus camaldulensis* Dehnhardt (Myrtaceae) in South Africa and Australia. Afr Entomol 14:88–92

Hall D, Pena J, Franqui R et al (2001) Status of biological control by egg parasitoids of *Diaprepes abbreviatus* (Coleoptera: Curculionidae) in citrus in Florida and Puerto Rico. BioControl 46:61–70

Hanks LM, Millar JG, Paine TD et al (2000) Classical biological control of the Australian weevil *Gonipterus scutellatus* (Coleoptera: Curculionidae) in California. Environ Entomol 29:369–375

Hassan R (2012) First record of the eucalyptus gall wasp, *Leptocybe invasa* Fisher and La Salle (Hymenoptera: Eulophidae) in Iraq. Acta Agrobot 65:93–98

Hesami S, Alemansoor H, Seyedebrahimi S (2005) Report of *Leptocybe invasa* (Hym.: Eulophidae), gall wasp of *Eucalyptus camaldulensis* with notes on biology in Shiraz vicinity. J Entomol Soc Iran 24:99–108

Huber JT, Prinsloo GL (1990) Redescription of *Anaphes nitens* (Girault) and description of two new species of *Anaphes haliday* (Hymenoptera: Mymaridae), parasites of *Gonipterus scutellatus* Gyllenhal (Coleoptera: Curculionidae) in Tasmania. Aust J Entomol 29:333–341

Huber J, Mendel Z, Protasov A et al (2006) Two new Australian species of *Stethynium* (Hymenoptera: Mymaridae), larval parasitoids of *Ophelimus maskelli* (Ashmead) (Hymenoptera: Eulophidae) on Eucalyptus. J Nat Hist 40:1916–1920

Huntley B, Birkes HJB (1989) An atlas of past and present pollen maps for Europe, 0–13 000 years ago. Cambridge University Press, Cambridge

Hurley B (2012) First discovery of *Selitrichodes neseri* in the field. Online at: http://www.forestry.co.za/firstdiscovery-of-selitrichodes-neseri-in-the-field

Hurley B (2014) New pest of Eucalyptus detected in South Africa. World Wide Web document. Available from: http://www.fabinet.up.ac.za/index.php/news-item?id=136. Accessed 21 Feb 2015

Inghilesi AF, Cervo R, Pennacchio F, Roversi PF, Tricarico E, Mazza G (2013) Alien insects on Eucalytpus spp.: an australian biocenosis in Tuscany. Redia 96:21–26

Kato K, Hijii N (1997) Effects of gall formation by *Dryocosmus kuriphilus* Yasumatsu (Hym, Cynipidae) on the growth of chestnut trees. J Appl Entomol 121:9–15

Kavallieratos N, Kontodimas D, Anagnou-Veroniki M et al (2006) First record of the gall inducing insect *Ophelimus eucalypti* (Gahan) (Hymenoptera: Chalcidoidea: Eulophidae) in Greece. Ann Benaki Phytopatol Inst 20:125–128

Kavitha K (2009) Bioecology and management of eucalyptus gall wasp, *Leptocybe invasa* Fisher & Salle (Hymenoptera: Eulophidae). Master's thesis, University of Agricultural Sciences, Bangalore

Kelly J, La Salle J, Harney M et al (2012) *Selitrichodes neseri* n. sp., a new parasitoid of the eucalyptus gall wasp *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae: Tetrastichinae). Zootaxa 3333:50–57

Kenis M, Auger-Rozenberg AM, Roques A et al (2008) Ecological effects of invasive alien insects. Biol Invasions. doi:10.1007/s10530-008-9318-y

Kim I, La Salle J (2008) A new genus and species of *Tetrastichinae* (Hymenoptera: Eulophidae) inducing galls in seed capsules of Eucalyptus. Zootaxa 1745:63–68

Kim I, Mendel Z, Protasov A et al (2008) Taxonomy, biology, and efficacy of two Australian parasitoids of the eucalyptus gall wasp, *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae: Tetrastichinae). Zootaxa 1910:1–20

La Salle J, Arakelian G, Garrison RW et al (2009) A new species of invasive gall wasp (Hymenoptera: Eulophidae: Tetrastichinae) on blue gum (*Eucalyptus globulus*) in California. Zootaxa 2121:39–42

Larson K (1998) The impact of two gall-forming arthropods on the photosynthetic rates of their hosts. Oecologia 115:161–166

Lawson S, Griffiths M, Nahrung H et al (2012) Biological control of eucalypt pests overseas and in Australia, Final report number FST/2011/028. Australian Centre for International Agricultural Research, Bruce

Lees DC, Lack HW, Rougerie R et al (2011) Tracking origins of invasive herbivores through herbaria and archival DNA: the case of the horse-chestnut leaf miner. Front Ecol Environ 9:322–328

Liang P, Li J, Wen X et al (2010) Observation on the male ratio of *Leptocybe invasa* adult. For Pest Dis 29:21–22

Lo Verde G, Rizzo R, Barraco G (2009) Dannosità e controllo di *Ophelimus maskelli* (Ashmead) su *Eucalyptus camaldulensis* in vivaio. Atti III Congresso Naz, Selvicoltura, 16–19 ottobre 2008, pp 1409–1412

Lo Verde G, Dhahri S, Ben Jamaa M (2010) First record in Tunisia of *Closterocerus chamaeleon* (Girault) parasitoid of the eucalyptus gall wasp *Ophelimus maskelli* (Ashmead) (Hymenoptera Eulophidae). Nat Sicil 34:208

Loch AD (2008) Parasitism of the Eucalyptus weevil, *Gonipterus scutellatus* Gyllenhal, by the egg parasitoid, *Anaphes nitens* Girault, in *Eucalyptus globulus* plantations in southwestern Australia. Biol Control 47:1–7

Luo J, Jiang J, Wang J et al (2011) Bionomics of *Leptocybe invasa* in Bobai of Guangxi Autonomous Region. For Pest Dis 30:10–12

Luo J, Arnold R, Lu W et al (2014) Genetic variation in *Eucalyptus camaldulensis* and *E. Tereticornis* for early growth and susceptibility to the gall wasp *Leptocybe invasa* in China. Euphytica 196:397–411

Mansilla Vazquez JP (1992) Presencia sobre *Eucalyptus globulus* Labill de *Gonipterus scutellatus* Gyll. (Col. Curculionidae) en Galicia. Bol San Veg Plagas 18:547–554

Mapondera TS, Burgess T, Matsuki M, Oberprieler RG (2012) Identification and molecular phylogenetics of the cryptic species of the *Gonipterus scutellatus* complex (Coleoptera: Curculionidae: Gonipterini). Aust J Entomol 51(3):175–188

Marelli C (1927) El gorgojo de los eucaliptos hallado en la Argentina no es la especie originaria de Tasmania “Gonipterus scutellatus” Gyll. Revista del Museo de La Plata (Argentina) 30:257–269

Mendel Z, Protasov A, Fisher N et al (2004) Taxonomy and biology of *Leptocybe invasa* gen. & sp. n. (Hymenoptera: Eulophidae), an invasive gall inducer on Eucalyptus. Aust J Entomol 43:103–106

Mendel Z, Protasov A, Blumberg D et al (2007) Release and recovery of parasitoids of the Eucalyptus gall wasp *Ophelimus maskelli* in Israel. Phytoparasitica 35:330–332

Mouna M (2013) Les insectes du cèdre (*Cedrus atlantica* Manetti) dans le Nord de l’Afrique. Série Zoologie, vol 48 (2012). Travaux de l’Institut Scientifique, Rabat

Nacambo S, Leuthardt FLG, Wan H et al (2014) Development characteristics of the box-tree moth *Cydalima perspectalis* and its potential distribution in Europe. J Appl Entomol 138:14–26

Nyeko P, Mutitu K, Otieno B et al (2010) Variations in *Leptocybe invasa* (Hymenoptera: Eulophidae) population intensity and infestation on *eucalyptus germplasms* in Uganda and Kenya. Int J Pest Manage 56:137–144

OEPP/EPPO (2005) *Gonipterus gibberus* and *Gonipterus scutellatus*. Data sheet on quarantine pests. OEPP/EPPO Bull 35:368–370

Pike C, Robison D, Abrahamson L (2006) Cynipid gall wasps in declining black oak in New York: relationships with prior tree history and crown dieback. In: Ozaki K, Yukawa J, Ohgushi T et al (eds) Galling arthropods and their associates, Ecology and evolution. Springer, Tokyo, pp 123–132

Price P (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251

Protasov A, Blumberg D, Brand D et al (2007a) Biological control of the eucalyptus gall wasp *Ophelimus maskelli* (Ashmead): taxonomy and biology of the parasitoid *Closterocerus chamaeleon* (Girault), with information on its establishment in Israel. Biol Control 42:196–206

Protasov A, La Salle J, Blumberg D et al (2007b) Biology, revised taxonomy and impact on host plants of *Ophelimus maskelli*, an invasive gall inducer on *Eucalyptus* spp. in the Mediterranean area. Phytoparasitica 35:50–76

Pujade-Villar J, Riba-Flinch J (2004) Dos especies australianas de eulófidos, muy dañinas para *Eucalyptus* spp., introducidas en el *Nordeste ibérico* (Hymenoptera: Eulophidae). Bol Soc Entomol Aragon 35:299–301

Quacchia A, Moriya S, Bosio G et al (2008) Rearing, release and settlement prospect in Italy of *Torymus sinensis*, the biological control agent of the chestnut gall wasp *Dryocosmus kuriphilus*. BioControl 53:829–839

Raman A, Withers T (2003) Oviposition by introduced *Ophelimus eucalypti* (Hymenoptera: Eulophidae) and morphogenesis of female-induced galls on *Eucalyptus saligna* (Myrtacea) in New Zealand. Bull Entomol Res 93:55–63

Ramanagouda S, Kumari K, Vastrad A et al (2010) Potential alien insects threatening eucalyptus plantations in India. Karnataka J Agric Sci 23:93–96

Reis AR, Ferreira L, Tomé M et al (2012) Efficiency of biological control of *Gonipterus platensis* (Coleoptera: Curculionidae) by *Anaphes nitens* (Hymenoptera: Mymaridae) in cold areas of the Iberian Peninsula: implications for defoliation and wood production in *Eucalyptus globulus*. For Ecol Manage 270:216–222

Rivera AC, Carbone SS (2000) The effect of three species of Eucalyptus on growth and fecundity of the Eucalyptus snout beetle (*Gonipterus scutellatus*). Forestry 73:21–29

Rizzo M, Lo Verde G, Rizzo R et al (2006) Introduzione di *Closterocerus* sp. in Sicilia per il controllo biologico di *Ophelimus maskelli* Ashmead (Hymenoptera, Eulophidae) galligeno esotico sugli eucalipti. Boll Zool Agr Bachic 38:237–248

Rosado-Neto GH, Marques MI (1996) Characteristics of adult, genitalia and immature forms of Gonipterus gibberus Boisduval and *G. scutellatus* Gyllenhal (Coleoptera, Curculionidae). Rev Bras Zooltec 13:77–90

Sanches MA (2000) Parasitismo de ovos de *Gonipterus scutellatus* Gyllenhal, 1833 e *Gonipterus gibberus* Boisduval, 1835 (Coleoptera, Curculionidae) por *Anaphes nitens* (Girault, 1928) (Hymenoptera, Mymaridae) em Colombo (Parana, Brasil). Rev Arq Inst Biol 67:77–82

Santolamazza-Carbone S, Fernández de Ana-Magán FJ (2004) Testing of selected insecticides to assess the viability of the integrated pest management of the Eucalyptus snout-beetle *Gonipterus scutellatus* in north-west Spain. J Appl Entomol 128:620–627

Sasso R, Laudonia S, Viggiani G (2008) Dati preliminari sul controllo biologico di *Ophelimus maskelli* (Ashmead) (Hymenoptera: Eulophidae) in Campania a seguito dell'introduzione del suo antagonista *Closterocerus chamaeleon* (Girault) (Hymenoptera: Eulophidae). Boll Lab Entomol Agrar Filipo Silvestri 62:51–55

Schauff ME, Garrison R (2000) An introduced species of *Epichrysocharis* (Hymenoptera: Eulophidae) producing galls on Eucalyptus in California with notes on the described species and placement of the genus. J Hymenopt Res 9:179–180

Serini GB (1990) Parasitoids of *Parectopa robiniella* Clemens and *Phyllonorycter robiniellus* (Clemens)(Lepidoptera Gracillariidae). Boll Zool Agr Bachic 22:139–149

Skuhravá M, Skuhravý V, Csóka G (2007) The invasive spread of the gall midge *Obolodiplosis robiniae* in Europe. Cecidology 22:84–90

Stohlgren TJ, Binkley D, Chong GW et al (1999) Exotic plant species invade hot spots of native plant diversity. Ecol Monogr 69:25–46

Stojanović A, Marković Č (2005) Parasitoid complex of *Phyllonorycter robiniella* (Clemens, 1859) (Lepidoptera, Gracillariidae) in Serbia. J Pest Sci 78:109–114

Thu PQ, Dell B, Burgess TI (2009) Susceptibility of 18 Eucalypt species to the gall wasp *Leptocybe invasa* in the nursery and young plantations in Vietnam. Sci Asia 35:113–117

Tooke FGC (1955) The Eucalyptus Snout. beetle, Gonipterus scutellatus Gyll. A study of its ecology and control by biological means, Entomology memoirs. Department of Agriculture and Forestry, Union of South Africa

Tóth P, Váňová M, Lukáš J (2011) Impact of natural enemies on *Obolodiplosis robiniae* invasion. Biologia 66:870–876

Tribe GD (2005) The present status of *Anaphes nitens* (Hymenoptera: Mymaridae), an egg parasitoid of the Eucalyptus snout beetle *Gonipterus scutellatus*, in the Western Cape Province of South Africa. S Afr For J 203:49–54

Udagedara U, Karunaratne W (2014) Biology, damage and parasitoids of the Eucalyptus gall wasp, *Leptocybe invasa* (Hymenoptera: Eulophidae), infesting *Eucalyptus camaldulensis* (Myrtaceae) in Maragamuwa plantation, Sri Lanka. Int J Trop Insect Sci 34:179–189

Viggiani G, Nicotina M (2001) L'Eulofide galligeno fogliare degli eucalipti *Ophelimus eucalypti* (Gahan) (Hymenoptera: Eulophidae) in Campania. Boll Zool Agr Bachic 33:79–82

Viggiani G, Laudonia S, Sasso R (2008) Gli stadi giovanili del parassitoide *Closterocerus chamaeleon* (Girault) (Hymenoptera: Eulophidae) e il loro sviluppo in rapporto all'eulofide galligeno *Ophelimus maskelli* (Ashmead). Boll Lab Entomol Agrar Filipo Silvestri 62:71–77

Walsh P (1996) Gall wasp on *Eucalyptus botryoides* and *Eucalyptus saligna* and possibilities for biological control. N Z For 41:40–41

Wan H, Haye T, Kenis M et al (2014) Biology and natural enemies of *Cydalima perspectalis* in Asia: is there biological control potential in Europe? J Appl Entomol 138:715–722

Williams M, Cronin J (2004) Response of a gall-forming guild (Hymenoptera :Cynipidae) to stressed and vigorous prairie roses. Environ Entomol 33:1052–1061

Withers TM (2001) Colonization of eucalypts in New Zealand by Australian insects. Austral Ecol 26:467–476

Withers T, Raman A, Berry J (2000) Host range and biology of *Ophelimus eucalypti* (Gahan) (Hym.: Eulophidae), a pest of New Zealand eucalypts. N Z Plant Prot 53:339–344

Zandigiacomo P, Cargnus E, Villani A (2011) First record of the invasive sawfly *Aproceros leucopoda* infesting elms in Italy. Bull Insectol 64:145–149

Zheng X, Li J, Yang Z et al (2014a) A review of invasive biology, prevalence and management of *Leptocybe invasa* Fisher & La Salle (Hymenoptera: Eulophidae: Tetrastichinae). Afr Entomol 22:68–79

Zheng X, Yang Z, Li J et al (2014b) Rapid identification of both sexes of Leptocybe invasa Fisher & La Salle (Hymenoptera: Eulophidae: Tetrastichinae): a morphological perspective. Afr Entomol 22:643–650

Chapter 9
Invasive Fruit, Cone and Seed Insects in the Mediterranean Basin

Marie-Anne Auger-Rozenberg and Thomas Boivin

Abstract Invasive fruit, cone and seed insects are considered the most important predators of tree seeds during the pre-dispersal phase of development. Although some species benefited from historical human movements across the Mediterranean Basin, the accelerating rate of international trade, travel and transport of wood products, including seeds, during the latter half of the twentieth century has increased the introduction of alien fruit, cone and seed insects in this area. The combination of almost inexistent phytosanitary regulations of tree seed trades and species biological characteristics favouring human-aided dispersal had a key role in successful invasions of Mediterranean forest ecosystems. Invasions may affect plant populations through increased direct trophic interactions such as seed parasitism and destruction, which can result in more complex indirect effects on natural regeneration processes. Many of the trees cone and seed insects feed upon have also been introduced by humans, but introduced insect species also may switch to native tree species congeneric to their original host and are then likely to interact with native seed feeders. In this chapter, we gathered current knowledge on seven insect species with invasive populations in the Mediterranean Basin. We put an emphasis on: (i) both anthropogenic and biological features involved in such invasion pathways, (ii) the ecological mechanisms involved in the establishment and the spread of invasive populations, (iii) the impacts of alien invasive species on Mediterranean ecosystems, and (iv) the issues related to the management of invasions in the fruit, cone and seed insect group.

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9.1 Introduction

The increase in worldwide exchange and trade of tree reproductive materials combined with phytosanitary regulations limited or non-existent in many countries, have resulted in the establishment of numerous species of fruit, cone and seed insects outside their native range (Langor and Sweeney 2009; Essl et al. 2011; Vaes-Petignat and Nentwig 2014). It is especially true for seed-borne insects and mites, because isolated seeds are preferred to whole cones and fruits for trade of conifers and of most broadleaved tree species (Roques et al. 2003, 2006). The guild of seed feeders/borers[1] is proportionally more represented in the alien fauna than in the European fauna (Kenis et al. 2007), but taxonomic difficulties related to this group could partly induce an underestimation of successful establishments in the Mediterranean Basin. Currently, a few alien species specialized on fruiting structures are recorded in Mediterranean forest ecosystems. Possible explanations are the low number of checklist of alien arthropods in many Mediterranean countries, the cryptic way of life of most of cone and seed insects, which does not usually allow detection easier than using X-ray radiography, and the lack of phytosanitary regulations in many countries (Auger-Rozenberg and Roques 2012).

The small number of invasive fruiting structure insects in Mediterranean ecosystems allows us to detail them on a case-by-case in this chapter. Their general biological traits and their guild characteristics are similar to those provided on native fruiting structure insects in Chap. 4. Once introduced in Sect. 9.2, we propose an overview of entering pathways of the species concerned (Sect. 9.3), of the factors that facilitate the invasion processes (Sect. 9.4) and then of the different kinds of impacts caused by the invasive pests to Mediterranean forest ecosystems (Sect. 9.5).

9.2 Diversity of Invasive Fruit, Cone and Seed Insects in the Mediterranean Basin

In this chapter, invasive fruiting structure species established in Mediterranean Basin will be referred to as *external invasives* when they originate from other continents. When different countries within the Mediterranean Basin constitute invasion sources, the species concerned will then be referred to as *internal invasives*. Each of the species mentioned in the literature as external or internal invasives in Mediterranean forest ecosystems will be presented in this section.

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[1] This term refers to both spermatophage and external seed predator feeding guilds defined in Chap. 4.

9.2.1 External Invasives (Introductions from Outside of the Mediterranean Basin)

Biogeographic Patterns Although Asia has supplied the major part of the alien arthropods occurring in Europe since the middle of the twentieth century, alien fruiting structure insects currently established in the Mediterranean Basin originate from North America, except those originating from Australasia that were mostly linked to the introduction of *Eucalyptus* and *Acacia* spp. in this area (Roques et al. 2010). A total of four external invasives have been recorded to date.

Taxonomy There are only three feeding guilds[2] of invasive fruiting structure insects introduced from outside of the Mediterranean Basin. The first invasive feeding guild corresponds to the *spermatophages* of the *Megastigmus* genus (Hymenoptera: Torymidae), which develop exclusively within seeds. Several native species belonging to this genus already exist in Mediterranean ecosystems, basically attacking Cupressaceae and Pinaceae species. These seed chalcids (also called seed wasps) associated with conifers are generally considered to be highly specialized, being either species-specific (even when several potential host species coexist in a same place) or restricted to a conifer genus (Auger-Rozenberg et al. 2006). *Megastigmus* invasive species are present throughout Europe on gymnosperms and angiosperms, but in Mediterranean forest ecosystems, only two North American *Megastigmus* species associated with firs are recorded and shifted from American to Mediterranean firs in south of France, *M. pinus* on *Abies alba*, and *M. rafni* on several Mediterranean firs (Fig. 9.1) (Roques and Skrzypczynska 2003). Likely benefiting from multiple introductions in France during the second half of twentieth century (Auger-Rozenberg et al. 2006), they are not yet recorded in other Mediterranean countries.

The second invasive feeding guild corresponds to the *inflorescence-feeders*, which are represented by a single species on *Eucalyptus* species, the chalcidoid wasp *Quadrastichodella nova* (Hymenoptera: Eulophidae; Fig. 9.1). Despite Eulophidae are often known as entomophagous,[3] this wasp is a gall-inducer in the placenta of one of the locules in the seed capsule of a flower bud (Klein et al. 2015). This prevents seed set (Kim and La Salle 2008). Although Australian in origin, *Q. nova* is now recorded from different Mediterranean countries including Tunisia (M. Branco, pers. observ.), Israel, Spain, Italy, and Turkey (Doğanlar and Doğanlar 2008; Kim and La Salle 2008), following its host tree.

The third invasive feeding guild corresponds to an *external seed predator* that feeds directly upon the seeds from the cone surface, namely the polyphagous Western conifer seed bug, *Leptoglossus occidentalis* (Hemiptera: Coreidae; Fig. 9.1). The third alien species is of particular interest because it is the only

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[2] See Chap. 4 for definitions of the terms used.

[3] Primary or hyper parasitoids.

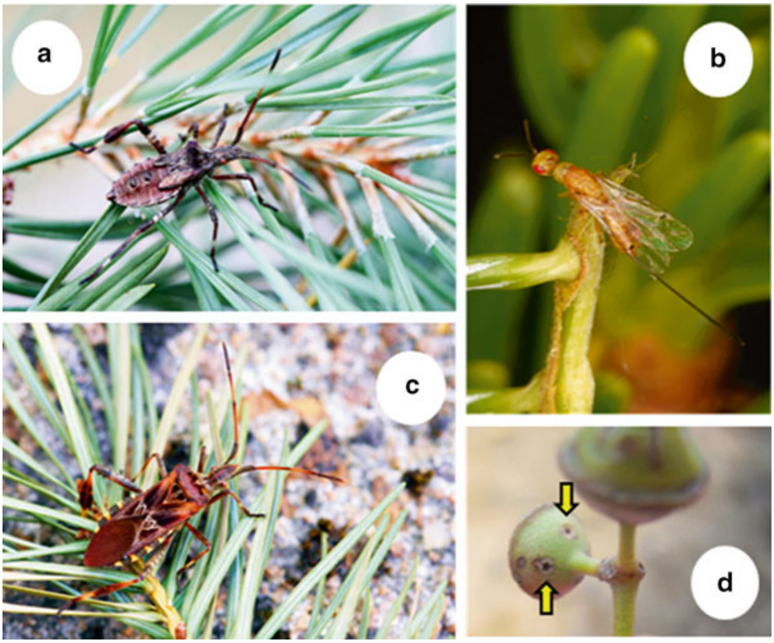

Fig. 9.1 The Western conifer seed bug, *Leptoglossus occidentalis* in south of France (**a**) immature nymph and (**b**) adults. The fir seed chalcid *Megastigmus rafni* in southeastern France (**c**). Eucalyptus seed capsule with two typical circular exit holes of the chalcidoid wasp *Quadrastichodella nova* in Tunisia (**d**) (Photos: D. Lees (**b**), V. Lesieur (**a**, **c**) and M. Branco (**d**))

polyphagous species of the list. *Leptoglossus occidentalis* is a pest widely distributed pest in western North America, which has been accidentally introduced in northern Italy in 1999. It expanded its range very quickly and spread over most Europe in about one decade (Lesieur et al. 2014). There is strong evidence that the fast invasion of this bug in Europe proceeds from multiple introductions (Lesieur 2014). Recorded for several years on the northern rim of Mediterranean Basin (EPPO 2014), it was recently found in North Africa (Ben Jamaa et al. 2013). This provides evidence that the bug is now becoming a highly successful worldwide invader that feeds on cones of a large number of conifer species. Both adults and immature nymphs consume individual seeds in developing and mature cones during the growing season, and whatever the already or soon invaded countries, Mediterranean forest ecosystems represents a suitable habitat of *L. occidentalis* (Zhu et al. 2014).

9.2.2 Internal Invasives (Introductions Within the Mediterranean Basin)

Biogeographic Patterns Invasions of fruiting structure insects can also occurred inside the Mediterranean Basin. Although little is currently known about the potential of Asia Minor and/or the Near East to provide such invaders, the three case studies presented in this section suggest an orientation of invasion movement in a northerly direction (according to the division of the main geographic sub-regions presented in Chap. 4, Sect. 4.3.2). This is consistent with greater interests of countries of the Northern Rim of the Mediterranean Sea (France, Greece, Italy, Spain and Portugal) for Mediterranean tree species importation and plantation than countries of the southwestern and southeastern Rim.

Taxonomy Internal invasive species belong to the sole feeding guild of spermatophages and genus *Megastigmus*. The first species is *Megastigmus wachtli*, a seed chalcid mainly associated with the Mediterranean cypress, *Cupressus sempervirens* (Fig. 9.2). This conifer is native to the eastern Mediterranean region and has been widely cultivated for millennia away throughout the whole Mediterranean region. Concurrently, *M. wachtli* populations have been accidentally introduced in most occidental Mediterranean countries probably by the ancient Greeks and the Romans inside the seeds (Roques et al. 1999).

Far more recently, two cedar seed chalcids have been introduced in cedar forests of southeastern France (Auger-Rozenberg et al. 2012). Most of such French cedar stands have been infested by *Megastigmus pinsapinis* (Fig. 9.3), which has probably been introduced from North Africa during the importation of seeds of *C. atlantica* for reforestation programs over more than a century ago. A second species, *M. schimitscheki* (Fig. 9.3), which native area covers *C. libani* and *C. brevifolia* forests in the Middle-East, has been accidentally introduced in southeastern France from seeds *of C. brevifolia* in the early 1990s. French populations of this chalcid were founded from a unique introduction event of an extremely restricted number of individuals that realized a host switch from *Cedrus brevifolia* to *C. atlantica* (Auger-Rozenberg et al. 2012). *M. schimitscheki* colonized most of southeastern French *C. atlantica* stands (Lander et al. 2014), which resulted in a niche overlap with *M. pinsapinis* (Boivin et al. 2008; Fabre et al. 2004) that led to strong competitive interspecific interactions between them (Gidoin et al. 2015).

9.3 Invasion Pathways

Many natural barriers between regions, countries and continents are bypassed due to the increase of international trades. Alien species favoured by such human activity are increasingly recognized as invasive species, posing great threats to biodiversity and economy (Walther et al. 2009). Whatever the insect group to be considered,

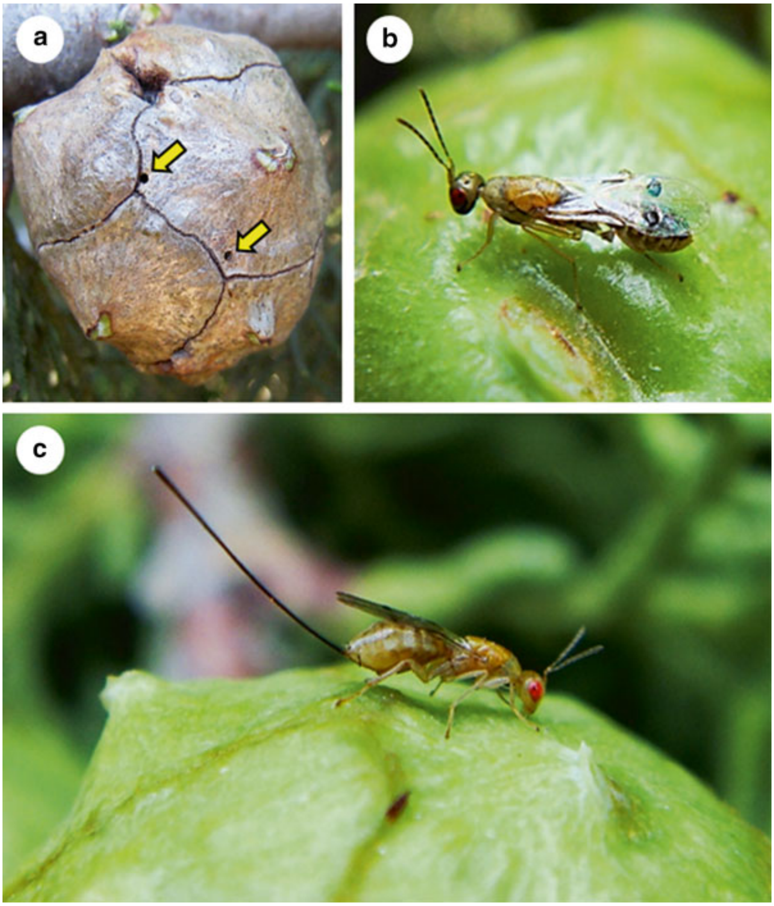

Fig. 9.2 The cypress seed chalcid *Megastigmus wachtli* in southeastern France. Two-year old cone of the evergreen cypress *Cupressus sempervirens* with two typical circular emergence holes of *M. wachtli* adults (**a**, *arrows*). Male and female of *M. wachtli* (respectively) on a 1-year old cone of *C. sempervirens* (**b**, **c**) (Photos: T. Boivin (**a**) and J. Safrana (**b**, **c**))

the invasion processes in invertebrates are commonly linked to the intensity of anthropogenic disturbance and hence to the pathways of introduction (Hulme et al. 2008; Pysek et al. 2010). Recent studies suggest that ca. 90 % of the alien invertebrates were introduced unintentionally through human activity (Roques 2010; Roques et al. 2009). Anthropogenic dispersal usually occurs from and to regions where important human activity coincides with a particular life stage that favours dispersal (e.g. Robinet et al. 2009; Kaňuch et al. 2013).

In the seminiphagous wasps *Quadrastichodella nova* and *Megastigmus* spp., the life stage that is most likely to be transported as a result of human activity is the

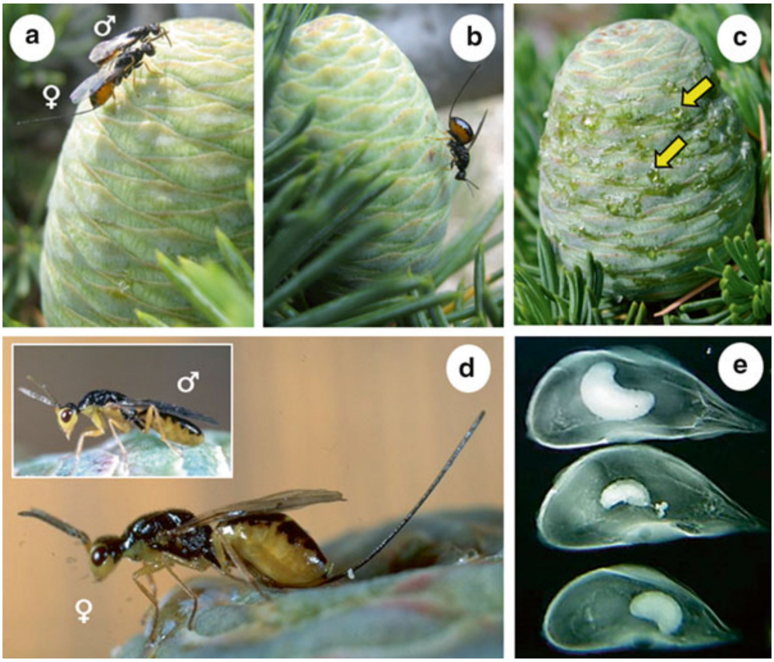

Fig. 9.3 The cedar seed chalcids *Megastigmus schimitscheki* (**a**, **b**) and *M. pinsapinis* (**d**) on 1-year cones of the Atlas cedar *Cedrus atlantica* in southeastern France. One-year old cone of *C. atlantica* with resin droplets (*arrows*) resulting from seed chalcid oviposition through the cone scales with their ovipositor. Note that the chalcids mainly target the central part of the cone during oviposition (**c**). X-ray radiography of seeds of *C. atlantica* parasitized by seed chalcids, whose larvae have consumed both seed embryo and reserve organs before entering diapause (**e**) (Photos: T. Boivin (**a**–**c**), J.-P. Fabre (**d**) and A. Chalon (**e**))

diapausing larval stage. Because all spermatophages have an endophytic life-cycle,[4] diapausing larvae remain within seeds from their harvest to their use in tree nurseries and may be transported as a result of seed trade at international, national and regional scales (Kim and La Salle 2008; Auger-Rozenberg and Roques 2012). Seminiphagous insect species require special attention because they can cause massive seed losses, and because the lack of regulatory measures on global trade in tree seeds facilitated their entry in Europe, including the Mediterranean Basin. They are actually considered as contaminants of traded goods, associated to commodities intentionally introduced by man (Hulme 2009), as in the case of seeds exchanges of exotic tree species[5] (Roques and Auger-Rozenberg 2006). As detailed in Sect. 9.2, the *Megastigmus* genus is becoming the major supplier of invasive seed insects in the Mediterranean Basin. In particular, the case of *M. schimitscheki* recently

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[4] Insects spending their entire pre-imaginal development (egg to pupa) within the fruiting structure.

[5] Mainly used in commercial seed market for plantations and ornamentals.

introduced from Near East to southeastern France highlights the implications of unregulated seed trade probably associated to seed imports for clandestine ornamental purposes (Auger-Rozenberg et al. 2012). Similarly, although introduction pathways of *Q. nova* in the Mediterranean Basin are not clearly known, it is likely that they were related to the *Eucalyptus* seed trade all over the world (Paine et al. 2011).

The introduction in Europe of the Western conifer seed bug *Leptoglossus occidentalis* resulted from another typical invasion pathway referred to as stowaway transport, in which species are directly associated with human transport but arrive independently of a specific commodity (e.g. Rabitsch 2010; Roy et al. 2011). Stowaway transport is the most likely vector of external seed predators, which feed and develop outside fruiting structures. The aggregative behaviour of *L. occidentalis* for the overwintering phase or the high mobility of isolated individuals probably favoured transportation of propagules by ship in containers, e.g. timber logs or wood panels related to timber shipments, from the USA to Europe (Dusoulier et al. 2007; Malumphy et al. 2008).

9.4 Factors of Invasion Success and Secondary Spread

Identifying the drivers of successful invasions is a key step in predicting and avoiding subsequent invasions of pest species belonging to the same guild. Invasion success refers to the ability of a species to increase from low population density (Shea and Chesson 2002). Characteristics of both the recipient community and the new environment are critical drivers of the demographic response of an introduced population, e.g. through the presence of natural enemies or by affecting resource availability.[6] Introduced populations generally face a heterogeneous world in which abiotic conditions, resource distribution and abundance, and density in native species[7] vary in both space and time. Such environmental heterogeneity is likely to affect population growth in both introduced and expanding populations. Displaying or evolving towards life-history traits that provide adaptive responses to such demographic and environmental constraints is a key to establishment, persistence and secondary spread in the new environment (Sakai et al. 2001). In this section, we will illustrate how these concepts can help understanding the successful invasion of Mediterranean forest ecosystems by the Western conifer seed bug and by *Megastigmus* seed chalcids (Fig. 9.4). Unlike *Quadristichodella nova*, these species have been well studied and have proved to be of particular interest for two reasons. First, they result from different introduction histories, i.e. multiple and single introductions. Second, they suggest that patterns of establishment success can drastically differ according to the species concerned.

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[6] Resource availability may depend the presence of native competitors and on spatio-temporal variation in fruiting structure abundance.

[7] Native species may be associated with facilitation, competition or predation.

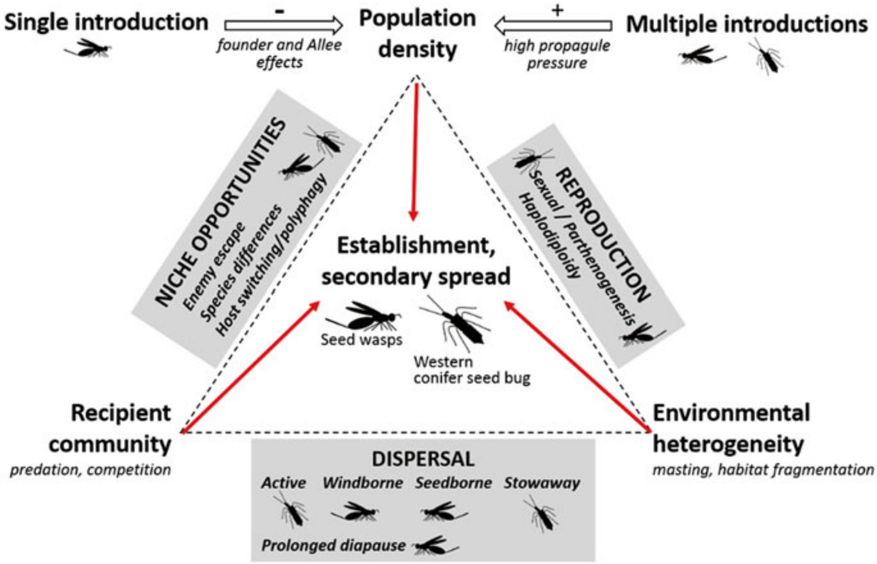

Fig. 9.4 Conceptual framework of the main drivers of invasion success in seed chalcids (*Megastigmus* spp.) and the Western conifer seed bug (*Leptoglossus occidentalis*) in the Mediterranean Basin. Establishment and secondary spread depend on the effects of the environment, the recipient community and population density on population growth of introduced populations. Such effects may vary in both space and time. Invasive populations may benefit from niche opportunities and both advantageous reproductive and dispersal strategies to grow and spread in their new environment

9.4.1 Reproduction

Reproductive strategies can play a key role in circumventing the demographic cost of severe founder effects in introduced populations or in those located at the front of expansion range (Sakai et al. 2001; Yamanaka and Liebhold 2009). Parthenogenesis is a typical reproductive strategy in seed chalcid wasps, in which females can produce asexually either males (i.e. arrhenotoky) or females (i.e. thelytoky) (Boivin et al. 2014). This trait is a likely factor of chalcids' invasion success in Mediterranean forests by reducing to risk of extinction and favouring population growth at low initial density (Auger-Rozenberg et al. 2012, Fig. 9.4). Recent work on the invasive cedar seed chalcid *M. schimitscheki* also demonstrated an absence of Allee effect as fertility reaches its maximum at low population density (Gidoin et al. 2015). Moreover, as all Hymenoptera, seed chalcids exhibit a haplodiploid sex-determination system, in which males develop from unfertilized eggs and are haploid, and females develop from fertilized eggs and are diploid. In haplodiploid organisms, a genetic load that is hidden in heterozygous female diploids should be expressed and thus purged by selection in the haploid males (Werren 1993). This might have limited adverse effects of inbreeding depression during the first steps of *Megastigmus* invasions (Auger-Rozenberg et al. 2012).

9.4.2 Niche Opportunities

Suitable Host Availability In any insect invasion the presence or absence of suitable resource and oviposition sites in the invaded range is a key factor of establishment success, even more in the context of climate change, which can facilitate a sustainable establishment of an invasive species in a new suitable ecosystem (Walther et al. 2009; Bacon et al. 2014). This may have a more critical meaning for specialists such as most of fruiting structure insects, for which the possibility of refugia on alternative habitats is generally almost null.[8] In this context, invasive seed feeders of the *Megastigmus* genus are unique because many of the trees they feed upon have also been introduced by humans in recent times, particularly since the development of international trade in the twentieth century. Because they are highly specialized seed feeders (Auger-Rozenberg and Roques 2012), the introduction of their host trees facilitates their own accidental introduction. Seed chalcids may also exhibit phenotypic plasticity and successfully switch to native tree species when these belong to the same genera as their original host (Roques et al. 2006). Host shifting generally results in a niche overlap with native specialized seed feeders that can lead to interspecific competition for the seed resource, as shown in Mediterranean fir and cedar stands (Auger-Rozenberg and Roques 2012; Gidoin et al. 2015). In the absence of suitable hosts in the native tree community, invasion of specialists succeeds at the sole condition that the original host has been also widely introduced. This was illustrated by the invasion of *Quadrastichodella nova* in *Eucalyptus* plantations across southern Europe and Middle-East (Kim and La Salle 2008; Paine et al. 2011). Conversely, invasion success in the Western conifer seed bug *Leptoglossus occidentalis* results from three typical features of host use in external seed predators: (1) generalist feeding habits, (2) external food intake,[9] and (3) strong active flight capability in adults (Fig. 9.4). *L. occidentalis* displays polyphagous feeding habits in the invaded European regions where it feeds on both native pine species and introduced exotic conifers. Such a combination of traits allows *L. occidentalis* to move rapidly and at rather long-distance to find suitable host trees (Lesieur et al. 2014).

Niche Use Differences between native and invasive specialist species are also important factors of invasion success as they may promote niche partitioning. Niche partitioning is a mechanism favouring coexistence provided invasive and resident species differ in their resource use (Byers and Noonburg 2003). Niche-based hypotheses to explain invasion success also rely on species differences that allow invaders to either access unused resources (empty niche hypothesis) or be more competitive in exploiting shared and limited resources (niche replacement hypothesis) (Ricciardi et al. 2013). In southeastern France, the successful invasion of *M.*

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[8] See Chap. 4 about host plant specialization in fruiting structure insects.

[9] Unlike most other fruiting structure insects that develop inside the cones or the seeds (see Chap. 4).

schimitscheki results from earlier phenology than its resident competitor *M. pinsapinis*. As cedar seeds are as yet unused by *M. pinsapinis* upon the adult emergence and oviposition of *M. schimitscheki*, this resource availability may be equivalent to an empty niche for *M. schimitscheki* and may have favoured its establishment. This scenario was supported by high probabilities of invasion failure in simulation approaches, in which *M. schimitscheki* has a similar phenology as *M. pinsapinis* (Gidoin et al. 2015). A similar empty niche mechanism may explain the successful invasion of *M. pinus* on French firs as this species has an earlier spring emergence than both the native *M. suspectus* and the invasive *M. rafni* (Boivin and Auger-Rozenberg, pers. observ.). By contrast, phenology cannot explain the great invasiveness of *M. rafni*, which it is the latest species related to firs in Europe to oviposit in spring. Alternatively, *M. rafni* has a longer ovipositor than any other fir chalcid species, which may allow oviposition in seeds that are not accessible to *M. pinus* and *M. suspectus* anymore due to the continuous development in size of cones (Auger-Rozenberg and Roques 2012). This may have facilitated the early stages of the invasion of *M. rafni*.

Enemy Escape Opportunity Another niche opportunity that a new environment can provide to invasive species is a low or null impact of natural enemies on population growth, a mechanism referred to as enemy escape opportunity (Shea and Chesson 2002). This may arise either in the absence of specialist enemies in the recipient community,[10] or when indigenous generalist and specialist enemies are inefficient in attacking invaders. Enemy escape opportunity may have contributed to successful invasions of both *Megastigmus* spp. and *L. occidentalis* in the Mediterranean Basin, as no specialist enemies known in the native areas of these species have been detected yet (Auger-Rozenberg and Boivin, pers. observ.; Lesieur 2014, Fig. 9.4).

9.4.3 Dispersal

Invasive species' range expansion occurs through many of the same mechanisms as range expansion of non-invasive species (Lawson Handley et al. 2011). Species may expand into adjacent habitats by regional diffusion as a function of population growth rate and a diffusion coefficient (Ciosi et al. 2010), or into distant patches and new environments by long-distance dispersal (Hastings et al. 2005). There may also be more complex dispersal patterns which combine short-distance diffusion with long-distance dispersal, referred to as stratified dispersal (Darling and Folino-Rorem 2009). Secondary spread of invasive fruiting structure insects can involve such diverse mechanisms, each depending on species' life-cycles or life stages (Fig. 9.4). In *L. occidentalis*, individuals live exclusively outside the cones and disperse primarily as adults, a highly mobile stage that can actively fly from a few

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[10] Because they did not successfully established or they were not introduced.

hundred meters to 30 km. Moreover, its habits to aggregate inside man-made structures in the fall to seek shelter for overwintering clearly facilitated stowaway secondary translocations within Europe (Lesieur et al. 2014). In seed chalcids, for which active flight capacity is unlikely to exceed host stand size (Jarry et al. 1997), passive long-distance dispersal, either windborne, seedborne[11] or both, was the most likely driver of colonization of new suitable sites across highly fragmented Mediterranean forest landscapes (Lander et al. 2014, Fig. 9.4).

As a temporal dispersal mechanism, strong propensity to prolonged diapause in seed chalcids may also help to buffer population collapses in years of low seed production by its obligate host, contributing to population sustainability following introduction and during expansion.[12] This has been demonstrated in *M. schimitscheki* (Suez et al. 2013). Similarly, *M. rafni* displays the strongest propensity to prolonged diapause among seed chalcid species feeding on French Mediterranean firs, which may have contributed to its successful establishment and expansion in this area (Boivin T., unpublished results).

9.5 Ecological and Economic Impacts

Alien species are considered as invasive when they have negative ecological and economic impacts in their novel environment. Their introduction contributes to damage ecosystems and affect economy and human health, and they are recognized as one of the major threats to biodiversity. Among them, alien insects cause a multitude of negative environmental impacts and billions of dollars in economic losses annually (Kenis et al. 2009; Vila et al. 2009; Roy et al. 2011; Simberloff et al. 2013; Jeschke et al. 2014). From a general point of view in forest ecosystems, it is mainly xylophagous invasive pests (e.g. the Asiatic *Anoplophora* species) that are responsible of higher environmental and economic impacts (Vaes-Petignat and Nentwig 2014). Fruiting structure insects are for their part generally considered the most important predators of tree seeds during the pre-dispersal phase of development (Turgeon et al. 1994; Auger-Rozenberg and Roques 2012). In this section, we will detail the different impacts that can be caused by the invasive fruiting structure insects in Mediterranean forest ecosystems. Because there is no specific data on the impacts of the *Eucalyptus* galling wasp *Quadrastichodella nova*, we will focus on those estimated in invasive conifer pests, namely the spermatophagous chalcid species (*Megastigmus* spp.), and the Western conifer seed bug.

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[11] Seedborne dispersal is referred to as man-aided displacement of infested seeds through seed trade.

[12] See Chap. 4 about the adaptive significance of prolonged diapause in populations of fruiting structure insects.

9.5.1 Ecological Impacts

The ecological impact of an invasion refers to the effect(s) that an established invasive species may have on a community at different levels of biological organization (Shea and Chesson 2002). Communities invaded by alien invasive species experience new species assemblages leading to novel interspecific interactions with potentially strong effects on the dynamics of both communities and invaders. This makes ecological impacts of invasive fruiting structure difficult to predict. They may occur at the genetic level through hybridization, and/or at the individual, population and community levels through seed consumption and competition for this resource or through transmission of diseases or parasites to native species (Kenis et al. 2009; Vaes-Petignat and Nentwig 2014).

9.5.1.1 Genetic Effects

Genetic effects through hybridization between invasive and native species of insects and other terrestrial invertebrates remain largely unexplored, whereas it is known to be the main type of impact for birds for example (Kenis et al. 2009; Langor and Sweeney 2009; Kumschick et al. 2015). Some examples are known on pollinating insects including species of honeybees and bumblebees in Mediterranean ecosystems, but cases of fruiting structure insects are largely unknown. The opportunities of hybridization depend on the presence of native species close to invasive species, which is not the case of the hymenopteran species on Eucalyptus (Kim and La Salle 2008, http://www.nhm.ac.uk/research-curation/research/projects/chalcidoids/database/). This is also not the case of *Leptoglossus occidentalis*, which is the only one species of the genus present in Europe, whereas the other occur only in Nearctic and sub-tropical regions (Brailovsky 2014). Conversely, resident and invasive species of the *Megastigmus* genus live in sympatry in the Mediterranean Basin, e.g. *M. pinsapinis* and *M. schimitscheki* on cedar (respectively), but no trace of genetic hybridization was yet detected between them. Intermediate morphotypes linked with intermediate genetic distances were however observed between the fir chalcid *M. suspectus* and *M. pinsapinis* (Auger-Rozenberg et al. 2006). This could indicate a species complex structured by host genus, rather than hybrids, so as both *M. suspectus* and *M. pinsapinis* exhibit thelytokous parthenogenesis and probably a loss of sexual function in females or in both sexes (Boivin et al. 2014).

9.5.1.2 Population and Community Effects

Effects on Host Populations As external seed predators and spermatophages, invasive populations of *L. occidentalis* and *Megastigmus* spp. (respectively) directly affect seed viability, potentially leading to similar demographic and evolutionary impacts on Mediterranean host populations as those associated with native insect communities.[13] Briefly, insect damages to seeds may influence: (1) host spatial dynamics through interferences with natural regeneration processes (Tamburini et al. 2012), and (2) host evolution if insects differentially decrease seed production among trees that vary individually in some heritable traits (Kolb et al. 2007). Invasions of seed insects might result in greater seed damages in invaded areas in the two following ways: (1) when hosts are evolutionarily naïve regarding their invasive seed predators so they did not develop adequate defence mechanisms (Raffa et al. 2008), or more likely (2) when seed predation rates by invasive predators cumulate to those of native seed predators (Auger-Rozenberg and Roques 2012; Lesieur et al. 2014). In the latter case, the impact of an invasive species on host dynamics can be hardly disentangled from that of native ones. Moreover, the long term effects of an invasive seed predator on a host population remain difficult to establish without clarifying the dynamics of the interactions that may arise with the other seed predators of the recipient community. In a community of seed specialists, niche overlap is the source of strong interspecific competition that may affect the demography of both invasive and native species, potentially maintaining global seed damage at a lower level than the sum of the damages caused by each species in the absence of a competitor. This has been shown in southern French natural stands of *Cedrus atlantica*, where the demographic growth of the invasive seed chalcid *M. schimitscheki* has progressively driven the sympatric populations of the resident *M. pinsapinis* to nearly extinction in about 10 years (Fig. 9.5). This contrasted with the stationary state of its allopatric populations escaping competition. As a result, the global seed infestation percentage in sympatric areas progressively converges towards that of the dominant chalcid species. This demonstrates that interspecific interactions in fruiting insects can modulate, in the long term, the cumulative effect of an invasion on seed outputs in invaded host populations.

Finally, invasive fruiting structure insects may affect native host populations through the potential transmission of diseases or parasites. Nevertheless, little data is available on the transmission of fungal diseases in the Mediterranean Basin, but *Leptoglossus occidentalis* may be a likely vector of *Diplodia pinea*, a native fungal disease which causes a tip-blight of the crown of Mediterranean pines (Luchi et al. 2012).

Effects on the Indigenous Entomofauna The outcome when an invasive species faces an indigenous species that uses the same resource may be coexistence, competitive displacement of the indigenous species or extinction (Sakai et al. 2001; Reitz and Trumble 2002). Shared ecological specialization on a discrete resource is perceived as one of the reliable predictors of competition in insect communities (Denno et al. 1995). Ecological specialization is indeed a mechanism that limits the possibility of refugia, which is particularly prone to enhance species niche overlap and consequently to strengthen interspecific competition. This may have a particular meaning for native and invasive fruiting structure insects that display high degrees of specialization at both the resource and host plant levels. Moreover,

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[13] See Chap. 4.

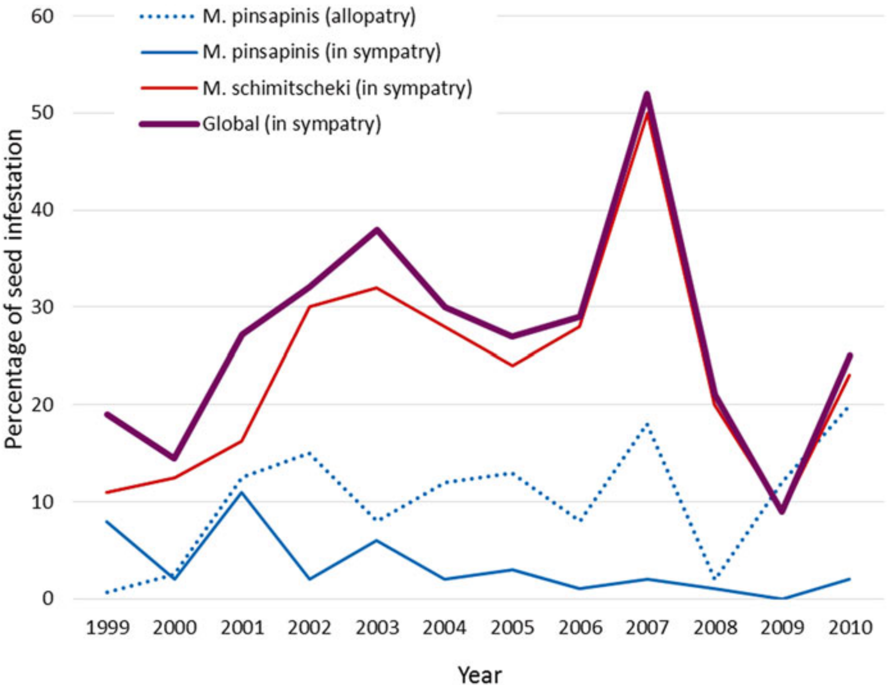

Fig. 9.5 Temporal pattern of the mean seed infestation percentages by the competing seed chalcids *Megastigmus schimitscheki* (invasive since 1994) and *M. pinsapinis* (resident) in southern French stands of *Cedrus atlantica*

biological invasions generally produce novel species assemblages of specialists that share the same host but that did not co-evolve, which may prevent diverse ecological factors (e.g. antagonists, mutualists and host plant effects) from modulating the strength of competition and then restrict coexistence opportunities (Ness and Bronstein 2004; Smith et al. 2008).

In southeastern France, cedar seed chalcids provided recent evidence that an absence of such ecological competitive trade-offs can lead to competitive displacement rather than stable coexistence in specialist invaded communities (Fig. 9.5). The invasive *Megastigmus schimitscheki* displays a long-term negative impact on the resident *M. pinsapinis*, through a resource pre-emption that results from both earlier phenology and larvae's cannibal behavior (Boivin et al. 2008; Gidoin et al. 2015). Similar niche replacement has been presumed in most French Mediterranean fir stands, where the invasive *M. rafni* has become the dominant seed chalcid species by displacing the native *M. suspectus*, following an important secondary spread in the 1990s (Roques 1983; Auger-Rozenberg and Roques 2012). Conversely to *M. schimitscheki*, *M. rafni* has the latest spring emergence, which results in a delayed access to the seed resource compared to other fir chalcid species and thus precludes niche replacement through resource pre-emption. If several factors may explain the invasion success of *M. rafni*,[14] the mechanisms driving its negative impact on native fir entomofauna are still unclear. However, interspecific competition in seed chalcids is not necessarily the rule as *M. pinus* has been increasingly observed in natural southeastern French stands of *Abies alba,* coexisting with *M. rafni* or with both *M. rafni* and *M. suspectus* (Auger-Rozenberg and Roques 2012).

9.5.2 Economic Impacts

Many recent studies review the socio-economic impacts of alien arthropods in Europe (Langor and Sweeney 2009; Vila et al. 2009; Vaes-Petignat and Nentwig 2014), and the importance of ecosystem services provided by insects is important and it is now obvious that their disruption can produce enormous costs. Nevertheless, few impact assessment studies exist for fruiting structure insects in Mediterranean forest ecosystems. When they do exist, they are often related with seed trade and have taken place in intensively-managed seed orchards and plantations for example, not in natural stands (Auger-Rozenberg and Roques 2012). Economic impacts due to the other invasive *Megastigmus* species (i.e. associated with firs) are far less known.

The seed bug *Leptoglossus occidentalis* is regarded as a major economic pest in the seed orchards designed to produce genetically superior tree seeds in the native American range. In France, bug damages could be a threat for yields in high-value seed orchards but they reached higher levels in natural stands (up to 25 % and 70 %, respectively) (Lesieur et al. 2014). Moreover, this pest could have a negative impact on the production of pine-seeds for human consumption in Italian stone pine stands (Bracalini et al. 2013). The bug is besides often considered an urban pest, causing alarm and social nuisance when swarms of adults invade buildings for overwintering and damage common plumbing material (Tamburini et al. 2012). Accurate identification of seed bug damage is very difficult because damage is not visible externally on fed-upon seeds, and internal damage (revealed through seed dissection or radiography, provided availability of such monitoring techniques in Mediterranean countries) may have been caused by weather, poor pollination, or other environmental factors rather than seed bug feeding. Bugs impacts are then easier to evaluate in planted and/or managed forests than in natural and unmanaged woodlands.

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[14] See Sect. 9.4.

9.6 Conclusion

Forest ecosystems of the Mediterranean Basin host only four non-native species of insect of tree reproductive structures. These include both the spermatophages *Megastigmus rafni* and *M. pinus* and the external seed predator *Leptoglossus occidentalis* that were introduced from North America, and the inflorescence feeder *Quadristichodella nova* that was introduced from Australia. To these species can be added three other spermatophages, *M. schimitscheki*, *M. wachtli* and *M. pinsapinis*, that are native to the Mediterranean Basin but that accidentally spread across this area from their native sub-regions. Thus, a total of seven species can be regarded as comprising invasive populations within forest ecosystems in the Mediterranean Basin. This contrasts with evidence of higher invasion pressure of fruiting structure insects in Northern Europe, where no less than 11 species have been introduced from all over the world as regards solely the *Megastigmus* genus (DAISIE European Invasive Alien Species Gateway: http://www.europe-aliens.org, accessed 29th May 2015). The multiple factors explaining such discrepancies are still difficult to assess, partly because many taxonomic uncertainties remain within such insect communities, and because many areas and host tree species remain to be sampled in the Mediterranean Basin. However, one could primarily speculate that both bioclimatic and vegetation specificities of the Mediterranean Basin provide a poor fit with those of the main provider areas of invasive forest insect species, e.g. China, Northern America or Africa. This may constitute a greater barrier to invasion success, especially since most fruiting structure insect species are specialists at both resource type and host scales. Little is known about the potential for other Mediterranean areas worldwide to be, or to become, substantial contributors to invasive entomofauna on tree reproductive structures in forest ecosystems of the Mediterranean Basin.

The case studies described in this chapter provide evidence that propagule pressure, chance events, ecological traits of invasive species and the properties of invaded ecosystems may be of primary importance to explain both invasion success and invasion impacts in Mediterranean forests. Once introduced and established, alien species may spread through both natural and human-aided dispersal (Hulme et al. 2008). A more and more common phenomenon is hereafter known as the bridgehead effect, namely a primary site of invasion with other territories subsequently invaded from this site. This process has been already revealed in diverse forest insects in the Mediterranean Basin, e.g. the maritime pine bast scale (Kerdelhue et al. 2014) and the red palm weevil (Rugman-Jones et al. 2013). We postulate here that the life cycle and the ecological features of fruiting structure insects make them ideal candidates for bridgehead effects, as recently demonstrated with the dispersal of the Western conifer seed bug *Leptoglossus occidentalis* in whole Europe (Lesieur 2014) and as suggested in the cedar chalcid *Megastigmus schimitscheki* (Auger-Rozenberg et al. 2012). It is likely that European populations of invasive fruiting structure insects could act as a bridgehead for latter invasions in the Mediterranean Basin, and beyond, especially in the context of unregulated international seed trade.

The management of this type of invasives may involve similar crop-monitoring and prophylactic techniques as those described for native species in Chap. 4 (Sect. 4.7). However, it is clear that an effective control of introduced populations would primarily rely on a considerable improvement of regulation measures in seed trade to minimize the risk of new introductions. Since the mid-1990s, globalization and worldwide movements of goods have drastically accelerated accidental introductions of exotic insects developing within seeds of cultivated or ornamental plants. Reasons for this include: (i) cones and seeds of woody plants are excluded by European Union directives from any controls at import from non-European countries, and (ii) cryptic insect life cycles impede detection and phytosanitary interventions (Auger-Rozenberg and Roques 2012). One such example is the *Megastigmus* genus cited in this chapter. In this context, the development of effective monitoring and control strategies that are specific to invasive populations strongly depend on our ability to disentangle the processes of post-establishment spread in the Mediterranean Basin. Most of current field survey methods detect populations only once they are relatively large and already serving as sources of emigrants. We emphasize a crucial need for monitoring programs aiming at detecting populations at an early stage of establishment, involving new alternative survey techniques, e.g. a suction trap network in case of windborne invasive populations (Lander et al. 2014). Given fruiting structure insects are generally highly host plant specialized, integrating specific monitoring of ornamental host specimens could provide valuable insights into the contribution of spatially isolated host individuals as stepping stones in population spread.

References

Auger-Rozenberg MA, Roques A (2012) Seed wasp invasions promoted by unregulated seed trade affect vegetal and animal biodiversity. Int Zool 7:228–246

Auger-Rozenberg MA, Kerdelhué C, Magnoux E et al (2006) Molecular phylogeny and evolution of host-plant use in conifer seed chalcids in the genus *Megastigmus* (Hymenoptera: Torymidae). Syst Entomol 31:47–64

Auger-Rozenberg MA, Boivin T, Magnoux E et al (2012) Inferences on population history of a seed chalcid wasp: invasion success despite a severe founder effect from an unexpected source population. Mol Ecol 21:6086–6103

Bacon SJ, Aebi A, Calanca P et al (2014) Quarantine arthropod invasions in Europe: the role of climate, hosts and propagule pressure. Divers Distrib 20:84–94. doi:10.1111/ddi.12149

Ben Jamaa ML, Mejri M, Naves P et al (2013) Detection of *Leptoglossus occidentalis* Heidemann, 1910 (Heteroptera: Coreidae) in Tunisia. Afr Entomol 21:165–167

Boivin T, Rouault G, Chalon A et al (2008) Differences in life history strategies between an invasive and a competing resident seed predator. Biol Invasions 10:1013–1025

Boivin T, Henri H, Vavre F et al (2014) Epidemiology of asexuality induced by the endosymbiotic Wolbachia across phytophagous wasp species: host plant specialization matters. Mol Ecol 23:2362–2375. doi:10.1111/mec.12737

Bracalini M, Benedettelli S, Croci F et al (2013) Cone and seed pests of *Pinus pinea*: assessment and characterization of damage. For Entomol 106:229–234

Brailovsky H (2014) Illustrated key for identification of the species included in the genus *Leptoglossus* (Hemiptera: Heteroptera: Coreidae: Coreinae: Anisoscelini), and descriptions of five new species and new synonyms. Zootaxa 3794:143–178

Byers J, Noonburg E (2003) Scale dependent effects of biotic resistance to biological invasion. Ecology 84:1428–1433

Ciosi M, Miller N, Toepfer S et al (2010) Stratified dispersal and increasing genetic variation during the invasion of Central Europe by the western corn rootworm, *Diabrotica virgifera virgifera*. Evol Appl 4:54–70

Darling JA, Folino-Rorem NC (2009) Genetic analysis across different spatial scales reveals multiple dispersal mechanisms for the invasive hydrozoan Cordylophora in the Great Lakes. Mol Ecol 18:4827–4840

Denno RF, McClure MS, Ott JR (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. Annu Rev Entomol 40:297–331

Doğanlar O, Doğanlar M (2008) First record of the eucalyptus seed gall wasp, *Quadrastichodella nova* Girault, 1922,(Eulophidae: Tetrastichinae) from Turkey. Turk J Zool 32:457–459

Dusoulier F, Lupoli R, Aberlenc H-P et al (2007) L'invasion orientale de *Leptoglossus occidentalis* en France: bilan de son extension biogéographique en 2007 (Hemiptera Coreidae). L'Entomologiste 63:303–308

EPPO (2014) Nouvelles données sur les organismes de quarantaine et les organismes nuisibles de la Liste d'alerte de l'OEPP. 11

Essl F, Dullinger S, Rabitsch W et al (2011) Socioeconomic legacy yields an invasion debt. Proc Natl Acad Sci U S A 108:203–207. doi:10.1073/pnas.1011728108

Fabre J-P, Auger-Rozenberg M-A, Chalon A et al (2004) Competition between exotic and native insects for seed resources in trees of a Mediterranean forest ecosystem. Biol Invasions 6:11–22

Gidoin C, Roques L, Boivin T (2015) Linking niche theory to ecological impacts of successful invaders: insights from resource fluctuation-specialist herbivore interactions. J Anim Ecol 84:396–406. doi:10.1111/1365-2656.12303

Hastings A, Cuddington K, Davies KF et al (2005) The spatial spread of invasions: new developments in theory and evidence. Ecol Lett 8:91–101

Hulme PE (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18

Hulme PE, Bacher S, Kenis M et al (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policy. J Appl Ecol 45:403–414

Jarry M, Candau JN, Roques A et al (1997) Impact of emigrating seed chalcid, *Megastigmus spermotrophus* Wachtl (Hymenoptera: Torymidae), on seed production in a Douglas-fir seed orchard in France and modelling of orchard invasion. Can Entomol 129:7–19

Jeschke JM, Bacher S, Blackburn TM et al (2014) Defining the impact of non-native species. Conserv Biol 28(5):1188–1194

Kaňuch P, Berggren A, Cassel-Lundhagen A (2013) Colonization history of *Metrioptera roeselii* in northern Europe indicates human-mediated dispersal. J Biogeogr 40:977–987

Kenis M, Rabitsch W, Auger-Rozenberg M-A et al (2007) How can alien species inventories and interception data help us prevent insect invasions? Bull Entomol Res 97:489–502

Kenis M, Auger-Rozenberg M-A, Roques A et al (2009) Ecological effects of invasive alien insects. Biol Invasions 11:21–45

Kerdelhue C, Boivin T, Burban C (2014) Contrasted invasion processes imprint the genetic structure of an invasive scale insect across southern Europe. Heredity 113:390–400. doi:10.1038/hdy.2014.39

Kim IK, La Salle J (2008) A new genus and species of Tetrastichinae (Hymenoptera: Eulophidae) inducing galls in seed capsules of *Eucalyptus*. Zootaxa 1745:63–68

Klein H, Hoffmann JH, Neser S, Dittrich-Schroder G (2015) Evidence that *Quadrastichodella nova* (Hymenoptera: Eulophidae) is the only gall inducer among four hymenopteran species associated with seed capsules of *Eucalyptus camaldulensis* (Myrtaceae) in South Africa. Afr Entomol 23:207–223

Kolb A, Ehrlén J, Eriksson O (2007) Ecological and evolutionary consequences of spatial and temporal variation in pre-dispersal seed predation. Perspect Plant Ecol 9:79–100

Kumschick S, Bacher S, Evans T et al (2015) Comparing impacts of alien plants and animals in Europe using a standard scoring system. J Appl Ecol 52(3):552–561

Lander TA, Klein EK, Oddou-Muratorio S et al (2014) Reconstruction of a windborne insect invasion using a particle dispersal model, historical wind data, and Bayesian analysis of genetic data. Ecol Evol 4:4609–4625. doi:10.1002/ece3.1206

Langor D, Sweeney J (2009) Ecological impacts of non-native invertebrates and fungi on terrestrial ecosystems. Biol Invasions 11:1–3

Lawson Handley LJ, Estoup A, Evans D et al (2011) Ecological genetics of invasive alien species. BioControl 56:409–428

Lesieur V (2014) Invasion de la punaise américaine *Leptoglossus occidentalis* en Europe: une contribution à la compréhension des invasions fulgurantes. Doctorat Biologie Forestière, Université d'Orleans

Lesieur V, Yart A, Guilbon S et al (2014) The invasive Leptoglossus seed bug, a threat for commercial seed crops, but for conifer diversity? Biol Invasions 16(9):1833–1849. doi:10.1007/s10530-013-0630-9

Luchi N, Mancini V, Feducci M et al (2012) *Leptoglossus occidentalis* and *Diplodia pinea*: a new insect-fungus association in Mediterranean forests. For Pathol 42:246–251

Malumphy C, Botting J, Bantock T et al. (2008) Influx of Leptoglossus occidentalis Heidemann (Coreidae) in England. Het News, 2nd Series, 12, Autumn

Ness J, Bronstein J (2004) The effects of invasive ants on prospective ant mutualists. Biol Invasions 6:445–461

Paine T, Steinbauer MJ, Lawson S (2011) Native and exotic pests of eucalyptus: a worldwide perspective. Annu Rev Entomol 56:181–201

Pysek P, Jarosik V, Hulme PE et al (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. Proc Natl Acad Sci U S A 107:12157–12162. doi:10.1073/pnas.1002314107

Rabitsch W (2010) True bugs (Hemiptera, Heteroptera). Biorisk 4:407–433

Raffa KF, Aukema BH, Bentz BJ et al (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58:501–517

Ricciardi A, Hoopes M, Marchetti M et al (2013) Progress toward understanding the ecological impacts of nonnative species. Ecol Monogr 83:263–282

Reitz SR, Trumble JT (2002) Competitive displacement among insects and arachnids. Annu Rev Entomol 47:435–465

Robinet C, Roques A, Pan H et al (2009) Role of human-mediated dispersal in the spread of the pinewood nematode in China. PLoS One 4(2):e4646. doi:10.1371/journal.pone.0004646

Roques A (1983) Les insectes ravageurs des cônes et graines de conifères en France. INRA, Versailles

Roques A (2010) Taxonomy, time and geographic patterns. Chapter 2. BioRisk 4:11–26

Roques A, Auger-Rozenberg M-A (2006) Tentative analysis of the interceptions of non-indigenous organisms in Europe during 1995–2004. EPPO Bull 36:490–496

Roques A, Skrzypczynska M (2003) Seed-infesting chalcids of the genus *Megastigmus* Dalman, 1820 (Hymenoptera: Torymidae) native and introduced to the West Palearctic region: taxonomy, host specificity and distribution. J Nat Hist 37:127–238

Roques A, Markalas S, Roux G et al (1999) Impact of insects damaging seed cones of cypress, *Cupressus sempervirens*, in natural stands and plantations of southeastern Europe. Ann For Sci 56:167–177

Roques A, Sun JH, Auger-Rozenberg M-A et al (2003) Potential invasion of China by exotic pests associated with tree seeds. Biodivers Conserv 12:2195–2210

Roques A, Auger-Rozenberg M-A, Boivin S (2006) A lack of native congeners may limit colonization of introduced conifers by indigenous insects in Europe. Can J For Res 36:299–313

Roques A, Rabitsch W, Rasplus JY et al (2009) Alien terrestrial invertebrates of Europe. In: DAISIE (ed) Handbook of alien species in Europe. Springer, Dordrecht, pp 63–79

Roques A, Kenis M, Lees D et al (eds) (2010) Alien terrestrial arthropods of Europe. Biorisk 4:1–1026

Roy H, Roy D, Roques A (2011) Inventory of terrestrial alien arthropod predators and parasites established in Europe. BioControl 56:477–504

Rugman-Jones PF, Hoddle CD, Hoddle MS et al (2013) The lesser of two weevils: molecular-genetics of pest palm weevil populations confirm *Rhynchophorus vulneratus* (Panzer 1798) as a valid species distinct from *R. Ferrugineus* (Olivier 1790), and reveal the global extent of both. PLoS One 8(10):e78379. doi:10.1371/journal.pone.0078379

Sakai AK, Allendorf FW, Holt JS et al (2001) The population biology of invasive species. Annu Rev Ecol Syst 32:305–332

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17:170–176

Simberloff D, Martin J-L, Genovesi P et al (2013) Impacts of biological invasions: what's what and the way forward. Trends Ecol Evol 28:58–66. doi:10.1016/j.tree.2012.07.013

Smith R, Mooney K, Agrawal A (2008) Coexistence of three specialist aphids on common milkweed, *Asclepias syriaca*. Ecology 89:2187–2196

Suez M, Gidoin C, Lefèvre F et al (2013) Temporal population genetics of time travelling insects: a long term study in a seed-specialized wasp. PLoS One 8(8):e70818

Tamburini M, Maresi G, Salvadori C et al (2012) Adaptation of the invasive western conifer seed bug *Leptoglossus occidentalis* to Trentino, an alpine region (Italy). Bull Insect 65:161–170

Turgeon JJ, Roques A, De Groot P (1994) Insect Fauna of coniferous seed cones: diversity, host plant interactions and management. Ann Rev Entomol 39:172–212

Vaes-Petignat S, Nentwig W (2014) Environmental and economic impact of alien terrestrial arthropods in Europe. Neobiota 22:23–42. doi:10.3897/neobiota.22.6620

Vila M, Basnou C, Pysek P et al (2009) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Front Ecol Environ 8:135–144

Walther G-R, Roques A, Hulme PE et al (2009) Alien species in a warmer world: risks and opportunities. Trends Ecol Evol 24:686–693

Werren JH (1993) The evolution of inbreeding in a haplodiploid organism. In: Thornhill NW (ed) The natural history of inbreeding and outbreeding. University of Chicago Press, Chicago, pp 42–94

Yamanaka T, Liebhold AM (2009) Mate-location failure, the Allee effect, and the establishment of invading populations. Popul Ecol 51:337–340

Zhu GP, Rédei D, Kment P et al (2014) Effect of geographic background and equilibrium state on niche model transferability: predicting areas of invasion of *Leptoglossus occidentalis*. Biol Invasions 16:1069–1081

Chapter 10
Invasive Sap-Sucker Insects in the Mediterranean Basin

Zvi Mendel, Manuela Branco, and Andrea Battisti

Abstract The chapter provides information on 15 species of invasive sacking insects on forest trees in the Mediterranean basin. Four Psyllids and one Thaumastocorid bug develop on *Eucalyptus* spp. and are native to Australia, although all of them possibly arrived in the Mediterranean area via South America. Among the five *Cinara* spp. those which develop on cedar trees spread inside the Mediterranean area, two of the aphids are North American species and one is probably from China. The discussed scale insects, two *Matsucoccus* spp. and *Marchalina hellenica* extent their range inside the Mediterranean basin. Finally, we report on two tingid species (*Corythucha* spp.) both originate from North America. We review their biology, the injury they inflect, their spread, as well as their natural enemies and the required management.

10.1 Introduction

Sap-sucker insects (Hemiptera) constitute the major feeding guild of invasive insect species affecting forest trees in the Mediterranean basin. They include mostly scale insects, aphids and psyllids (Sternorrhyncha) as well as some phytophagous bugs (Heteroptera). Some of these invasive insect species affect exotic tree species in the Mediterranean, such as *Eucalyptus*, whereas others mainly affect native ones, such as some Mediterranean conifers. Many invasive species originated from other regions outside the Mediterranean basin, such as those affecting *Eucalyptus*, which are all native to Australia (Table 10.1). Still, some species are distinguished to be simultaneously native in some regions of the Mediterranean basin and invasive on

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Table 10.1 List of sap-suckers insects invasive in the Mediterranean basin

Species	Family	Host trees	Origin	Distribution in the invaded range
Ctenarytaina eucalypti	Psyllidae	*Eucalyptus*	Australia	Western Europe
Ctenarytaina spatulata	Psyllidae	*Eucalyptus*	Australia	Mediterranean
Glycaspis brimblecombei	Psyllidae	*Eucalyptus*	Australia	Mediterranean
Blastopsylla occidentalis	Psyllidae	*Eucalyptus*	Australia	Mediterranean
Thaumastocoris peregrinus	Thaumastocoridae	*Eucalyptus*	Australia	Mediterranean
Cinara cedri[a]	Aphididae	*Cedrus*	Turkey, Syria	Mediterranean
Cinara cupressi	Aphididae	*Cupressacea*	North America	Mediterranean
Cinara tujafilina	Aphididae	*Cupressacea*	Iran, Asia	Mediterranean
Cinara fresai	Aphididae	*Juniperus*	North America	Europe
Cinara laportei[a]	Aphididae	*Cedrus*	North Africa	Mediterranean
Marchalina hellenica[a]	Marchalinidae	*Pinus*	Caucasus,Turkey	Greece, Italy
Matsucoccus feytaudi[a]	Matsucoccidae	*Pinus*	Morocco, Iberian Peninsula, SW France	Southern Europe
Matsucoccus josephi[a]	Matsucoccidae	*Pinus*	Turkey, Syria, Lebanon, Crete	Middle East
Corythucha ciliata	Tingidae	*Platanus*	North America	Europe
Corythucha arcuata	Tingidae	*Quercus*	North America	Europe

[a] Native in some parts of the Mediterranean and invasive in other parts

other regions of the basin, such as two pine bast scales, *Matsucoccus* spp. The mode of life of sap-suckers, frequently concealed on foliage, wind dispersed, small sized, and rapid development of high population densities on young trees, facilitates their easy spread on nursery stock.

The piercing of the parenchyma or the phloem tissues and the uptake of plant sap, characteristic of their feeding habit, cause plant damage resulting in leaf bruising, leaf and twigs distortion, inhibition of new shoot formation, loss of apical dominance and eventually dieback when trees are intensively attacked. The honeydew produced by the phloem sucker species often lead to subsequent development of sooty mold fungi on the foliage, have further negative effects on tree physiology, interfering in the photosynthesis and transpiration. Additionally, the honeydew, the sooty mold fungi, and the dead bodies and waxy residues produced by some of the species have a substantial unaesthetic impact by soiling the ground covering surfaces and parked vehicles, which might be particular important in urban and recreation areas.

10.2 Eucalyptus Sap-Suckers

Sap-suckers is the major group of invasive insect species affecting *Eucalyptus* in the Mediterranean basin, most of the species become established during the last two decades. Currently they comprise four Psyllidae species, *Ctenarytaina eucaliptii* Maskell, *Ctenarytaina spatulata* Taylor, *Glycaspis brimblecombei* Moore and *Blastopsylla occidentalis* Taylor and one Thaumastocoridae, *Thaumastocoris peregrinus* Carpintero et Dellape. All these insect pests originated from Australia, but most of them, if not all, found their way to the Mediterranean basin through other regions; South Africa, South America and North America are the most plausible important regions, which served as bridgehead to the Mediterranean basin (Paine et al. 2011).

All these species have several overlapping generations per year. In the Mediterranean climate conditions their population growth starts with the development of news shoots and leaves in spring and develops through summer. Irrigation and nitrogen fertilization are favorable for the outbreak of the populations, especially in urban areas.

10.2.1 Psyllids

The blue gum psyllid *C. eucaliptii* was the first eucalyptus feeding invasive species established in the Mediterranean basin. The psyllid was primarily observed in 1971 in Portugal (Azevedo and Figo 1979). The severity of damage recorded by that time on *E. globulus* plantations was so high that it caused alarm among forest owners (Azevedo and Figo 1979). Still, since this psyllid only affects the juvenile's growth, before leaf differentiation takes place, only the young plantations were at risk. A specialized parasitoid *Psyllaephagus pilosus* Noyes (Hymenoptera: Encyrtidae) was introduced in Southeastern France in 1997 to control *C. eucalypti* (Malausa and Girardet 1997). Later, the parasitoid was introduced in Ireland from individuals collected in France (Chauzat et al. 2002). In both locations, the success was very high, the parasitoid quickly established and in a few months the parasitism rates reached almost 100 % in the released areas. Currently, *C. eucalypti* may episodically pose slight concern in nurseries but not in forest stands (Ferreira and Ferreira 1991).

Three decades later a congener species *C. spatulata* become also established in the Mediterranean basin (Fig. 10.1). The species was first recorded in 2002 in central Portugal affecting several *E. globulus* plantations. In 2003 the psyllid was observed all over the country and in Spain (Valente et al. 2004). Like *C. eucaliptii*, *C. spatulata* was mostly found on *E. globulus*, but large populations were also found on other tree species, namely *E. nitens* and *E. dalrympleana*. *C. spatulata* feeds on adult shoots and is more damaging to Eucalyptus trees than the congener *C. eucaliptii*. Before its introduction in the Mediterranean basin, *C. spatulata* was first observed in South America in 1994 (Burckhardt et al. 1999; Santana et al. 1999),

Fig. 10.1 *Ctenarytaina spatulata*, nymph (*left*) and adult (*right*) (Photos: C. Valente)

which suggests that this region might have acted as bridgehead for its introduction in Europe. On the contrary, *C. eucaliptii* was observed in South America only in 1999 (Burckhardt et al. 1999), 20 years before its first observation in Europe, suggesting a reverse flux of invasions. A new species of the same genus *C. peregrina* was described from UK, where it was first found in 2006 in *Eucalyptus parvula*. Until present, this species did not expand to the Mediterranean Basin.

More recently, two other psyllids were found in the Mediterranean basin, the red gum lerp psyllid *Glycaspis brimblecombei* and the eucalyptus psyllid *Blastopsylla occidentalis*. Both species were found in the Mediterranean basin about 10 years after its first detection in South and North America in the late 1990s (Gill 1998; Brennan et al. 1999; Halbert et al. 2001). The red gum lerp psyllid *G. brimblecombei* was observed in the Iberian Peninsula in 2007 (Borrajo et al. 2009; Valente and Hodkinson 2009). In a few years multiple first records were registered, and this insect species became an invasive pest all over the Mediterranean basin, first in Italy in 2009 (Laudonia and Garonna 2010) and in the following years in Tunisia, Morocco, Turkey and Israel (Maatouf and Lumaret 2012; Dhari et al. 2014; Spodek et al. 2015). *G. brimblecombei* nymphs are characteristically concealed by shield-like conical white waxy coverings, lerps, which the nymphs secrete to protect themselves from natural enemies (Fig. 10.2). This particularity allows its easy distinction from the other invasive psyllid species feeding on *Eucalyptus*. In other psyllid species, such as *B. occidentalis*, the nymphs may be protected by white flocculent wax but do not form lerps. *Blastopsylla occidentalis* was observed in the eastern Mediterranean, in 2006 in Italy and 1 year later in Turkey (Aytar et al. 2011). Its occurrence in the western Mediterranean is dated from 2009 (Otero et al. 2011). Due to the low temporal distance and the high geographical distance among these regions, multiple introductions in the Mediterranean basin are plausible.

Both *G. brimblecombei* and *B. occidentalis* were found mainly associated with *E. camaldulensis*, although infestations may also be observed in other *Eucalyptus* species (Laudonia 2006; Valente and Hodkinson 2009; Otero et al. 2011). Since

Fig. 10.2 *Glycaspis brimblecombei*, nymphs covered by the lerp and an adult (*left*), uncovered nymph (*right*) (Photos A. Garcia)

E. globulus is a less susceptible tree species, the forest owners and the pulp industry in Southern Europe are not particularly alarmed. Still, the two psyllids may cause concern in urban parks and side roads, especially due to the honeydew production and sooty mold fungi. In North Africa and Middle East countries, *E. camaldulensis* is one of the most used Eucalyptus tree species for soil conservation, in recreation areas for shade, as windbreaks, as source of pollen and nectar for honeybees and for fuelwood. In these regions the two psyllids are considered a menace as they threat these services provided by these trees.

The parasitoid *Psyllaephagus bliteus* Riek (Hymenoptera: Encyrtidae) was found established in the Mediterranean basin more or less at the same time as its host *G. brimblecombei*, which suggest that the host and the parasitoid might be introduced together. No country reported its deliberate introduction, but the parasitoid occurred all over the Mediterranean as documented in Spain (Otero et al. 2011), Italy (Caleca et al. 2011), Greece (Bella and Rapisarda 2013), Algeria and Morocco (Reguia and Peris-Felipo 2013). No parasitoid species was so far introduced for the control of *B. occidentalis.*

Many non-specific predators native to the invaded regions may feed on the eucalypts psyllids, especially those that feed on other sap-sucker insects, including green lacewings (Chrysopidae: Neuroptera), ladybeetles (Coccinellidae: Coleoptera), hoverflies (Syrphidae: Diptera), pirate bugs (Anthocoridae: Hemiptera) and spiders (Azevedo and Figo 1979; Valente and Hodkinson 2009; Laudonia and Garonna 2010; Otero et al. 2011). European native parasitoids (Ichneumonidae: Hymenoptera) were also found parasitizing *C. eucalypti* and *C. spatulata* (Azevedo and Figo 1979). These generalist natural enemies are usually considered ineffective in reducing psyllid populations to satisfactory levels (Hodkinson 1999). Nevertheless, the activity of these predators may contribute to reduce the psyllids abundance. Apart from biological control, no other measures have been extensively used for the control of these psyllids in the Mediterranean basin.

10.2.2 Thaumastocoris peregrinus

The Eucalyptus bronze bug *Thaumastocoris peregrinus* Carpintero et Dellape (Hemiptera Thaumastocoridae), is a small bug, 2–3 mm in length, which feeds on the Eucalyptus leaves. Thaumastocoridae is a small family occurring mainly in the southern Hemisphere, and believed to be closely related to the widespread family Anthocoridae (Drake and Slamr 1957). Both nymphs and adults are found gregariously on the *Eucalyptus* leaves and spread rapidly when disturbed. Aggregation and possible alarm pheromones determine its peculiar behavior (Martins et al. 2012; Garcia et al. 2013). Egg masses are laid in small dark clusters on the surface of leaves (Fig. 10.3).

The Eucalyptus bronze bug was first reported in South Africa in 2003 (Jacobs and Neser 2005) and 2 years later in Argentina (Nadel et al. 2010). DNA bar-coding distribution of the haplotypes indicates that several distinct introductions of this insect occurred into several regions of the southern Hemisphere, probably originated from Sydney, where populations frequently reach outbreak levels in urban areas (Nadel et al. 2010).

In Europe the Eucalyptus bronze bug was first reported on the eastern Mediterranean basin, in Italy in 2011 (Laudonia and Sasso 2012). Only 1 year later it was found on the most extreme of the western Mediterranean (Garcia et al. 2013). Again, the proximity of dates in two opposite sides of the Mediterranean basin suggests that multiple introductions might have occurred. Yet, in this case the introductions were most probably from other regions in the Southern Hemisphere where the species was already present, and which served as bridgehead and not directly from Australia. At the same time in the western Mediterranean, an alien predator *Hemerobius bolivari* Banks (Neuroptera Hemerobiidae) was also observed preying on *T. peregrinus* nymphs. This predator species is native to South America and was then first recorded in Europe (Garcia et al. 2013; Monserrat et al. 2013). Therefore,

Fig. 10.3 *Thaumastocoris peregrinus* adults and small dark clusters of egg masses on *Eucalyptus camaldulensis* leaves (Photo A. Garcia)

the authors hypothesized that the predator may have reached Europe together with prey species, either *T. peregrinus* or previously introduced sap-suckers.

Surveys confirmed a long list of host species of the bronze bug. Out of 30 Eucalyptus species present in a Eucalyptus arboretum in Portugal, 19 were infested by *T. peregrinus*, being *E. camaldulensis*, *E. pauciflora* and *E. viminalis* the most infested species. Although, *T. peregrinus* may occasionally infest *E. globulus*, this species was found to be less preferred. No specific biological agent was so far recorded in the Mediterranean and no control strategies were developed.

In Australia where Eucalyptus bronze bug represent a problem in urban trees, specially *E. nicholii* and *E. scoparia*, chemical control based on tree microinjection with imidacloprid proved to be efficacious for the control of *T. peregrinus* as the bug populations declined significantly on treated trees for more than a year (Noack et al. 2009).

10.3 Pine Scale Insects

A few invasive species of aphids and scale insects affect conifers, *Abies*, *Cedrus*, *Cupressus* and *Pinus* in the Mediterranean basin. Some of these species are also native to the Mediterranean or neighbor areas (Table 10.1). Among these species, the most destructive ones have been the pine bast scales (*Matsucoccus* spp.) and the Greek pine scale *Marchalina hellenica*

10.3.1 Matsucoccus *spp. (Hemiptera: Matsucoccidae)*

Pine bast scales (Hemiptera: Matsucoccidae) are among the oldest known organisms closely associated with pines (Koteja 1990) and currently include the oldest known scale insect fossils (Foldi 2004). The stenophagous character of bast scales and their prolonged co-evolution with the genus *Pinus*, can explain not only the present distribution of *Matsucoccus* spp. but also the past geographic distribution of pine (Mendel 1998). Cockerell named the genus in 1909 from material originating from both Japan; the etymology is from the Japanese ‘Matsu’ meaning pine, and Greek ‘coccus’ for berry or a small ball. *Matsucoccus* spp. feed exclusively on pine; each species develops on one or a few host species of a given section or subsection of the genus *Pinus*. The genus is exclusive to the Northern Hemisphere including both Palearctic and Nearctic regions. Among the 33 modern *Matsucoccus* species, 20 have survived in North America, and only five occur in the west Palearctic region (Booth and Gullan 2006). Three European native *Matsucoccus* species occur in the Mediterranean basin, *M. pini* (Green), *M. feytaudi* Ducasse and *M. josephi* Bodenheimer and Harpaz Foldi (2004). According to Ray’s (1982) classification of the North American *Matsucoccus* spp., *M. feytaudi* and *M. pini* belong to Apachecae section whereas *M. josephi* may assign to Alabamae section. The three species

Fig. 10.4 Lures with the *Matsucoccus feytaudi* female sex pheromone with male attracted (*left*) and larvae of *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae) (*right*) (Photos M. Branco)

differ in their distinct host range and by number of annual generations. *M. pini* is a bivoltine species which has a broad geographic distribution in Europe; it develops on *P. nigra, P. sylvestris P. pumilio, P. uncinata* and *P. mugo*. In the Mediterranean basin at high elevation, its area of distribution overlaps those of the other two *Matsucoccus* species, which are endemic to restricted regions of the Mediterranean. *Matsucoccus feytaudi* naturally occurs in the Iberian Peninsula, southwestern France and North Africa and feeds exclusively on the maritime pine, *Pinus pinaster. M. josephi* is indigenous in the north rim of the East Mediterranean and develops on several closely species of Mediterranean pines, including *Pinus brutia*, *P. halepensis,* but may be found also on *P. canariensis* and *P. pinea*.

Speciation and evolutionary processes of the two Mediterranean species are considered to be linked to the glacial periods during which the ancestors of these *Matsucoccus* species become isolated together with its host pines in the specific areas of the Mediterranean basin. During the twentieth century the two species spread to neighbor regions of the Mediterranean, where they cause considerable devastation to pine forests. *M. feytaudi* spread to eastern France, Italy and Corsica, *M. josephi* spread southward to Israel and Jordan. Therefore, both species are considered invasive within the Mediterranean basin. All three *Matsucoccus* species are biparental, males are attracted to the female sex pheromone (Fig. 10.4). All three are rather rare in their native habitat or occur in very low population densities. Yet, severe outbreaks, resulted in the destruction of large forest areas due to tree mortality inflicted by both *M. feytaudi* and *M. josephi* in its introduced range. Susceptible tree genotypes of their pine hosts or genetically closely related host species has been suggested as one of the main reasons of the aggressive attacks on their introduced range, justified by lack of a co-evolutionary history. *Matsucoccus* spp. are not attacked by hymenopteran or dipteran parasitoids, but several predators are known from its native range. There is probably a linkage among the triad *Pinus*, *Matsucoccus* and the predatory bugs (Anthocoridae) of the genus *Elatophilus* (Mendel et al. 1991).

10.3.1.1 *Matsucoccus feytaudi*

The maritime pine bast scale *M. feytaudi* was first recorded from France in 1938, by that time identified as *M. matsumurae* Kuwana, from specimens collected from *P. pinaster* trees in the region of Bordeaux. Later, in 1942 the species was described by Ducasse as *M. feytaudi*. In the early 1960s, extensive damage to *P. pinaster* plantations was reported in the Massif of Maures, southeast of France (Riom and Gerbinot 1977). Initially the damage was assigned to the attack of bark beetles, such as *Ips sexdentatus*, *Tomicus destruens*, *Orthotomicus erosus* and *Pissodes castaneus*, which attacked the dying trees, later it was found that the primary cause for the tree decline was *M. feytaudi*. The symptoms of attack comprise yellowing of the crown, exudation of resin and tree death, which can be confused with injury inflicted by bark beetles. About 120,000 ha of maritime pine forest were seriously affected and thousands of pine trees died in a few years (Schvester 1967). During this period *M. feytaudi* was also found to occur endemically in Spain, Portugal and Morocco, which corresponds to its native range, but causing no damage. In the late 1970s the pine bast scale expanded its invasive range from the eastern of France till the north of Italy (Covassi and Binazzi 1992). In 1994 the insect was found in Corsica for the first time causing tree mortality on large area (Jactel et al. 1996). Currently *M. feytaudi* is still expanding southwards in Italy and in Corsica where it spreads at a rate of 2 km/year (Jactel et al. 2012). Molecular markers showed that the population in Corsica originated from individuals coming both from the populations in Italy and southeastern France (Kerdelhué et al. 2014).

The maritime pine bast scale is univoltine. The adults emerge in February–March when they mate and lay eggs. The first instar nymphs (L1) appear about 1 month later. This is the dispersal stage, L1 are crawlers which are easily dispersed by the wind from one tree to another. Once they reach a suitable host, they become sedentary and begin feeding on the parenchyma layer. Second instar nymphs (L2) are dark, about 1.3 mm long, and develop through August until December–January living fixed on the tree trunk inside bark crevices (Riom and Gerbinot 1977). By December–January the males pupate within waxy cocoons hidden in the bark. The females emerge from L2 after molting and are mobile. The males are short lived and attracted by the sex pheromone emitted by the females. Each female lays a single egg mass, containing usually more than 300 eggs, inside bark crevices and protected by silky wax. The dead body of the female is usually attached to the egg mass.

In its native regions *M. feytaudi* populations can be found in all *P. pinaster* stands at low density and the impact on the host tree is negligible (Tavares et al. 2014). The insect only becomes a serious pest on the invaded range. Genetic differences among *P. pinaster* populations may explain this outcome. The populations of the maritime pine and *M. feytaudi* were isolated together in small areas in the Iberian Peninsula and North Africa during the last glaciations, from where both *P. pinaster* and *M. feytaudi* spread to north (Burban et al. 1999). As both host tree and insect pest share the same geographical range of origin, probably also where the speciation of *M. feytaudi* occurred, a co-evolutionary history leading to highly resistant genotypes.

In the invaded areas, a lack of tree defense mechanism is probably the reason for the high susceptibility of the trees (Schvester and Ughetto 1986).

Matsucoccus feytaudi is accompanied by several species of natural enemies, all of them are predators. Interestingly, many of these predators, both adult and larvae, are attracted to the sex pheromone of the scale. This is the case of Anthocoridae belonging to the genus *Elatophilus*, namely *E. nigricornis* (Zetterstedt) and *E. crassicornis* Reuter, the Hemerobiidae, *Hemerobius stigma* Stephens (Fig. 10.7), and three Coleopteran species, *Aplocnemus raymondi* Deville, (Dasytidae), *Malachiomimus pectinatus* (Kiesenwetter) (Malachiidae), and *Iberorhyzobius rondensis* (Eizaguirre) (Coccinellidae) (Fig. 10.4) (Mendel et al. 2004; Branco et al. 2006a, 2011; Rodrigo et al. 2013). Other generalist predators such as of ladybirds of the genus *Scymnus* and *Rhyzobius chrysomeloides* are also found preying on the egg masses of *M. feytaudi* (Toccafondi et al. 1991), although these do not display a kairomonal attraction to the sex pheromone of the prey. In the invaded range, *E. nigricornis*, *H. stigma* (Fabre et al. 2000) and *Aplocnemus brevis* Rosenhauer are also found preying on *M. feytaudi*. Possibly by shifting from *M. pini* to the new prey as they also respond to sex pheromone of *M. matsumurae* (Branco et al. 2006b, c; Jactel et al. 2006). Nevertheless, these predators do not seem to effectively reduce *M. feytaudi* population densities to acceptable levels in its invaded range (Schvester and Fabre 2001).

Direct insecticide applications did not show to be efficient or economically justified for the control of *M. feytaudi*, in part due to the concealed living habitats of its life stages. Silvicultural methods, eliminating susceptible and symptomatic trees, have been the most used practices. Since tree vigor and bark thickness were found positively correlate with tree resistance, selective thinning by promoting tree vigor was also proposed as an adequate strategy to reduce the damage caused by the pine bast scale (Gaulier et al. 2001). Due to the differences in susceptibility to *M. feytaudi* for different *P. pinaster* provenances, genetic improvement was further considered a possibility to explore (Schvester and Ughetto 1986). Following the identification and synthesis of the *M. feytaudi* sex pheromone (Jactel et al. 1994), studies were conducted to optimize pheromone baited traps for monitoring *M. feytaudi* populations and its principal predators (Branco et al. 2004).

10.3.1.2 *Matsucoccus josephi*

The Israeli pine bast scale *Matsucoccus josephi* Bodenheimer et Harpaz was first recorded in newly afforested area in Ramot Menashe in North Samaria, in the early 1930s (Bodenheimer and Neumark 1955). It was named ‘*josephi*’ after Joseph Weitz, the first head of the Forests Department of the Land and Development Authority (KKL) in Israel. The scale was probably spread southern with prevailing winds from old *Pinus halepensis* stands on Mt Carmel to Ramot Menashe. Until the 1980s *M. josephi* was considered to be an endemic insect of Aleppo pine, and in Israel was known only on Aleppo pine. In the early 1990s the scale was found in *P. brutia* forests in Cyprus and Turkey (Mendel 1992; Mendel and Schiller 1993).

The patterns of DNA fragments displayed a positive association between the Israeli and Cypriot populations and a negative association between the Israeli and the Turkish populations. Hence, *M. josephi* probably arrived in Israel on fresh timber of *P. brutia* that was brought from Cyprus by the British forces during the First World War (Mendel et al. 1994c).

Speciation of *M. josephi* could have occurred in the south of the areas between the Black and the Caspian Seas from a progenitor that came into contact with *P. brutia* ssp. *brutia,* brutia pine after speciation of brutia pine and *P. halepensis* (Mendel 1998). The primary range of *M. josephi* encompasses the entire distribution area of brutia pine in western Turkey, including the Turkish European areas in Thrace and the islands of Cyprus and Crete. The scale is probably also present on the islands off the Anatolian coast. *M. josephi* also occurs on *P. halepensis* in small enclaves near Adana and Marmaris in Turkey (which were planted over there for harvesting the resin for production of Greek retsina win), and on brutia pine in southern Lebanon. Its natural range most probably also includes the brutia pine forests along the coastal mountain range of Syria and northern Lebanon. *M. josephi* may be found in natural relic stands of brutia pine in Kurdistan (northern Iraq) and eastern Turkey. It is also infests the *P. halepensis* forest in Jordan. About 80 % of the area covered with *Pinus halepensis* in Israel is affected to some degree by the scale (Mendel et al. 1994a) (Fig. 10.5).

The adult males emerge from their pupation sites in the forest litter are attracted to the sex pheromone emitted by the females (Mendel et al. 1990b; Dunkelblum

Fig. 10.5 Chronic injury inflicted *by Matsucoccus josephi* on *Pinus halepensis* in Israel (Photo Z. Mendel)

Fig. 10.6 Egg masses (*right*) and first and second instar larvae (*left*) of *Matsucoccus josephi* (Photos A. protasov)

et al. 1993, 2000). They live for about 8 h, during which time each may fertilize several females. The female may be successfully inseminated up to 10 days after emergence. Soon after mating the females seek an oviposition spot, usually under bark scales or in crevices, but when there are high population densities egg mass may also be found on main branches and twigs (Mendel et al. 1998). Adult females weigh between 40 and 340 mg, and fertility is closely correlated with body weight. Thus, an egg mass may consists of 44–350 eggs (Fig. 10.6). Ovipositing females tend to congregate, and thus produce large combined egg masses. Egg laying occurs 24 h after mating (Mendel et al. 1990a). Soon after hatching the crawlers start to disperse along the host plant. They tend to leave the egg mass site and on adult trees they go up the trunk seeking for loose bark scales under which live bark can be reached (Bodenheimer and Neumark 1955). In case of 2–3-year-old saplings they prefer to descend and to colonize the lower part of the plant. However, they may settle on any part of the tree, including the bases of the brachyblasts, branches, twigs and flower stalks, and exposed roots. On growth that is covered with thick rhytidome, their settling is limited to lenticell openings. *M. josephi* displays low temperature thresholds of the feeding stages (larvae) and the non-feeding stages (eggs and pupae) are 2.4 °C and 7.4 °C, respectively (Mendel et al. 1988).

M. josephi is well adapted to the Mediterranean climate and thus occurs at all altitudes of its principal host, brutia pine; it has been found from sea level up to 1200 m. The scale is invasive in the natural areas of *P. halepensis* in the Near East. The pest does not favor areas with a long dry summer and a short period of width growth of the plant host. Thus, in the desert areas in Israel the population of the scale is very low, with the exception of rare episodes of rainy years, following which the population increases steeply (Mendel 1987, 1992, 1998; Mendel and Schiller 1993). Unlike other studied *Matsucoccus* spp. *M. josephi* displays multivotinouos characteristics (Bodenheimer and Neumark 1955; Mendel et al. 1990b). In Israel, on Aleppo pine trees, it breeds through 5–7 generations annually, with the peaks in the spring and early summer, and the autumn (Mendel et al. 1997a). The population density coincides closely with the physiological activity of the host tree, displaying intensive width growth from February till May and in September (Mendel et al. 1997b). The pest displays a typical clumped distribution (Nestel et al. 1995).

M. josephi develops and reproduces on all five taxa of subsection Halepenses in the Section Pinea: (1) *Pinus brutia* ssp. *brutia*, is highly resistant to infestation; (2) *Pinus brutia* ssp. *stankewiczii* (Sukaczew) Nahal; (3) *Pinus brutia* ssp. *pithyusa* (Stevenson) Nahal; (4) *Pinus brutia* ssp. *eldarica*; and (5) *P. halepensis*. It may develop on *Pinus pinea* L. (section Pinea, subsection Pinea) and on *P. canariensis* Smith and *Pinus roxburghii*; these belong to a sister pine section, Sula (subsection Canarienses) (Liphschitz and Mendel 1989b). It is suggested that the host specificity to *M. josephi* relates to the suitability of the pest's saliva composition (Liphschitz and Mendel 1987, 1989a). Infestation by closely related species is prevented, since the growing larvae trigger the development of wound periderm which eventually leads to the death of the pest (Liphschitz and Mendel 1989a). In pine species that are genetically remote from the suitable host, the tree's hypersensitive reaction prevents any development of the scale's crawlers (Liphschitz and Mendel 1989b). Provenances of *P. halepensis* from Greece and the Near East are relatively resistant, as compared with those of the West Mediterranean which are highly susceptible. The Caucasian subspecies of brutia pine, *Pinus brutia pithyusa*, *P. brutia stankewiczii*, and *P. brutia eldarica* are highly susceptible. Even brutia pine or less susceptible *P. halepensis* provenances may be severely affected under irrigation and fertilization. Hybrids of brutia pine x *P. halepensis* and brutia pine x *Pinus nigra* (the latter species is immune to *M. josephi*) display similar susceptibility to that of *P. halepensis* (Madmony et al. 2003; Mendel 1992, 1998).

The typical injury consists of accelerated drying of infested growth. The injuries include drying of buds, shortened needles, twig flagging, twisting of twigs and young branches, yellowish dry or sparse crowns. Drying of young trees within a few months of infestation is common on natural regeneration sites and on 2–5-years-old plantations close to adult stands (Bodenheimer and Neumark 1955; Mendel et al. 1994a). High seedling mortality rates caused by the scale occur from the winter (February) till early summer (early June) (Mendel et al. 1997b). Seedling mortality deceases steeply from the sixth year onward. In older stands, 18–40 years after planting or regeneration, as soon as the tree canopy is closed and typical cork scale peeling of the stem appears the *M. josephi* population increases. The damage is characterized by progressive drying of branches from the lowest ones upwards, a process which may last for several decades. Heavily infested sections of the trunk become reddish, with typical premature cork scale peeling, which leads to excretion of numerous resin drops, cracked bark and separation of numerous bark flakes.

Fig. 10.7 (*Left*), *Elatophilus hebraicus* feeding on *Matsucoccus josephi* female (Israel), (*right*) *Hemerobius stigma* (Portugal) (Photos Z. Mendel)

When it switches from the latent to the epidemic state, *M. josephi* covers much of the branch bases and 1–2-years-old shoots, resulting in the dying of the tree crown.

The spread of the scale into Aleppo stands in the Near East has gradually led to heavy losses of those stands (Mendel et al. 1994a), and introduction of *M. josephi* into the natural Aleppo pine areas around the western Mediterranean poses a serious risk to large forest areas in north Africa and along the Mediterranean coast of Italy and France (Mendel 1998).

Elatophilus hebraicus Péricart, a specific predator, is the most common enemy of *M. josephi* (Mendel et al. 1995) (Fig. 10.7). Similar to other principal predators of pine bast scale *E. hebraicus* is highly attracted to the sex pheromone of its prey (Mendel et al. 2004). Apart from *E. hebraicus* all predators associated with *M. josephi* are polyphagous and occur in several different sylvan and agricultural ecosystems. The main associates (in Israel) are: *Dufouriellus ater* (Heteroptera: Anthocoridae) that preys on other natural enemies of the scale. *Cryptolestes halevyae* Thomas (Coleoptera: Laemophleoidae), *Ulrike Syriaca* (Steinmann) (Rhaphidioptera: Raphidiidae), *Anystis baccarum* L. (Acari; Anystidae) and *Hysterochefiler gracilimanus* Beier (Pseudoscorpiones; Cheliferidae).

The inspection of stands for typical chronic injury symptoms is based on the observation of the extent of the tree canopy drying up, the distinct twisting of twigs, flagging and dry needles (Bodenheimer and Neumark 1955; Liphschitz and Mendel 1989a). *Matsucoccus josephi* is confirmed by examining occurrences of larvae or remains of larvae and empty ovisacs, at the base of the brachyblasts, when removing loose bark flakes of partial scaly-bark stem sections. The population density of *M. josephi* can be estimated by counting the number of ovisacs, on jute belt wrapped around each tree, at breast height (Mendel and Rosenberg 1988). Sticky traps baited with female sex pheromone are also used to determine the presence of the scale (Dunkelblum et al. 2000; Mendel et al. 1997a). The traps are highly selective and strongly attractive to males of *M. josephi* as well as to the adults, both male and female, of its specific predator, *E. hebraicus* (Mendel et al. 1997a, 2004).

Prevention of injury to newly established stands or to young natural regeneration by *M. josephi* is achieved by pruning the lower branches, and extensive thinning of dense regeneration. Planted stands of Aleppo pine more than 10 years old should be thinned, in at least two thinning cycles, to open the canopy and avoid tree stress. Trees with big crowns are less susceptible to the scale epidemic.

Matsucoccus josephi spreads between pine stands by crawlers carried by the prevailing wind, and it may be transferred between regions on fresh timber that is harvested in the areas of *P. brutia* and *P. halepensis* in the eastern Mediterranean. The pest may be moved on young saplings older than 6 months. No precautionary measures are taken to prevent the spread of *M. josephi* from infested to non-infested areas.

10.3.2 Marchalina hellenica

Marchalina hellenica (Gennadius) (Hemiptera: Coccoidea, Marchalinidae) is a scale insect feeding on Pinaceae. The insect species is distributed in the eastern part of the Mediterranean Basin, in the Turkish and Greek coastal zones of the Aegean and Black seas up to 1200 m (Petrakis et al. 2011). The family Marchalinidae is one of 10 families previously grouped as “Margarodidae” and contains a single genus *Marchalina* with two described species, *M. azteca* Ferris from Mexico and *M. hellenica* (Kozár et al. 2013). A similar species distributed in Caucasus was described by Hadzibeyli in 1969 as *M. caucasica* and later synonymised with *M. hellenica* (Hodghson and Gounari 2006). Still, differences in morphological traits, life history, host species and geographic distribution, all support that *M. caucasica* and *M. hellenica* are probably two separate species (Hodghson and Gounari 2006).

It is believed that *M. hellenica* was introduced in northern Greece from Turkey by late Romans and Byzantines; there are no records of its presence in Greece at prehistoric and classical times (Petrakis et al. 2011). The recent expansion of the pine scale was due to the activity of beekeepers which exploit the abundant honeydew excreted by the scale insect to produce the so much appreciated “Greek pine honey”. With the intent of increasing honeydew production, beekeepers deliberately introduced *M. hellenica* in sites where the insect did not existed before, in particular at high elevation in mountain areas (Bacandritsos 2004). It was introduced in the 1960s in the Italian island of Ischia, where it does still occur and threaten ornamental pine trees (EPPO 2007).

M. hellenica has one generation a year presenting three immature instars for females, and four for the males, before reaching the adult stage. Only the second and third instars feed on the sap phloem in the tree trunk and branches, 1st instar are crawlers. Overwintering occurs at the third instar. All stages are yellow colored. The adult females start to occur by the end of March and may be easily observed on the branches and trunk of pine trees due to its large size and bright color until the end of April, beginning of May. Female are large and oval, about 8–13 mm length and 4–5.5 mm width. Males are apterous with elongated body and dark-yellow legs. Yet, males are rare. *M. hellenica* reproduces mostly by parthenogenesis, a trait which further distinguishes this species from *M. caucasica* (Hodgson and Gounari 2006). Females lay a woolly ovisac containing 130–400 eggs on the bark of the host tree (Gounari 2006).

In its distribution range, *M. hellenica* feeds on a few pine species, namely *P. halepensis*, *P. brutia*, *P. pinea, P. nigra* and *P. silvestris* and sporadically on *Abies* sp. The insect usually attacks mature and old pines, with about 35 years or older (Yesil et al. 2005).

In Turkey many native predators were found preying on immature and adult stages of *M. hellenica* (Ülgentürk et al. 2013). The most important and most widespread predator was *Neoleucopis kartliana* (Diptera: Chamaemyiidae). Other predators include three species of mites (Acarina), ladybird species (Coleoptera: Coccinellidae), *Myrrha octodecimguttata*, *Rodolia cardinalis* and *Scymnus subvillosus*, generalist Neuropteran predators, both from Chrysopidae and Hemerobiidae families, and two Anthocoridae, *Cardiastethus nazarenus* and *Elatophilus pachycnemis*. Whereas *N. kartliana* appeared to be a monophagous predator of *M. hellenica*, the other predators are mostly generalists feeding on other scale insects occurring on pines. In other regions, many predators were also found associated with *M. hellenica*, including Chameamyiidae (Diptera), Coccinellidae (Coleoptera), Raphidiidae (Raphidioptera) and Chrysopidae (Neuroptera) Ben-Dov et al. (2013). Some of these predators also feed on honeydew produced by the scale insects. The honeydew also attracts ants which may play an important role in protecting the scale insect from its natural enemies (Petrakis et al. 2011).

M. hellenica is an economically important scale insect due to the honeydew produced by the insect which is one of the most important resources for Greek and Turkish apiculture. In fact, pine honey represents 60–65 % of total honey production in Greece (Thrasyvoulou and Manikis 1996) and approximately 50 % of Turkish honey production (Miguel et al. 2014). The density of beehives may attain more than 225 hives/km^2 in the sites most populated with the pine scale (Gounari 2006). To keep the honey production at high levels, beekeepers intentionally introduce the scale insect into new areas and increase infestations with new inoculations.

The high densities of *M. hellenica* populations observed in the affected areas are severe, causing tree growth loss, crown transparency and tree decline (Yesil et al. 2005). The phenomenon is further considered to negatively affect the biodiversity in the affected areas (Petrakis et al. 2011). The beekeepers are blamed to “kill the goose that laid the golden egg” as reductions and fluctuations of the quantity of honeydew produced has further caused some concern among beekeepers (Petrakis et al. 2011).

Silvicultural practices such as thinning, removing of decaying trees, and the use of genetic materials resistant to the scale insect in afforestation and plantation programs, have been proposed as major measures to control this pine scale on the affected areas (Gallis 2007).

10.4 Conifer Aphids

The conifer aphids of the genus *Cinara* Curtis are soft-bodied, generally gregarious insects that often found in large groups. Most members of the genus are known from North and Central America (Blackman and Eastop 1994); in the West Palaearctic region the genus is represented by 47 species (Nafria et al. 1984). These aphids do not perform host alternate, but remain on their chosen host species throughout the year. They may feed on the roots, branches, or foliage. In the Mediterranean, these species mainly occur on members of the genera *Pinus* and *Cedrus* (Pinaceae) and *Juniperus* and *Cupressus* (Cupressaceae).

Most species feed on a single or a few closely related congeners. Species of *Cinara* have specific feeding sites on their host plants (Bradley 1959); those in the Mediterranean usually feed on young shoots and 2–3 year old branches. The life cycles of *Cinara* spp. in their holocyclic sequence include males and egg laying females, which after pairing, give rise to overwintering eggs. Where favorable climatic and host plant conditions persist, the sexual reproduction may be omitted altogether and anholocyclic colonies may persist for many generations (Binazzi 1978; Carter and Maslen 1982). Many *Cinara* spp. are attended by ants and the host plants benefit from this association. Honeydew supply usually increases the frequency of ant interactions with the aphids (Mooney and Tillberg 2005). Although tending ants not always benefit their hemipteran partners (e.g. Styrsky and Eubanks 2007), the host trees usually gain from this interaction as the ants decrease the soiling of the canopy with honeydew and sooty mold and encourage arthropod predation by the ants (Bach 1991; Rosengren and Sundström 1991). *Cinara* spp. display limited dispersal ability, compared to other aphid species (Voegtlin 1988; Blackman and Eastop 1994). However, few species have become invasive pests and spread on large areas. Among these, few species have become a major pests while other did not reach any significant economic status although there were not accompanied by their principal natural enemies.

Several *Cinara* spp. are considered invasive pests in the Mediterranean region and are presented below. Two of these species are invasive within the region: *Cinara* (*Cedrobium*) *laportei* spread from *Cedrus atlantica* forests in the Atlas Mountains in North Africa (Fabre and Rabasse 1987a) and *Cinara* (*Cinarela*) *cedri* which is probably indigenous to *Cedrus libani* forests in the North East Mediterranean (e.g. Michelena et al. 2005). Three other species arrived from other regions. *Cinara* (*Cupressobium*) *tujafilina* is common in the Mediterranean region on oriental thuja (e.g. Halperin et al. 1988) probably spread from the Far East. Two other species are from North America, *Cinara* (*Cupressobium*) *fresai*, which was reported in Israel (Mendel and Zehavi 1987), and *Cinara cupressi sensu stricto* (Watson et al. 1999) which is distributed over the distribution range of *Cupressus* spp. in the Mediterranean basin. It is interesting to note that none of the invasive *Cinara* spp. in the Mediterranean inflicts any serious damage on native trees, with the only exception of *C. cupressi* which is known to cause rapid dieback of tree canopy in spring (Roques and Battisti 1999).

Fig. 10.8 *Cinara laportei* on *Cedrus atlantica*, aphid colony (*left*) and dying branches with typical damage (Photos Z. Mendel)

10.4.1 Cinara *(*Cedrobium*)* laportei *Remaudière*

Cinara laportei is a rather small aphid, the apterous adult length is 1.7–2.0 mm rather flat, pale brown and grey-greenish with a narrow pale spinal stripe from head to anterior abdomen and shiny, legs and antennae are pale (Fig. 10.8). The alates are a bit small 1.6–1.9 mm long and darker. The colonies are usually small and located at the base of the needles or on 1-year-old twigs. These colonies seemed to develop in low dry areas in early spring (February) and reach a high number of individuals during the succeeding months, until June–July. In higher elevations of its range, it occurs in high number in mid-summer. In Israel, the population almost disappeared in the second half of the summer and became conspicuous again in early February. Detection of small populations of *C. laportei* may be difficult since the aphids settle deep in small crevices in the outer bark and are not always attended by ants (see also Covassi and Binazzi 1974; Notario et al. 1984). The overwintering eggs are black and deposited on the needles. They may be found also during aestivation periods on the roots of the host plants (e.g. Binazzi and Pennacchio 1996).

C. laportei is indigenous to the Atlas Mountains, North Africa, where it occurs on the Atlantic cedar. Conclusive evidence of the aphid out of its natural range was first recorded in the early 1970s in the cedar populations of southeast France. Since then the aphid spread to vast areas where Atlantic cedar is planted in the Mediterranean, but also in other European regions, Africa and Asia (Nafria et al. 1984).

Infested trees are evidenced by the typical injury; lower branches may be covered with sooty-mold, while honeydew is usually not noticeable (Fig. 10.8). Intensive feeding of *C. laportei* may cause rapid loss of needles (Notario et al. 1984). Often, trees, especially from most susceptible host species, do not recover from the damage inflicted by the aphid. Fabre et al. (1988) tested the susceptibility of provenances of cedar to *C. laportei* and found that *Cedrus atlantica* was most susceptible to *C. laportei*, while infestation on Himalayan cedar *C. deodara* were moderate and Lebanon Cedar *C. libani* and Cyprus cedar *C. brevifolia* were not susceptible. Damage was more severe in elevated regions above 700 m. Similar susceptibility picture was obtained in Israel (Saphir et al. 2000). This geographical pattern may be related to the typical feeding habit of the aphid (Fabre and Chalon 2005). *C. laportei* consumes relatively low amount of the phloem sap and thus there is a reduced flow of honeydew, especially when compared with that produced by *C. cedri* (see below), but its feeding involves the injection of toxins causing plant injury.

We may safely assume that the effective biological control of the aphid in it native area initially prevents the injury inflicted on *C. atlantica.* Typical aphid predators, such as green lacewings and lady beetles were observed in *Cinara laportei* infestations (Fabre 1990). However, only after the introduction of *Pauesia cedrobii* (Hym.: Aphidiidae) from High Atlas range to France, in 1981, the aphid was efficiently controlled (Fabre and Rabasse1987a). The wasp spread fast and 12 years later it was found in the forests of Vincennes, 600 km away from where they had been introduced (Fabre and Rabasse1987b; Remaudiere and Starý 1993). The successful biological control in France was repeated in Israel by releasing several hundred individuals originated from parasitized aphids collected in Avignon (Saphir et al. 2000).

10.4.2 Cinara *(*Cinarella*)* cedri *Mimeur*

Cinara cedri is probably native to the natural distribution range of the Lebanese cedar where its principal parasitoid was located (Michelena et al. 2005). The aphid is well known for many years on planted cedars trees in Europe, Asia and South America (Covassi and Binazzi 1974; Carter and Maslen 1982; Notario et al. 1984). In Israel and Turkey the aphid forms small colonies on the twigs and small to large colonies on branches (Fig. 10.9).

The apterae forms of the large cedar aphid are dark gray in color; its body length reach up 3.8 mm; a pair of bracket longitudinal band on the body is rather conspicuous as well as its black *siphunculi*. The alates have similar appearance but lack the dark band and their wings are grayish –yellow (Carter and Maslen 1982; Notario

Fig. 10.9 Colony of *Cinara cedri* on a branch of *Cedrus atlantica* (*left*) and tree covered with sooty mold (*right*) (Photos Z. Mendel)

et al. 1984). The aphid covered large compact colonies on the twigs and the branches and even trunks (5–6 cm diameter) of *C. atlantica, C. libani* and *C. deodora.* Populations start to build up early in the spring (February–March in Israel) and reach high densities during the succeeding months. In mid-summer the populations decline and become quite rare although small colonies may be found by tracing ant activity on the trees.

The feeding involves secretion of large amount of honeydew which cover the foliage and the bark upon which dense layer of sooty mold develops (e.g. Covassi and Binazzi 1974; Fabre 1976; Carter and Maslen 1982; Saphir et al. 2000). Susceptible provenances may suffer more from the infestation which may lead to significant loss of needles (e.g. Nafría et al. 1984).

On the background of severe infestation in Israel during the late 1990 a search for its principal parasitoid was initiated with the idea that the aphid was originated from Asia Minor. From parasitized individuals collected in this region *Pauesia anatolica* nov. sp. immerged (Michelena et al. 2005). Releasing of the wasps in Israel helped to decrease the population of the aphid, although, unlike the very effective control of *C. laportai*, the populations of *C. cedri* are still easily detected and responsible for the infrequently soiling of the lower branches canopy with honeydew, although the damage is limited.

10.4.3 Cinara *(*Cupressobium*)*

Cinara (*Cupressobium*) *tujafilina* **(del Guercio)** It is a relatively large aphid; the alates are 1.7–3.5 mm long, brownish-yellow in color and slightly covered with a dorsal pattern of bluish-white wax layer. They display a broad body with long legs;

siphunculi are broad, short, and cone-shaped and two dark brown divergent curved bands running from head to *siphunculi* level are visible (Blackman and Eastop 1994; Binazzi and Scheurer 2009). *Cinara tujafilina* develops on variety of Cupressaceae genera, such as *Callitris, Chamaecyparis, Cupressus, Juniperus, Libocedrus, Thuja* and *Widdringtonia* (Nafria 2007; Blackman and Eastop 2010). Apparently, almost all known populations are anholocyclic, but sexual forms, oviparae and males have been recorded from Iran and Kirghizia (Remaudiѐre and Binazzi 2003; Zhuravlev 2003). Although it produces a huge amount of honeydew, it is scarcely attended by ants.

The area of origin of the aphid is not clear. The occurrence of several *Cinara* spp. on oriental thuja in Iran (Hodjat 1993) and the finding the principal parasitoid *Pauesia hazratbalensis* Bhagat (Starý et al. 2005) may suggest that Iran may be source of the aphid in the Mediterranean. However, this plant is probably naturalized in Iran; whereas Oriental thuja is actually *Platycladus orientalis* originated from China and therefore we may assume that *C. tujafilina* is native in that area (Wikipedia 2014, http://en.wikipedia.org/wiki/). Many coniferous species have been distributed by humans to other areas over the world. Hence, we may suggest that associated *C. tujafilana*, like other *Cinara* spp., often followed its host plant species more or less simultaneously or successively (Starý et al. 2005). *Cinara tujafilina* become cosmopolitan (Eastop and Lambers 1976; Binazzi 1978) and is widely distributed in the Mediterranean region (Nafría et al. 2012). It usually infests well-lignified twigs, produces large quantities of honeydew and often attended by ant and bees. Development of conspicuous sooty mold is not common and usually the aphid is not considered a pest in the Mediterranean region.

Cinara* (*Cupressobium*) *fresai *Cinara fresai* is probably indigenous in North America where it is widespread in different areas in both Northern and Southern hemisphere on several conifer genera. In the Mediterranean it is known from Israel and Spain in *Juniperus* spp. (Bustillo 1975; Mendel and Zehavi 1987; Carter and Watson 1991; Remaudiѐre and Binazzi 2003; Lázzari et al. 2004; Nafría et al. 2012). In the Mediterranean and Europe the aphid does not seem to inflict any significant damage. *Cinara fresai* is anholocyclic with no sexual morphs (Blackman and Eastop 1994). Apterae individuals are 3.4–4.2 mm long, pinkish-grey to dark brownish-grey, dusted with white wax, especially on the sides of thorax. It has also characteristic pairs of black patches on thoracic and anterior abdominal tergites diverging in an inverted "V" (Blackman and Eastop 1994). This aphid usually prefers the branches and trunk of a host plant and forms very small colonies always visited by ants (Durak 2012; Durak et al. 2014).

***Cinara* (*Cupressobium*) *cupressi* (Buckton)** The cypress aphid *Cinara cupressi* Buckton is native to North America (Watson et al. 1999) and widely distributed in Southwest Asia, India, Africa, and South America (Carter and Maslen 1982; Murphy 1994; Blackman and Eastop 1994; Mujtar et al. 2009). *C. cupressi* is particularly known for causing extensive dieback and mortality of *Cupressus lusitanica* Miller. The tree species is native to Mexico and Guatemala and was introduced in Europe

Fig. 10.10 Damage of *Cinara cupressi* on *Cupressus sempervirens* (Photo A. Battisti)

by the Portuguese in the seventeenth century. From Portugal, *C. lusitanica* was introduced in other Mediterranean countries as well as in Brazil. The tree species is also widely planted in the East and Central African region on farmlands where it is grown for timber production.

In the Americas and Africa, *C. cupressi* develops on *Juniperus, Cupressus, Thuja, Chamaecyparis, Widdringtonia* and other Cupressaceae. In the Mediterranean basin outbreak of the aphid were observed is several countries on *Cupressus* spp., including native and exotic species (Fig. 10.10). In Italy and Israel the first outbreaks were recorded in late 1970s and early 1980s (Binazzi 1997; Mendel and Golan 1983, respectively). In Italy, the outbreaks were repeated in 1997 when the effect on the tree was much tougher than in the past; an unusual spring frost that destroyed much of the insect enemies of the aphid held responsible for the outbreak (Binazzi 1997). In Israel, no damage was recorded since the last and single outbreak.

Apterae and alatae are orange-brown to yellowish-brown, the dorsum dusted with pale grey wax making a pattern of cross-bands, with two dark wavy longitudinal stripes (Fig. 10.11). Body length is 1.8–3.9 mm. The alates are similar in appearance to the apterous viviparae. It may produce more than ten annual generations (Binazzi 1997). The life cycle is holocyclic, but in warmer and drier areas, *C.*

Fig. 10.11 Aphids of *Cinara cupressi* (*left*) and the honeydew (*right*) on *Cupressus sempervirens* (Photo A. Battisti)

cupressi shows an anholocyclic way of life (Delfino and Binazzi 2005). Although it produces a huge amount of honeydew, it is scarcely attended by ants. The aphids feed on small twigs, less than 1 cm thick, in the foliated part of the crown and inject salivary toxins which may cause branch dieback. Reddening is first recorded in the inner part and later on the whole crown, but very quickly, generally in about 10–15 days. Damage is generally associated to cool summers followed by mild winters. Surveillance of aphid colonies under such situation is thus essential, and it may lead to applications of insecticides or just water to disperse founder colonies in the very early spring (Roques and Battisti 1999).

The taxonomy of *C. cupressi sensu lato* is controversial (Remaudière and Binazzi 2003) and the fact that *C. cupressi* is an invasive species in the Mediterranean is not all clear. Watson et al. (1999) suggested that *C. cupressi* appear to belong to a species complex, *C. sabinae*, *C. canadensis* and *C. cupressi* all occurring in North America. These authors also proposed that populations introduced from the Middle East to Africa eventually belong to a separate species, *C.* (*Cupressobium*) *cupressivora* whose origin is related to the Italian cypress *Cupressus sempervirens* forests native from eastern Greece to south of the Caspian Sea. Still, Remaudière and Binazzi (2003) rejected the proposal of *C. cupressivora* as a new species. They indicated that nearly 25 % of the specimens of the type series could not be identified using the discrimination function and since morphologically intermediate populations are found in Pakistan the distinction of the former species from *C. cupressi* is unjustified. However, the absence of specific *Cinara* sp. (if *C. cupressivora* is not a valid species) in *C. sempervirens* suggests that a molecular analysis is needed in order to clarify this question.

Murphy et al. (1991 and cited literature) listed five aphidiid species reared from *C. cupressi* from different areas, *Aphidius* sp., *Adialytus salicaphis*, *Lysephedrus validus*, *Pauesia antennata* and *Praon volucre*, and the syrphid *Scaeva selentica*. Yet, it may be important to note that both on Italy and Israel parasitoids were not recovered from the aphid population. In Chile the aphid is attacked by the fungus *Neozygites osornensis* (Retamal et al. 2013)

10.5 Broadleaves Invasive Sap–Suckers: *Corythuca* spp.

Two species from the genus *Corythucha* (Heteroptera Tingidae), native to North America are invasive in the Mediterranean basin affecting broadleaved trees (Fig. 10.12).

Corythucha ciliata The sycamore lace bug *C. ciliata* is a species associated with *Platanus occidentalis* in its native range. The bug has colonized southern Europe by infesting native *Platanus orientalis* and introduced sycamore trees, and their hybrids, either in towns or in forests. Being sycamore trees growing often on roadsides, the pest behaves like a hitchhiker and has quickly occupied the whole sycamore range after its introduction in the 1960s. The sycamore lace bug has three generations a year and overwinters as an adult under the bark scales. A female lays about 100 eggs on the lower side of the leaves, close to the ribs, and the nymphs suck out the cytoplasm of the leaf cells, causing discoloration of the blade. In case of heavy infestation, the trees turn yellow in the middle of the summer and lose the leaves earlier than usual. The species has a great potential to adapt to temperature extremes, and can tolerate exposure to temperatures as high as 41 °C (Ju et al. 2013), making it a serious threat at lower latitudes and elevations where its hosts are widely planted. In spite of active searches of natural enemies in the native range, so far no species has been shown suitable for biological control of this pest, and the management relies mainly on cultural control methods.

Corythucha arcuata The oak lace bug *C. arcuata* has a similar colonization history of the sycamore lace bug but it has arrived to Europe more recently (Bernardinelli 2006) and since then it has slowly expanded to other countries and to Middle East. Life history and damage are similar to those of the sycamore lace bug, although more limited so far. It seems that the species requires special conditions of light and water, avoiding drought-stressed trees (Barber 2010). Its role in the general syndrome of oak decline has to be further investigated.

Fig. 10.12 Adults of *Corythuca arcuata* (*left*) and *C. ciliata* (*center*) and damage of *C. arcuata* on *Quercus* indicated by the *red arrow* (*right*) (Photos: I. Bernardinelli)

References

Aytar F, Dağdaş S, Duran C (2011) Australian insects affecting eucalyptus species in Turkey. Silva Lusit 19:41–47

Azevedo F, Figo ML (1979) *Ctenarytaina eucalyptii* Mask (Homoptera, Psyllidae). Boletin del Servicio de Defensa contra Plagas 5:41–46

Bacandritsos N (2004) Establishment and honeydew honey production of *Marchalina hellenica* (Coccoidea Margarodidae) on fir tree (Abies cephalonica). Bull Insectol 57:127–130

Bach E (1991) Direct and indirect interactions between ants (*Pheidole megacephma*), scales (*Coccus viridi*s) and plants (*Pluchea indica*). Oecologia 87:233–239

Barber NA (2010) Light environment and leaf characteristics affect distribution of *Corythuca arcuata* (Hemiptera: Tingidae). Environ Entomol 39:492–497

Bella S, Rapisarda C (2013) First record from Greece of the invasive red gum lerp psyllid *Glycaspis brimblecombei* Moore (Hemiptera Psyllidae) and its associated parasitoid *Psyllaephagus bliteus* Riek (Hymenoptera Encyrtidae). Redia 96:33–35

Ben-Dov Y, Miller DR, Gibson GAP (2013) ScaleNet: a database of the scale insects of the World. Scales in a region query results. http://www.sel.barc.usda.gov/scalenet/scalenet.htm. Accessed 9 Mar 2015

Bernardinelli I (2006) Potential host plants of *Corythucha arcuata* (Het., Tingidae) in Europe: a laboratory study. J Appl Entomol 130:480–484

Binazzi A (1978) Contributions to the knowledge of aphids on conifers I. The species of the genera *Cinara* Curt., *Schizolachnus* Mordv., *Cedrobium* Remaud. and *Eulachnus* D.Gu. present in Italy (Homoptera, Aphidoidea, Lachnidae). Redia 41:291–400

Binazzi A (1997) Further observations on the biology and ecology of the cypress aphid *Cinara (Cupressobium) cupressi* (Buckton) in Tuscany (I) (Lachninae). Redia 80:45–52

Binazzi A, Pennacchio F (1996) Note su alcuni lacnidi cinarini della Sardegna Nord-Orientale (Homoptera Aphididae). Redia 79:187–193

Binazzi A, Scheurer S (2009) Atlas of the honeydew producing conifer aphids of Europe. Aracne editrice S.r.l, Roma

Blackman R, Eastop V (1994) Aphids on the world trees: an identification and information guide. The Natural History Museum, London

Blackman R, Eastop V (2010) Aphids on the world's trees – an identification and information guide, 2nd edn. Published online at http://www.aphidsonworldsplants.info

Bodenheimer FS, Neumark S (1955) The Israeli pine Matsucoccus. Kiryat Sepher, Jerusalem

Booth JM, Gullan PJ (2006) Synonymy of three pestiferous *Matsucoccus* scale insects (Coccoidea: Margarodidae) based on morphological and molecular evidence. Proc Entomol Soc Wash 108:749–760

Borrajo P, Lopez G, Ruiz F (2009) Primera cita de *Glycaspis brimblecombei* Moore (Homoptera: Psyllidae) en SO de España. Bol San Veg Plagas 35:355–361

Bradley G (1959) Feeding sites of aphids of the genus *Cinara curtis* (Homoptera: Aphididae) in Northwestern Ontario. Can Entomol 91:670–671

Branco M, Jactel H, Silva EB et al (2004) Effect of trap design, trap size and pheromone dose on male capture of two pine bast scales species (Hemiptera: Matsucoccidae): implications for monitoring and mass-trapping. Agric For Entomol 6:233–239

Branco M, Franco JC, Dunkelblum E et al (2006a) A common mode of attraction of larvae and adults of insect predators to the sex pheromone of their prey (Hemiptera: Matsucoccidae). Bull Entomol Res 96:179–185

Branco M, Jactel H, Franco JC et al (2006b) Modelling response of insect trap captures to pheromone dose. Ecol Model 197:247–257

Branco M, Lettere M, Franco JC et al (2006c) Kairomonal response of predators to three pine bast scale sex pheromones. J Chem Ecol 32:1577–1586

Branco M, van Halder I, Franco JC et al (2011) Prey sex pheromone as kairomone for a new group of predators (Coleoptera: Dasytidae, *Aplocnemus* spp.) of pine bast scales. Bull Entomol Res 101:667–674

Brennan EB, Gill RJ, Hrusa GF et al (1999) First record of *Glycaspis brimblecombei* (Moore) (Homoptera: Psyllidae) in North America: initial observations and predator associations of a potentially serious new pest of eucalyptus in California. Pan Pac Entomol 75:55–57

Burban C, Petit RJ, Carcreff E et al (1999) Rangewide variation of the maritime pine bast scale Matsucoccus feytaudi Duc (Homoptera: Matsucoccidae) in relation to the genetic structure of its host. Mol Ecol 8:1593–1602

Burckhardt D, Santana DLQ, Terra AL et al (1999) Psyllid pests (Hemiptera, Psylloidea) in South American eucalypt plantations. Mitt Sch Ent Gesell 72:1–10

Bustillo A (1975) El pulgon gris del cipres, *Cinara fresai* Blanchard (Homoptera: Aphididae). Rev Colomb Entomol 1:33–34

Caleca V, Lo Verde G, Maltese M (2011) First record in Italy of *Psyllaephagus bliteus* Riek (Hymenoptera; Encyrtidae) parasitoid of *Glycaspis brimblecombei* (Hemiptera Psyllidae). Nat Sicil 35:435–444

Carter C, Maslen N (1982) Conifer lachnids, vol 58, Forestry Commission Research Station, bulletin. HMSO, London

Carter C, Watson G (1991) The ecology of conifer aphids and its bearing on forest establishment and productivity. In: Proceedings of the workshop on exotic aphid pests of conifers: a crisis in African forestry, Kenya Forestry Research Institute, FAO, Rome

Chauzat MP, Purvis G, Dunne R (2002) Release and establishment of a biological control agent, *Psyllaephagus pilosus* for eucalyptus psyllid (*Ctenarytaina eucalypti*) in Ireland. Ann Appl Biol 141:293–304

Covassi M, Binazzi A (1974) Note corologiche e morfologiche sulla *Cinara cedri*. Mim. in Italia (Homoptera, Aphidoidea, Lachnidae). Redia 55:331–341

Covassi M, Binazzi A (1992) Primi focolai di *Matsucoccus feytaudi* Duc. nella Liguria orientale (Homoptera: Margarodidae). Redia 75:453–466

Delfino MA, Binazzi A (2005) Further data on conifer aphids from Argentina (Aphididae Lachninae Eulachnini). Redia 88:3–7

Dhari S, Ben Jamaa ML, Garcia A et al (2014) Presence of *Glycaspis brimblecombei* and its parasitoid *Psyllaephagus bliteus* in Tunisia and Portugal. Silva Lusit 22:99–115

Drake CJ, Slamr JA (1957) The phylogeny and systematics of the family Thaumastocoridae (Heniiptera: Heteroptera). Ann Entomol Soc Am 50:353–370

Dunkelblum E, Mendel Z, Assael F et al (1993) Identification of the female sex pheromone of the Israeli pine bast scale *Matsucoccus josephi*. Tetrahedron Lett 34:2805–2808

Dunkelblum E, Harel M, Assael F et al (2000) Specificity of pheromonal and kairomonal response of the Israeli pine bast scale *Matsucoccus josephi* (Homoptera: Matsucoccidae) and its predator *Elatophilus hebraicus* (Hemiptera: Anthocoridae). J Chem Ecol 26:1649–1657

Durak R (2012) *Cinara fresai* (Blanchard, 1939) (Hemiptera: Aphidoidea) an aphid species new to Poland. Wiad Entomol 31:73–77

Durak R, Lachowska-Cierlik D, Bartoszewski S (2014) Relationships within aphids *Cinara* (Cupressobium) (Hemiptera) based on mitochondrial and nuclear DNA sequences. J Appl Genet 55:89–96

Eastop V, Lambers D (1976) Survey of the world's aphids. Dr. W. Junk, The Hague

EPPO (2007) Panel opinion on *Marchalina hellenica* 2006/130. Available on www.eppo.int

Fabre J (1976) On the presence in France of *Cinara cedri* (Mimeur), an aphid injurious to cedar. C R Acad Ag Fr 62:771–775

Fabre J (1990) Insectes Introduıts sur les Cèdres (Genre *Cedrus*) en France. International cedar symposium, Antalya, pp 743–753

Fabre J, Chalon A (2005) Multiplication possibilities of an ecotype of the aphid *Cedrobiunm laportei* (Homoptera Lachnidae) on various provenances of the genus *Cedrus*. In: Lieutier F, Ghaioule D (eds) Entomological research in Mediterranean forest ecosystems. INRA, Versailles, pp 123–138

Fabre J, Rabasse J (1987a) Introduction dans le sud-est de la France d'un parasite: *Pauesia cedrobii* (Hym.: Aphidiidae) du puceron, *Cedrobium laportei* (Hom.: Lachnidae) du cèdre de l'Atlas, *Cedrus atlantica*. Entomophaga 32:127–141

Fabre R, Rabasse P (1987b) Parasitic infestation and biological antagonists in *Cedrus atlantica*. In: Proceedings of the international conference on *Cedrus atlantica*, Ifrane. Bull Inst Scientif Maroc 23–27, Rabat

Fabre J, Chalon A, Chizky J et al (1988) Possibilites d'infestation par les pucerons : *Cedrobium laportei* Remaudière, *Cinara cedri* Mimeur (Homoptera, Lachnidae), chez le genre Cedrus. Ann Sci For 45:125–140

Fabre JP, Menassieu P, Foing JJ et al (2000) Biology and ecology of *Elatophilus nigricornis* Zetterstedt (Hemiptera Anthocoridae) predator of *Matsucoccus feytaudi* Ducasse (Homoptera Matsucoccidae) in the South-East of France. Ann For Sci 57:777–792

Ferreira MC, Ferreira GWS (1991) Pragas das folhosas. Guia de campo. Serie Divulgacao – DGPA. No. 5. Ministério da Agricultura e Produção Animal, Lisboa, 191 p

Foldi AI (2004) The Matsucoccidae in the Mediterranean basin with a world list of species (Hemiptera: Sternorrhyncha: Coccoidea). Ann Soc Entomol Fr 40:145–168

Gallis AT (2007) Evaluation of the damage by insect *Marchalina hellenica* (Genn.) in Eastern Attica, Greece. Conclusions for sustainable management of forest ecosystems. In: Lekkas TD (ed) Proceedings of the 10th international conference on environmental science and technology. G-NEST and University of Aegean, Greece, pp 191–196.

Garcia A, Figueiredo E, Valente C et al (2013) First record of *Thaumastocoris peregrinus* in Portugal and of the neotropical predator Hemerobius bolivari in Europe. Bull Insectol 66:251–256

Gaulier A, Menassieu P, Hoguet F et al (2001) Towards a sylvicultural method of pest control for *Matsucoccus feytaudi* Ducasse, the Maritime pine bast scale (Hemiptera: Margarodidae). Bol Zool Agr Bachicoltura 33:455–465

Gill RJ (1998) New state record: Redgum lerp psyllid, *Glycaspis brimblecombei*. Calif Plant Pest Dis Rep 17:7–8

Gounari S (2006) Studies on the phenology of *Marchalina hellenica* (gen.) (Hemiptera: Coccoidea, Margarodidae) in relation to honeydew flow. J Apic Res 45:8

Halbert SE, Gill RJ, Nisson JN (2001) Two *Eucalyptus* psyllids new to Florida (Homoptera: Psyllidae). Department of Agriculture and Consumer Services, Division of Plant Industry, Gainesville

Halperin J, Binazzi A, Swirski E (1988) Aphids of forest and ornamental trees and shrubs of Israel. Isr J Entomol 22:27–44

Hodgson CJ, Gounari S (2006) Morphology of *Marchalina hellenica* (Gennadius) (Hemiptera: Coccoidea: Marchalinidae) from Greece, with a discussion on the identity of *M. causcasica* Hadzibeyli from the Caucasus. Zootaxa 1196:1–32

Hodjat SH (1993) A list of aphids and their host plants in Iran. Shahid-Chamran University, Ahvaz, 150 pp

Hodkinson ID (1999) Biocontrol of eucalyptus psyllid *Ctenarytaina eucalypti* by the Australian parasitoid *Psyllaephagus pilosus*: a review of current programmes and their success. Biocontrol News Inf 20:129–134

Jacobs DH, Neser S (2005) *Thaumastocoris australicus* Kirkaldy (Heteroptera: Thaumastocoridae): a new insect arrival in South Africa, damaging to Eucalyptus trees. S Afr J Sci 101:233–236

Jactel H, Menassieu P, Lettere M et al (1994) Field response of maritime pine scale, *Matsucoccus feytaudi* Duc. (Homoptera: Margarodidae), to synthetic sex pheromone stereoisomers. J Chem Ecol 20:2159–2170

Jactel H, Ménassieu P, Burban C (1996) Découverte en Corse de *Matsucoccus feytaudi* Duc (Homoptera: Margarodidae), cochenille du pin maritime. Ann Sci For 53:145–152

Jactel H, Menassieu P, Vetillard F et al (2006) Tree species diversity reduces the invasibility of maritime pine stands by the bast scale, *Matsucoccus feytaudi* (Homoptera: Margarodidae). Can J For Res 36:314–323

Jactel H, Barbaro L, Vetillard F et al (2012) Rapport final du project: lutte biologique contre la cochenille du pin maritime, *Matsucoccus feytaudi*, en Corse

Ju RT, Gao L, Zhou XH et al (2013) Tolerance to high temperature extremes in an invasive lace bug, *Corythucha ciliata* (Hemiptera: Tingidae), in subtropical China. PLoS One 8(1), e54372

Kerdelhué C, Boivin T, Burban C (2014) Contrasted invasion processes imprint the genetic structure of an invasive scale insect across southern Europe. Heredity 113:390–400

Koteja J (1990) Paleontology. In: Rosen D (ed) Armored scale insects, World crop pests ser, 4B. Elsevier, Amsterdam, pp 149–163

Kozár F, Konczné Benedicty Z, Fetykó K et al (2013) An annotated update of the scale insect checklist of Hungary (Hemiptera, Coccoidea). Zookeys 309:49–66

Laudonia S (2006) *Blastopsylla occidentalis* Taylor (Homoptera: Psylloidea) on Italian Eucalyptus spp. a new exotic pest for European fauna. Poster presented at the VIIIth European Congress Entomology, Izmir, 17–22 Sept 2006. Supplementary abstract book-2, RVPP-74, p 26

Laudonia S, Garonna AP (2010) The red gum lerp psyllid, *Glycaspis brimblecombei*, a new exotic pest of *Eucalyptus camaldulensis* in Italy. Bull Insectol 63:233–236

Laudonia S, Sasso R (2012) The bronze bug *Thaumastocoris peregrinus*: a new insect recorded in Italy, damaging to Eucalyptus trees. Bull Insectol 65:89–93

Lázzari F, Trentini R, Carvalho R (2004) Occurrence of *Cinara* spp. (Hemiptera, Aphididae) on *Pinus* spp. (Pinaceae), in the county of Lages-SC, Brazil. Rev Bras Entomol 48:2

Liphschitz N, Mendel Z (1987) Histological studies of *Pinus halepensis* stem xylem affected by *Matsucoccus josephi* (Homoptera: Margarodidae). IAWA Bull 8:369–378

Liphschitz N, Mendel Z (1989a) Pathological changes in the cortex of *Pinus halepensis* are related to injury by *Matsucoccus josephi*. Can J Bot 67:2692–2703

Liphschitz N, Mendel Z (1989b) Interactions between hosts and non-hosts of *Pinus* spp. and *Matsucoccus josephi*: anatomical responses of the stem to infestation. New Phytol 113:135–142

Maatouf N, Lumaret JP (2012) Eco-ethology of new invasive pest species on eucalyptus plantation of Morocco. Ann Soc Ent Fr 48:289–297

Madmony A, Riov Y, Schiller G et al (2003) Controlled and open pollination between *P. brutia* and *P. halepensis* in Israel. Isr J Bot 51:213–222

Malausa JC, Girardet N (1997) Lutte biologique contre le psylle de l'eucalyptus: acclimatation sur la Côte d'Azur d'un auxiliaire prometteur, *Psyllaephagus pilosus*. Phytoma-La Défense des végétaux 498:49–51

Martins CBC, Soldi RA, Barbosa LR et al (2012) Volatile chemicals of adults and nymphs of the Eucalyptus pest, *Thaumastocoris peregrinus* (Heteroptera: Thaumastocoridae). Psyche 2012:ID 275128. doi:10.1155/2012/275128

Mendel Z (1987) Major pests of man-made forests in Israel: origin, biology, damage and control. Phytoparasitica 15:131–137

Mendel Z (1992) The occurrence of *Matsucoccus josephi* in Cyprus and Turkey and its relation to decline of Aleppo pine. Entomol Gener 17:299–306

Mendel Z (1998) Biogeography of *Matsucoccus josephi* (Homoptera: Matsucoccidae) as related to host resistance in *Pinus brutia* and *P. halepensis*. Can J For Res 28:323–330

Mendel Z, Golan Y (1983) The cypress aphid (*Cinara cupressi*), a new pest of cypress in Israel. Hassadeh 63:2690–2691

Mendel Z, Rosenberg U (1988) Trials to control the Israeli pine bast scale *Matsucoccus josephi* (Homoptera: Margarodidae) with Fenoxycarb. J Econ Entomol 81:1143–1147

Mendel Z, Schiller G (1993) Biogeography of *Matsucoccus josephi* in Crete and mainland Greece. Ann Sci For 50:383–388

Mendel Z, Zehavi A (1987) Cinara fresai – new juniper aphid in Israel. Phytoparasitica 15:258

Mendel Z, Saphir N, Madar Z et al (1988) The effect of habitat and age of Aleppo pine plantations on damage caused by *Matsucoccus josephi*. Hassadeh 68:2203–2207

Mendel Z, Dunkelblum E, Robison D (1990a) Sexual behavior of *Matsucoccus josephi* (Homoptera: Margarodidae): asynchronous adult emergence and sex pheromone release. J Chem Ecol 16:2341–2351

Mendel Z, Saphir N, Robinson D (1990b) Mass rearing of the Israeli pine bast scale *Matsucoccus josephi* (Homoptera: Margarodidae), with notes on its biology and mating behavior. Ann Entomol Soc Am 83:532–537

Mendel Z, Carmi E, Podoler H (1991) Relations between the genera *Matsucoccus* (Homoptera: Margarodidae) and *Elatophilus* (Hemiptera: Anthocoridae) and their significance. Ann Entomol Soc Am 84:502–507

Mendel Z, Assael F, Saphir N et al (1994a) New distribution records of *Matsucoccus josephi* and *Pineus pini* (Homoptera) in parts of the near east. Phytoparasitica 22:9–18

Mendel Z, Assael F, Saphir N et al (1994b) The role of *Matsucoccus josephi* and drought in the early stages of natural regeneration after fire of Aleppo pine in Israel. Isr J Entomol 29:169–177

Mendel Z, Nestel D, Gafny R (1994c) Examination of the origin of the Israeli population of *Matsucoccus josephi* (Homoptera: Matsucoccidae) using random amplified polymorphic DNA – polymerase chain reaction method. Ann Entomol Soc Am 87:165–169

Mendel Z, Carmi E, Podoler H et al (1995) Reproductive behavior of the specialist predator *Elatophilus hebraicus* Pericart (Hemiptera: Anthocoridae). Ann Entomol Soc Am 88:856–861

Mendel Z, Adar K, Dunkelblum E et al (1997a) Sex pheromone traps as a tool to study population trends of the principal predator of a scale insect and to select potential predators for biological control. "Technology Transfer in Mating Disruption". IOBC Bull 20:231–240

Mendel Z, Assael F, Saphir N et al (1997b) Seedling mortality in natural regeneration after fire of Aleppo pine in Israel. Int J Wildland Fire 7:327–333

Mendel Z, Assael F, Dunkelblum F (2004) Kairomonal attraction of predatory bugs (Heteroptera: Anthocoridae) and brown lacewings (Neuroptera: Hemerobiidae) to sex pheromones of *Matsucoccus* species (Hemiptera: Matsucoccidae). Biol Control 30:134–140

Michelena J, Assael F, Mendel Z (2005) Description of *Pauesia* (*Pauesia*) *anatolica* (Hymenoptera:Braconidae, Aphidiinae) sp. nov., a parasitoid of the cedar aphid *Cinara cedri*. Phytoparasitica 33:499–505

Miguel S, Pukkala T, Yesil A (2014) Integrating pine honeydew honey production into forest management optimization. Eur J For Res 133:423–432

Monserrat VJ, Triviño V, Acevedo F et al (2013) Nuevos datos sobre algunas especies de Hemeróbidos de la península Ibérica e islas Canarias, incluyendo una nueva especie invasora de origen neotropical en Portugal (Insecta, Neuroptera, Hemerobiidae). Graellsia 69:157–168

Mooney K, Tillberg C (2005) Temporal and spatial variation to ant omnivory in pine forests. Ecology 86:1225–1235

Mujtar V, Covelli J, Delfino MA et al (2009) Molecular identification of *Cinara cupressi* and *Cinara tujafilina* (Hemiptera, Aphididae). Environ Entomol 38:505–512

Murphy ST, Abraham YJ, Cross AE (1991) Prospects for the biological control of exotic forest aphid pests in southern and eastern Africa. In: Proceedings of the workshop, exotic aphid pests of conifers: a crisis in African forestry. Kenya Forestry Research Institute, Muguga, 3–6 June 1991. FAO, Rome, pp 124–132

Murphy ST, Chilima CZ, Cross AE et al (1994) Exotic conifer aphids in Africa: ecology and biological control. In: Leather SR, Watt AD, Mills NJ, Walters KFA (eds) Individuals, populations and patterns in ecology. Intercept, Andover, pp 233–242

Nadel RL, Slippers B, Scholes MC et al (2010) DNA bar-coding reveals source and patterns of *Thaumastocoris peregrinus* invasions in South Africa and South America. Biol Invasions 12:1067–1077

Nafria JMN (2007) *Cinara* (*Cupressobium*) *tujafilina* (Del Guercio, 1909). Fauna Europaea: Aphididae. Fauna Europaea version 13 at http://www.faunaeur.org/full_results.php

Nafria JMN, González D, Durante M (1984) Catálogo de los pulgones (Aphidoidea) de España y de sus plantas hospedadoras. Universidad de León, León

Nafría JM, Andreev AV, Binazzi A et al (2012) Hemiptera: Aphidoidea. In: de Jong YSDM (ed) Fauna Europaea version 2.5. http://www.faunaeur.org. Accessed April 2013

Nestel D, Cohen H, Saphir N et al (1995) Spatial distribution of scale insects: a comparative study using Taylor's "power law". Environ Entomol 24:506–512

Noack AE, Kaapro J, Bartimote-Aufflick K et al (2009) Efficacy of imidacloprid in the control of *Thaumastocoris peregrinus* on Eucalyptus scoparia in Sydney, Australia. Arboricult Urban For 35:192–196

Notario A, Binazzi A, Castresana L et al (1984) Los pulgones del cedro: *Cinara cedri* Mimeur y Cedrobium laportei Remaudier. Min Agr Pesca Alimentacion, Instituto Nacional para la Conservacion de la Naturaleza (ICONA). Monografia 33:1–75

Otero RP, Mansilla JP, Borrajo P et al (2011) Primera cita en la península ibérica de *Blastopsylla occidentalis* Taylor (Homoptera: Psyllidae). Bol San Veg Plagas 37:139–144

Paine TD, Steinbauer MJ, Lawson SA (2011) Native and exotic pests of eucalyptus: a worldwide perspective. Annu Rev Entomol 56:181–201

Petrakis PV, Spanos K, Feest A (2011) Insect biodiversity reduction of pinewoods in southern Greece caused by the pine scale (*Marchalina hellenica*). For Syst 20:27–41

Ray CR (1982) Revision of the genus *Matsucoccus* (Homoptera: Coccoidea: Margarodidae) in North America. PhD thesis, Auburn University, Auburn, pp 1–282

Reguia K, Peris-Felipo FJ (2013) *Glycaspis brimblecombei* Moore, 1964 (Hemiptera Psyllidae) invasion and new records in the Mediterranean area. Biodiv J 4:501–506

Remaudière G, Binazzi A (2003) Les *Cinara* du Pakistan II. Le sous-genre *Cupressobium* (Hemiptera, Aphididae, Lachninae). Rev Fr Entomol 25:85–96

Remaudiere G, Starý P (1993) Spontaneous settlement in the Paris area of the *Pauesia cedrobii* (Hymenoptera: Aphidiidae), parasite of the Cedrus aphid *Cedrobium laportei*. Rev Fr Entomol 15:157–158

Retamal CM, Barta M, Pérez ER et al (2013) *Neozygites osornensis* sp. nov., a fungal species causing mortality to the cypress aphid *Cinara cupressi* in Chile. Mycologia 105:661–669

Riom J, Gerbinot B (1977) Étude biologique et écologique de la cochenille du pin maritime *Matsucoccus feytaudi* Ducasse, 1942 (Coccoidea, Margarodidae, Xylococcinae) dans le Sud-Est de la France. I – Biologie générale et phénologie. Ann Zool Ecol Anim 9:11–50

Rodrigo E, Catalá-Oltra M, Pérez-Laorga E, Baena M (2013) Monitoring of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae) and its natural enemies in Spain using sticky tapes and pheromone traps. Eur J Entomol 110(2):301–310

Roques A, Battisti A (1999) Cypress pests. In: TeissierduCros E (ed) Cypress. A practical handbook. Studio Leonardo, Florence, pp 75–96

Rosengren R, Sundstrom L (1991) The interaction between red wood ants, Cinara aphids, and pines. A ghost of mutualism past? In: Huxley N, Cutler D (eds) Ant–plant interactions. Oxford University Press, New York, pp 80–91

Santana DLQ, Iede ET, Penteado SRC et al (1999) Ctenarytaina eucalypti (Maskell, 1890) (Hemiptera, Psyllidae) em eucaliptos no Brasil. Bol Pesq Florest 39:139–144

Saphir N, Assael F, Zehavi A et al (2000) The cedar lachnid, *Cedrobium laportei*, a new pest of cedar trees in Israel. In: Abstracts of presentations at the 18th conference of the Entomological Society of Israel, ARO, The Volcani Center, Bet Dagan, 18 May 2000

Schvester D (1967) Observations générales sur le dépérissement du pin maritime dans les Maures. Rev For Fr 6:374–384

Schvester D, Ughetto F (1986) Differences in susceptibility to *Matsucoccus feytaudi* (Homoptera: Margarodidae) in maritime pine (*Pinus pinaster*) according to provenance. Ann Sci For 43:459–474

Schvester D, Fabre JP (2001) Le dépéressiment du pin maritime des Maures et de l'Estérel provoqué par *Matsucoccus feytaudi* Ducasse (Homoptera, Matsucoccidae), connaissances acquises de 1964 à 1990. I. Historique et rôle des insectes. Forêt Méditerran 22:213–234

Spodek M, Burckhardt D, Protasov A, Mendel Z (2015) First record of two invasive eucalypt psyllids (Hemiptera: Psylloidea) in Israel. Phytoparasitica 43:401–406

Starý P, Rakhshani E, Talebi A (2005) Parasitoids of aphid pests on conifers and their state as biocontrol agents in the Middle East to Central Asia on the world background (Hym., Braconidae, Aphidiinae; Hom., Aphididae). Egypt J Biol Pest Control 15:147–151

Styrsky J, Eubanks M (2007) Ecological consequences of interactions between ants and honeydew-producing insects. Proc R Soc B 274:151–164

Tavares C, Jactel H, Halder I et al (2014) A case of ecological specialization in ladybirds: *Iberorhyzobius rondensis* (Coleoptera: Coccinellidae), potential biocontrol agent of *Matsucoccus feytaudi* (Hemiptera: Matsucoccidae). Bull Entomol Res 104:367–375

Thrasyvoulou A, Manikis I (1996) Some physiochemicals and microscopic characteristics of Greek unifloral honeys. Apidologie 26:441–452

Toccafondi P, Covassi M, Pennacchio F (1991) Studies on the entomophagous predators of scale insects of the genus *Matsucoccus* Cock. in Italy. II Bio-ethological notes on *Rhyzobius chrysomeloides* (Herbst) in pine forests of Liguria (Coleoptera: Coccinellidae). Redia 74(2):599–620

Ülgentürk S, Szentkirályi F, Uygun N et al (2013) Predators of *Marchalina hellenica* (Hemiptera: Marchalinidae) on pine forests in Turkey. Phytoparasitica 41:529–537

Valente C, Hodkinson I (2009) First record of the red gum Lerp Psyllid, *Glycaspis brimblecombei* Moore (Hem.: Psyllidae), in Europe. J Appl Entomol 133:315–317

Valente C, Manta A, Vaz A (2004) First record of the Australian psyllid *Ctenarytaina spatulata* Taylor (Homoptera: Psyllidae) in Europe. J Appl Entomol 128:369–370

Voegtlin D (1988) Bridges CA: catalog of the *Cinara* species of North America (Homoptera: Aphididae). Ill Nat Hist Surv Spec Publ 8:1–55

Watson G, Voegtlin D, Murphy S et al (1999) Biogeography of the *Cinara cupressi* complex (Hemiptera: Aphididae) on Cupressaceae, with description of a pest species introduced into Africa. Bull Entomol Res 89:271–283

Wikipedia (2014) *Platycladus orientalis* (known as oriental thuja). http://en.wikipedia.org/wiki/Platycladus page, last modified on 29 Oct 2014

Yeşil A, Gürkan B, Saraçoğlu O et al (2005) Effect of the pest *Marchalina hellenica* Gennadius (Homoptera, Margarodidae) on the growth parameters of *Pinus brutia* Ten in Mugla Region (Turkey). Pol J Ecol 53:451–458

Zhuravlev V (2003) The aphids of the genus *Cupressobium* (Homoptera, Aphidoidea, Lachninae) of Eastern Europe, Caucasus and Middle Asia. Vestnik Zoologii 37:13–50

Chapter 11
Alien Wood-Boring Beetles in Mediterranean Regions

Davide Rassati, François Lieutier, and Massimo Faccoli

Abstract The suitable climate and the high diversity of woody plants and ecological conditions characterizing the Mediterranean regions have favored the establishment of several alien species in the Mediterranean Basin during the last decades. Among them, the vast majority is represented by wood-boring beetles, which can be easily transported between continents within all kinds of woody materials. Up to now, 34 alien wood-boring beetles are recorded as established in Mediterranean countries, and the bulk of them is represented by Scolytinae and Cerambycidae. Italy, France and Spain report the highest number of established alien species. Besides giving an overview of their origin, introduction pathways, biology and distribution in the Mediterranean Basin, we discuss the potential impact of these insects in the invaded environment, the survey and early-detection protocols, the main ecological processes driving their establishment and spread, and how climate change could affect their invasion process in the near future.

11.1 Introduction

Wood-boring beetles are known as one of the most important threats to forests worldwide (Brockerhoff et al. 2006a). They can cause severe damage in their native ecosystems, and large amount of economic resources are invested for their management every year (Wermelinger 2004). At the same time, they are considered as one of the most successful group of invasive species, as they can be transported in almost all kinds of wood products (Brockerhoff et al. 2006a). Following the increase of international trade, the rate of introduction of alien wood-boring beetles has sharply increased in the last decades (Haack 2001, 2006; Work et al. 2005; Brockerhoff

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et al. 2006a; Kirkendall and Faccoli 2010), and new species are intercepted or recorded as established almost every year (Roques and Auger-Rozenberg 2006; Kirkendall and Faccoli 2010; Rassati et al. 2015a). Although the group of wood-boring beetles includes a number of families, four are considered more important than the others: the bark beetles (Scolytinae), the longhorn beetles (Cerambycidae), the jewel beetles (Buprestidae) and the pinehole borers (Platypodinae) (Kirkendall and Faccoli 2010; Sauvard et al. 2010). These families are, in fact, the most commonly intercepted at points of entry worldwide (Haack 2001; Brockerhoff et al. 2006a), and include the most threatening species of the last decades (Nowak et al. 2001; Kovacs et al. 2010). Furthermore, Mediterranean countries have been identified as especially suitable to alien wood-boring beetles (Kirkendall and Faccoli 2010; Marini et al. 2011). The wet and warm climate, as well as the wide variety of ecosystems, with a high diversity of woody plants and ecological conditions, have favored the establishment of several species (Kirkendall and Faccoli 2010; Marini et al. 2011). This trend will probably continue, or even increase, in the next future, as the raising speed and frequency of movement of goods around the globe and climate change (Levine and D'Antonio 2003) will intensify the probability of alien wood-boring beetle arrival and establishment in Mediterranean countries.

11.2 Species Diversity, Origin and Distribution

Up to now, 34 alien wood-boring beetles are recorded as established in Mediterranean countries. The bulk of them is represented by Scolytinae (15 genera, 18 species) and Cerambycidae (12 genera, 14 species), whereas Buprestidae and Platypodinae are represented by only one species each (Tables 11.1 and 11.2). Among Scolytinae, *Xylosandrus* is the most represented genera with four species, whereas, among Cerambycidae, the richest genera are *Anoplophora* and *Phoracantha*, with two species each. Apart from feeding and breeding habits (Sect. 11.3), there are three main reasons explaining why alien species are more often scolytids than cerambycids or buprestids: first, the small size, which render them more difficult to detect than bigger beetles; second, the number of individuals arriving at points of entry, which is usually higher for scolytids than for the other families third, the availability of specific aggregation pheromones, which allow scolytids to locate in the invaded environment other individuals of the same species, increasing the possibilities of their mating and establishment.

Given that the introduction of alien wood-boring beetles has always been unintentional, it is difficult to determine precisely when a certain species arrived (Kirkendall and Faccoli 2010). An alien species can be, in fact, detected years or even decades after its arrival (Kenis et al. 2007; Mattson et al. 2007; Roques et al. 2009). Anyway, analyzing the first records of the alien species, it is possible to point out that there has been a constant increase of their introductions from 1900 to 2015 (Fig. 11.1). Particularly evident is the trend of alien Scolytinae, with 9 out of 18 species introduced in the last 15 years. The oldest records of alien species in

Table 11.1 List of alien Scolytinae and Platypodinae established in Mediterranean countries, with details on their distribution, country of origin, feeding habit and host species

	Distribution in med countries	Native to	1st record	Feeding guild	Hosts
Scolytinae					
Ambrosiodmus rubricollis (Eichhoff)	IT	East Asia	2008	AB	Polyphagous, broadleaf trees
Ambrosiophilus atratus (Eichhoff)	IT	East Asia	2007	AB	Polyphagous, broadleaf trees
Cyclorhipidion bodoanum (Reitter)	CR, FR, IT	North Asia	1960	AB	Oligophagous, Fagaceae
Cyrtogenius luteus (Blandford)	IT	East Asia	2009	BB	Oligophagous, Pinaceae
Dryocoetes himalayensis Strhomeyer	FR	India	2009	BB	Polyphagous, *Juglans regia*, *Pyrus lanata*
Gnathotrichus materiarius (Fitch)	FR, IT, SP	North-East USA	1933	AB	Polyphagous, conifers
Hypocryphalus scabricollis (Eichhoff)	IT, MA	East Asia	1991	BB	Monophagous, *Ficus* spp.
Hypothenemus eruditus Westwood	CR, EG, FR, IT, IS, MA, MO, SP, TK	American tropics?	1924	BB	Polyphagous
Monarthrum mali (Fitch)	IT	North-East USA	2008	AB	Polyphagous, broadleaf trees
Phloeosinus rudis Blandford	FR	East Asia	1940	BB	Oligophagous, Cupressaceae
Phloeotribus liminaris (Harris)	IT	East USA	2004	BB	Monophagous, *Prunus* spp.
Pityophthorus juglandis Blackman	IT	South-West USA	2013	BB	Monophagous, *Juglans* spp.
Xyleborinus attenuatus (Blandford)	SP	North USA	1987	AB	Polyphagous, broadleaf trees
Xyleborus pfeilii (Ratzeburg)	AG, CR, FR, GR, IT, MO, SI, SP, YU	East Asia	1837	AB	Polyphagous, broadleaf trees
Xylosandrus crassiusculus (Motschulsky)	IT, FR	Asia	2003	AB	Polyphagous
Xylosandrus compactus (Eichhoff)	IT	South-East Asia	2011	AB	Polyphagous

(continued)

Table 11.1 (continued)

	Distribution in med countries	Native to	1st record	Feeding guild	Hosts
Xylosandrus germanus (Blandford)	CR, FR, IT, SI, SP	East Asia	1950	AB	Polyphagous
Xylosandrus morigerus (Blandford)	FR, IT	Globally distributed	1916	AB	Polyphagous, greenhouse orchards in Europe
Platypodinae					
Megaplatypus mutatus (Chapuis)	IT	South America	2000	AB	Polyphagous, broadleaf trees

Country abbreviation: *AG* Algeria, *CR* Croatia, *EG* Egypt, *FR* France, *GR* Greece, *IT* Italy, *IS* Israel, *MA* Malta, *MO* Morocco, *SI* Slovenia, *SP* Spain, *TK* Turkey, *YU* Serbia and Montenegro. Feeding guild abbreviation: *AB* ambrosia beetles (xylomycetophagous), *BB* bark beetles (phloeophagous)

Mediterranean countries concern the scolytid *Xyleborus pfeilii* (Ratzeburg) in 1837 and the longhorn beetle *Callidiellum rufipenne* (Motschulsky) in 1906. The first species, *X. pfeilii*, is a largely polyphagous ambrosia beetle living on broadleaf trees and native to Asia (southern China, Japan, and Korea), although in the past it was considered to be indigenous to Europe. This ambrosia beetle is considered rare but it can be found in most Europe as well as in northern Africa and Turkey. Morphologically it apparently belongs to groups of species of Asian origin, and it is not similar to any of the species of *Xyleborus* native to Europe. Furthermore, it shows a clearly disjunct spatial distribution, which is a characteristic of introduced species (Kirkendall and Faccoli 2010). This species and the longhorn beetle *C. rufipenne* were probably introduced to Europe following the increase of importations from the Far East recorded at the beginning of the nineteenth century.

The alien wood-boring beetles established in Mediterranean countries were introduced from six world regions: Africa, Asia, Australia, North-America, Central-America and South-America. Asia is the most represented continent, with 10 species of Scolytinae and 8 species of Cerambycidae, whereas 7 species – 5 Scolytinae and 2 Cerambycidae – are from Americas (Tables 11.1 and 11.2). The habitat diversity, offering a large number of possible host-trees, and the dry and warm climate with mild winters occurring in Mediterranean regions, have been identified as the main features favoring the establishment of alien species (Kirkendall and Faccoli 2010; Marini et al. 2011). Although the smaller extension, the Mediterranean Basin is, in fact, disproportionately rich in alien wood-boring beetles compared to temperate areas of Europe (Kirkendall and Faccoli 2010). Large differences, however, exist also among Mediterranean countries. Italy, France and Spain have the largest number of alien wood-boring beetle species (24, 15 and 10, respectively), followed by Israel (6), Malta, and Croatia (5) (Fig. 11.2). The majority of Mediterranean countries, instead, counts between one and five established alien species. Analyzing the four families separately, it is possible to notice that Italy hosts the 83 % of alien

Table 11.2 List of alien Cerambycidae and Buprestidae reported in Mediterranean countries, with details on their distribution, country of origin and host species

	Distribution in Med countries	Native to	1st Record	Hosts
Cerambycidae				
Acrocinus longimanus (Linnaeus)	PT	Brazil	1977	Polyphagous, broadleaf trees
Anoplophora chinensis (Förster)	IT	South-Central China	2000	Polyphagous, broadleaf trees
Anoplophora glabripennis (Motschulsky)	FR, IT	South-Central China	2001	Polyphagous, broadleaf trees
Aromia bungii (Faldermann)	IT	China, Korea	2011	Polyphagous, broadleaf trees
Batocera rufomaculata (De Geer)	IS	Asia	1956	Polyphagous
Callidiellum rufipenne (Motschulsky)	FR, IT, SP	East Asia, Japan	1906	Oligophagous, Cupressaceae
Chlorophorus annularis (Fabricius)	SP	Asia	1991	Polyphagous, mainly bamboo
Neoclytus acuminatus (Fabricius)	CR, FR, IT, SI, YU	South-Central USA	1908	Polyphagous
Phoracantha recurva Newman	GR, IT, IS, LB, LE, MA, MO, PT, SP, TU	Australia	1992	Oligophagous, *Eucalyptus* spp.
Phoracantha semipunctata (Fabricius)	AG, EG, FR, GR, IT, IS, LB, LE, MA, MO, PT, SP, SY, TU	Australia	1948	Oligophagous, *Eucalyptus* spp.
Phryneta leprosa (Fabricius)	FR, MA	South Tropical Africa	1997	Monophagous, *Morus nigra*
Psacothea hilaris (Pascoe)	IT	East Asia	2005	Oligophagous, Moraceae
Xylotrechus stebbingi (Fabricius)	FR, GR, IT, IS, SI, TU	Central Asia	1990	Polyphagous, broadleaf trees
Xystrocera globosa (Olivier)	IS	South Asia	2002	Polyphagous
Buprestidae				
Chrysobothris dorsata (Fabricius)	PT, SP	Tropical Africa	1986	Polyphagous, broadleaf trees

Country abbreviation: *AG* Algeria, *CR* Croatia, *EG* Egypt, *FR* France, *GR* Greece, *IT* Italy, *IS* Israel, *LB* Libya, *LE* Lebanon, *MA* Malta, *MO* Morocco, *PT* Portugal, *SI* Slovenia, *SY* Syria, *SP* Spain, *TU* Tunisia, *YU* Serbia and Montenegro

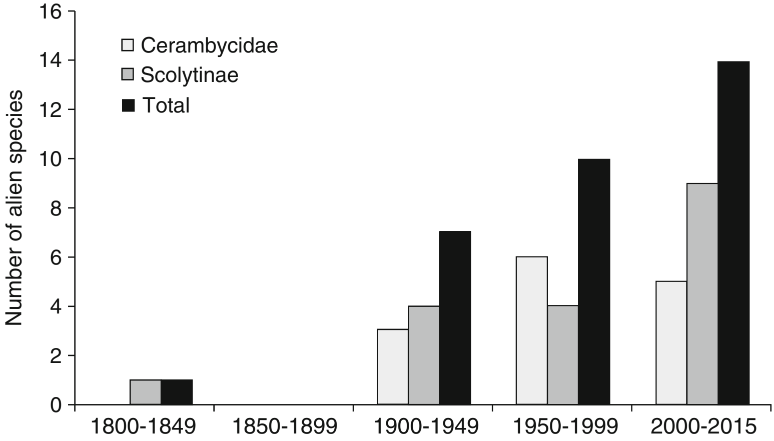

Fig. 11.1 Number of scolytids and cerambycids recorded in Mediterranean countries from 1800 to 2015

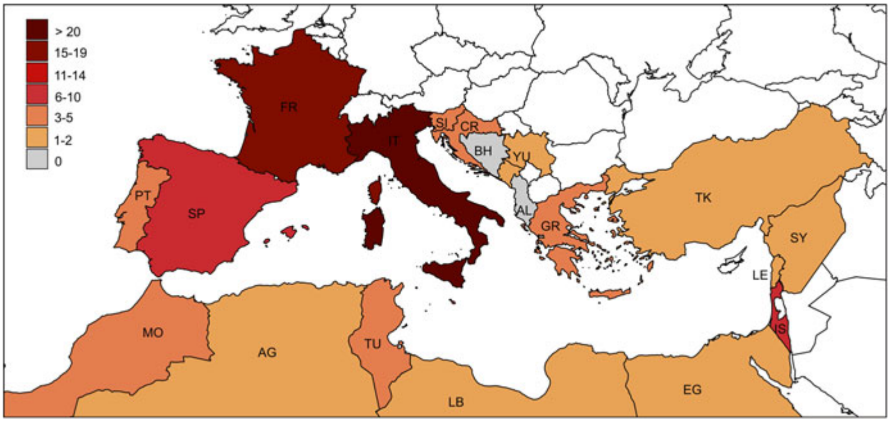

Fig. 11.2 Comparative colonization of Mediterranean countries by alien wood-boring beetles (Scolytinae, Cerambycidae, Buprestidae and Platypodinae)

Scolytinae, among which 7 species occur exclusively in this country, the 64 % of alien Cerambycidae, among which three exclusive species, and the only alien Platypodinae. France, on the contrary, counts the 50 % of alien Scolytinae, among which two exclusive, and the 43 % of alien Cerambycidae, which are all shared with other countries. Such differences can be due to different reasons, such as the length of coastline, the number and size of ports of entry, and the composition of their surrounding forests (Haack 2001, 2006; Rassati et al. 2015a). Furthermore, the occurrence of specific monitoring or early-detection programs in a given country can affect the possibility of alien species recording (Kirkendall and Faccoli 2010).

11.3 Feeding and Breeding Habits

The vast majority (80 %) of alien wood-boring beetles occurring in Mediterranean countries develops in sap-wood. They include both true wood borers (48 %), like cerambycids and buprestids, and ambrosia beetles (52 %), like platypodids and some scolytids. The other species (20 %), all belonging to the scolytid family, are bark beetles developing in the phloem of the host trees.

Most of alien wood-boring beetles are polyphagous species (68 %, including 12 scolytids, nine cerambycids, one buprestid and one platypodid) breeding in different genera often belonging to different families, or oligophagous (20 %, including three scolytids and four cerambycids) breeding in one family of host plants. Only four (12 %) of the aliens established in Mediterranean regions are monophagous, i.e. breeding in only one species or genus of woody plants, in particular they are phloeophagous species. They are one cerambycid and three bark beetles (Tables 11.1 and 11.2). Concerning scolytids and platypodids, most of the established alien species are ambrosia beetles, mainly from Asia or North America. Ambrosia beetles are usually polyphagous (Beaver 1979; Kirkendall 1983), and the lack of host specificity is considered to be a major reason why they are such successful invaders (Kirkendall and Faccoli 2010). Among the species developing in a more restricted number of hosts (i.e., monophagous or oligophagous), two are specific of alien tree species (*Eucalyptus* spp.), two of Fagaceae and Cupressaceae (dominant families in much of Mediterranean area), and four in widely planted fruit trees like *Ficus*, *Juglans*, *Morus* and *Prunus*.

Breeding habits also play a key role in determining the possibilities of their establishment in a new country (Jordal et al. 2001; Marini et al. 2011). Particularly important are the demographic, ecological and genetic problems related with low population densities, known as Allee effect (Liebhold and Tobin 2008; Brockerhoff et al. 2014). Single small populations are always at risk of extinction from random local hazards, and, when they arose from large outbreeding populations, they usually suffer from inbreeding depression (Kirkendall and Faccoli 2010). Mate location can also lower the reproductive rate of small populations. Species which usually have a brother-sister mating, such as ambrosia beetles, circumvent many of these problems: mating takes place among siblings, before dispersal, and regular inbreeders presumably suffer much less from inbreeding depression than do outbreeders (Jordal et al. 2001). About 35 % (12) of the alien wood-boring beetles are inbreeders, but this proportion increases until up to 66 % considering only scolytids, which is roughly twice as high as the proportion of the European scolytid fauna which inbreeds (Kirkendall 1993), supporting the importance of inbreeding in colonization of new areas. In this respect, 90 % of alien inbreeding scolytids are polyphagous while 84.6 % of polyphagous species are inbreeders, suggesting that both inbreeding and polyphagy favor invasiveness.

11.4 Life History of the Most Important Alien Wood-Boring Beetle Species Established in Mediterranean Countries

The high diversity in the origin and impact of alien wood-boring beetles established in Mediterranean countries has led to a strong heterogeneity in the information available on their biology and ecology. In fact, if the most damaging species have been deeply studied in the last decades, the less important ones are still largely underinvestigated. Here we report the main biological and ecological traits of those species that had or could have ecological or economic impacts in Mediterranen countries.

11.4.1 Ambrosiodmus rubricollis *(Eichhoff)*

Biology and Ecology *A. rubricollis* (Fig. 11.3a, b) is the only species belonging to the genus *Ambrosiodmus* known to be established in Europe (Faccoli et al. 2009). It is a highly polyphagous species that is able to colonize broadleaf trees, shrubs and, occasionally, also conifers (Faccoli et al. 2009). Although its biology and ecology has not been deeply investigated yet, it is known that *Ambrosiodmus* species inbreed (Kirkendall and Jordal 2006), so newly matured females mate with siblings before emerging from the host (Faccoli et al. 2009). The voltinism of this species is still unclear, but studies conducted in the USA highlighted only one peak of flying adults in early May (Coyle et al. 2005).

Possible Damage Developing mainly in dead wood, *A. rubricollis* is not considered as an aggressive species (Faccoli et al. 2009). It can be regarded, however, as an invasive species with a very high expansion rate, spreading in 11 US states in less than 40 years (Faccoli et al. 2009). Furthermore, the strong infestation recorded in an Italian peach orchard in 2008 could be a first indicator of the potential harmfulness of this species in a new continent (Faccoli et al. 2009).

11.4.2 Cyrtogenius luteus *(Blandford)*

Biology and Ecology *C. luteus* is a 2.2–2.4 mm long bark beetle of Asiatic origin. Although most aspects of its biology are still unknown, this species is considered to be associated with conifers, especially pines, but it has also been collected from larch and spruces (Faccoli et al. 2012; Gómez et al. 2012). The life cycle is likely to be very similar to the closely related species *C. brevior* (Eggers), which has been better studied (Gómez et al. 2012) and which has been considered for a long time as synonymous of C. luteus. In the phloem of the host tree adults bore irregular galleries several centimeters long, where eggs are laid singly on each side (Gómez et al.

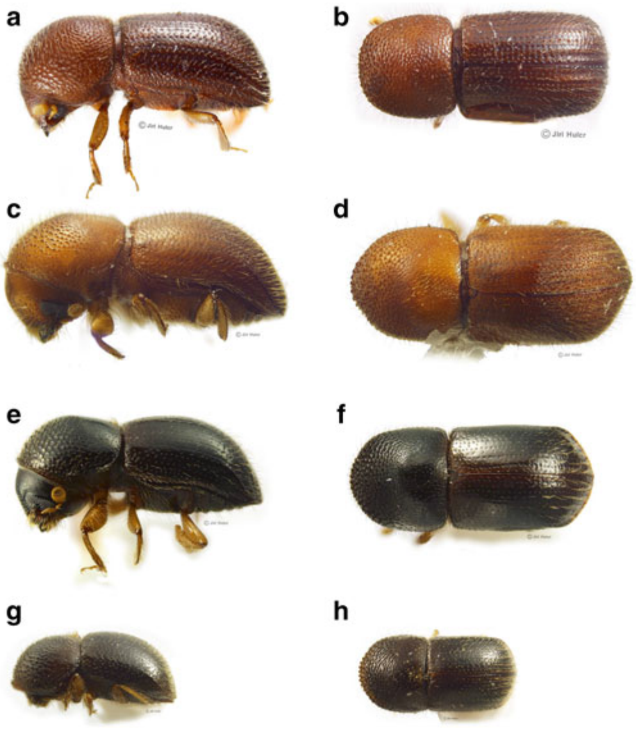

Fig. 11.3 *Ambrosiodmus rubricollis* female, (**a**) habitus lateral; (**b**) habitus dorsal; *Xylosandrus crassiusculus* female, (**c**) habitus lateral; (**d**) habitus dorsal; *Xylosandrus germanus* female, (**e**) habitus lateral; (**f**) habitus dorsal; *Xylosandrus compactus*, (**g**) habitus lateral; (**h**) habitus dorsal (Photos: J. Hulcr)

2012). Larvae make irregular galleries and pupation occurs in the outer phloem or in the bark (Gómez et al. 2012). Research on phenology and seasonality is currently ongoing in Italy.

Possible Damage Although *C. luteus* appears to behave as a secondary pest in its native range, attacking only dying or dead trees, several infested areas including dead individuals of *Pinus taeda* L. were reported in Uruguay (Gómez et al. 2012). Its possible impact in Mediterranean countries is, however, still unknown.

11.4.3 Gnathotrichus materiarius *(Fitch)*

Biology and Ecology *G. materiarius* is a small (3.2–3.5 mm) ambrosia beetle characterized by a cylindrical, narrow, and elongated body (Faccoli 1998). In Europe this beetle colonizes several conifer species (*Pinus*, *Abies*, *Picea*, *Larix* and

Pseudotsuga), excavating slightly winding and branched galleries that provide ideal conditions for the growth of the black fungus *Endotnycopsisfa sciculata* Batra, which is used as food by the larvae (Faccoli 1998). In Europe the adults fly between April and the middle of June, but it is possible that a second flight takes place at the end of the summer (Faccoli 1998). This species overwinters as mature larvae or young adult. Males are very rare (Balachowsky 1949).

Possible Damage Although *G. materiarius* has been recorded only on dead or dying trees, it can cause economic damage to wood products both directly, through the excavation of the galleries, and indirectly, through the black discoloration caused by its associated fungi (Faccoli 1998).

11.4.4 Phloeosinus rudis *Blandford*

Biology and Ecology *P. rudis* is a small (2.5–3.0 mm long), dark brown bark beetle. It colonizes species belonging to the family Cupressaceae, mainly *Thuja, Chamaecyparis*, and *Juniperus.* Females bore into the trunk of trees weakened by drought or other stress factors (Moraal 2010). Galleries are about 5–16 cm long and the feeding activity of the larvae usually kills the host (Moraal 2010). This species overwinters mainly as larvae, whereas the percentage of overwintering adults is usually low (Moraal 2010). Only one generation per year is produced.

Possible Damage Although this species is not considered as a main pest, the feeding activity of the larvae can lead weakened host trees to death (Moraal 2010). Solitary trees, as well as complete hedges located in domestic gardens of city and urban peripheries or along streets, can be heavily damaged (Moraal 2010).

11.4.5 Phloeotribus liminaris *(Harris)*

Biology and Ecology *P. liminaris* is a small (1.9–2.3 mm long) bark beetle characterized by an oval, wide, and short body (Pennacchio et al. 2004). The colour is dark brown to almost black (Pennacchio et al. 2004). This species, also known as "Peach Bark Beetle", is associated with *Prunus serotina* Ehrh. and other spontaneous and cultivated *Prunus* species (Pennacchio et al. 2004). It overwinters as adult in short, single and transverse galleries excavated, mainly by the female, in the cortical tissue (Wood 1982). In May the beetle emerges searching for weakened host trees where to reproduce (Pennacchio et al. 2004). *P. liminaris* has two generations per year in North America, but it is able to start a third one in the southernmost latitudes of its native range (Wood 1982).

Possible Damage The galleries dug by overwintering beetles in the vital internal bark of trees in good vegetative condition can be particularly harmful, especially when the beetle density is high, causing irregular growth of tissues and a strong decrease of wood value (Rexrode 1982). This is of particular concern in the USA for *P. serotina*, whose wood is used for valuable items (Pennacchio et al. 2004). Although its potential impact in the Mediterranean Basin is still unclear, it could become a pest in peach orchards (Pennacchio et al. 2004).

11.4.6 Pityophthorus juglandis *Blackman*

Biology and Ecology *P. juglandis* is a minute (1.5–1.9 mm) bark beetle reproducing under the bark of many walnut species (Wood 1982). In spring the beetle colonizes the base of twigs in rough areas of bark, although large branches and even the trunk can be infested; the underside of branches is preferred, typically on the warmer side of the tree (Newton and Fowler 2009). *P. juglandis* has 2–3 generations per year, with adults that emerge in April/May, initiating the excavation of horizontal galleries where eggs are laid by the females (Newton and Fowler 2009). Although the beetle itself is not considered as a main pest, it is of utmost importance for its role as vector of the fungus *Geosmithia morbida* Kolařik, causal agent of the thousand cankers disease (Montecchio and Faccoli 2014).

Possible Damage Trees affected by thousand cankers disease initially exhibit yellowing and wilting of the foliage followed by progressive branch dieback and crown thinning (Newton and Fowler 2009), and dark wet cankers are found near the entrance hole of *P. juglandis* (Montecchio and Faccoli 2014). Although cankers caused by *G. morbida* are small, repeated feeding and egg laying by *P. juglandis* on the same tree lead to the production of a high number of cankers which can cause the death of the tree within 3–4 years (Newton and Fowler 2009). The association *P. juglandis*/*G. morbida* clearly represents a threat to the cultivation of *Juglans* species in Mediterranean countries, especially considering that also the English walnut *J. regia* L., that is cultivated for both fruit and timber production, has found to be susceptible to the thousand cankers disease (Montecchio et al. 2014).

11.4.7 Xylosandrus crassiusculus *(Motschulsky)*

Biology and Ecology *X. crassiusculus* is a 2.1–2.9 mm long beetle (Fig. 11.3c, d) characterized by a stout body and reddish elytra with vestiture of long setae arranged in irregular rows. It colonizes several tree species, both conifers and broadleaves (Faccoli 2010a). It exhibits the typical ambrosia habit, with larvae living in wood and feeding on the mycelium of ambrosian-type fungi (Pennacchio et al. 2003). Mated females bore small chambers within the wood where eggs are laid in groups

(Faccoli 2010a). During the burrowing, the female compacts and pushes frass out of the nest, forming a characteristic cylinder which stick out from the entrance hole (Pennacchio et al. 2003). Beetles are usually active from March to the autumn, and the life cycle takes about 55 days, with usually two generations per year.

Possible Damage Although data on the economic impact of *X. crassiusculus* in forests and wood production is lacking, it is considered as a potential pest in nurseries, orchards and plantations, as diffuse colonization inevitably leads to the death of host tree (Pennacchio et al. 2003). Moreover, many woody plants known as potential hosts of this species are important fruit crops, forest trees or woody ornamentals in Mediterranean regions. For example, given its ability to colonize chestnut trees (Oliver and Mannion 2001), it is considered as potentially detrimental for chestnut silvilcultre in Italy (Pennacchio et al. 2003), where some infestations has been already recorded (Faccoli, unpublished data).

11.4.8 **Xylosandrus germanus** ***(Blandford)***

Biology and Ecology *X. germanus* is a 2.0–2.3 mm long ambrosia beetle with shiny black elytra (Fig. 11.3e, f) that is considered as a successful invasive species (Faccoli 2010b). It is able, in fact, to spread over tens of kilometers per year (Henin and Versteirt 2004) and to attack a very wide range of both deciduous (such as *Fagus, Castanea, Buxus, Ficus, Carpinus, Quercus* and *Juglans*) and coniferous trees (*Picea*, *Pinus*) (Wood 1982). Furthermore, the species is not size-selective, and it is able to breed both in small branches and in large logs and stumps (Henin and Versteirt 2004). Both adults and larvae feed on the symbiotic ambrosia fungus *Ambrosiella hartigii* Batra, which is introduced by the adults into the gallery system before oviposition (Henin and Versteirt 2004). The size of the brood varies considerably, but it is usually of about 16 individuals (Weber and McPherson 1983). *X. germanus* is generally considered to be monovoltine, but in Italy two generations per year have been observed (Faccoli 2010b).

Possible Damage Although it is considered as a secondary species, attacks by *X. germanus* can occur also on healthy trees (Faccoli 2010b). The economic impact results both from the direct excavation of the larval galleries and the wood staining caused by the ambrosia fungus (Faccoli 2010b). Previous studies suggested that this species could become the dominant ambrosia beetle in the invaded forests due to a decline in native species abundance, which is probably related to the occupation of potential breeding sites by *X. germanus* (Grégoire et al. 2001; Bouget and Noblecourt 2005).

11.4.9 Xylosandrus compactus *(Eichhoff)*

Biology and Ecology *X. compactus* is a small ambrosia beetle (1.4–1.9 mm long) with dark brown to almost black body (Garonna et al. 2012; Fig. 11.3g, h). This species can colonize more than 225 species of plants, belonging to 62 families (Ngoan et al. 1976). *X. compactus* mainly breeds in seedlings, shoots and small twigs, rarely in material larger than 6 cm of diamater (Garonna et al. 2012). The female digs a tunnel into the pith or wood of the host plant which consists of a simple or bifurcated entrance and a longitudinal chamber where eggs are layed (Garonna et al. 2012). Larvae feed on an ambrosia fungus growing on the walls of the brood chamber (Ngoan et al. 1976). Although in tropical areas breeding is continuous with overlapping generations (Browne 1961), it is reasonable to assume that *X. compactus* can complete at least two generations per year in Mediterranean countries (Pennacchio et al. 2012).

Possible Damage *X. compactus* can attack live twigs and branches causing their death in few weeks through the excavation of the galleries (Ngoan et al. 1976). This can be especially important as it weakens and retards the fruiting of young plants and makes the replacement of trees very difficult (Ngoan et al. 1976). Among the many described cases, very intense attacks were observed on *Castanea* spp. in China (Yan et al. 2001) and on laurel in Italy (Pennacchio et al. 2012).

11.4.10 Xylosandrus morigerus *(Blandford)*

Biology and Ecology *X. morigerus* is a very small ambrosia beetle (1.4–1.7 mm), also known as "brown twig borer", that can colonize a very wide variety of host plants, mainly broadleaf trees (Wood 1982). This species usually breeds in shoots, twigs and small branches, but can also attack seedlings and larger stems up to a diameter of about 20 cm (Roberts 1977). Both females, which initiate attacks, and larvae feed on the ambrosia fungi that are introduced by the adults into the gallery system (Roberts 1977). Only a single male is usually present within each gallery, and it mates with his sisters leading to a rapid increase of the population level (Roberts 1977). In its native range, breeding is continuous, with overlapping generations, so that this species is active at all times (Roberts 1977).

Possible Damage Although *X. morigerus* is not known to have established populations in natural forests, it seems to have a permanent presence in European greenhouses (Balachowsky 1949; Kirkendall and Faccoli 2010). Similar to other ambrosia beetles, this species is considered as a potential pest of ornamental trees and as a borer in orchid stems (Kirkendall and Faccoli 2010).

11.4.11 Megaplatypus mutatus *(Chapuis)*

Biology and Ecology *M. mutatus* is the only alien pinehole borer known as established in the Mediterranean Basin. It is 7–8 mm long, characterized by a cylindrical body that is dark-brown in males and reddish-yellow in females (Alfaro et al. 2007). It is a serious pest in commercial plantations of a number of broadleaf and fruit tree species, but *Populus* spp. are considered as the main hosts in Europe (see also Sect. 11.7.1). This beetle is univoltine in both South America, its native range, and Italy, where it overwinters as mature larvae or immature adults (OEPP/EPPO 2009). After emergence, males bore into host trunk and release a pheromone to attract the females; then, after copulation, the latter dig deep galleries, laying 100–200 eggs (OEPP/EPPO 2009) and introducing the symbiotic ascomycete *Raffaelea santoroi* Guerrero (OEPP/EPPO 2009). Larvae develop slowly in about 5 months (OEPP/EPPO 2009). They are initially mycetophagous but become xylophagous in the last stages before pupation (OEPP/EPPO 2009).

Possible Damage *M. mutatus* is recognized as an important pest of timber trees, especially poplars, as it can reduce both the wood volume through the excavation of the galleries and the wood quality through the dark staining produced by the ambrosial mycelia (Alfaro et al. 2007). In Italy, this beetle caused significant economic losses also to fruit tree plantations, including apple (*Malus domestica* Borkh), walnut (*Juglans regia* L.) and hazel (*Corylus avellana* L.) (Alfaro et al. 2007). Although this species has been recorded so far only in Italy, many countries of the Mediterranean Basin, especially those where poplar plantations and fruit crops are widely spread, are at risk of introduction (Alfaro et al. 2007).

11.4.12 Aromia bungii *(Faldermann)*

Biology and Ecology *A. bungii* is a large black cerambycid (approximately 40 mm long) with glossy elytra and a distinctively red pronotum (Garonna et al. 2013). It is considered as a fruit tree pest in its native range, and its main host plants are *Prunus* species (Rosaceae), in particular peach (*Prunus persica* L.) and apricot (*P. armeniaca* L.), and to a lesser extent plum (*P. domestica* L.) and cherry (*P. avium* L.) (Garonna et al. 2013). Although data on the biology and ecology of *A. bungii* is generally lacking, it has been observed that larvae bore galleries in the trunk and in the main lateral branches, infesting the subcortical area between the bark and the sapwood (Garonna et al. 2013). Eggs are laid by females in bark crevices at the beginning of July. It is also reported that in Northern China one generation may take 2–3 years (Garonna et al. 2013).

Possible Damage The excavation of the larval galleries within the trunk and the main branches leads to the loss of fruit production and the weakening of the trees. Given that *Prunus* species are widely present across Mediterranean regions for ornamental purposes and fruit production, this beetle is considered of major economic importance (Garonna et al. 2013). The fact that it may also attack other important species cultivated either for fruit, such as olive, or wood production, such as *Populus alba* L., makes this species particularly dreaded.

11.4.13 Anoplophora glabripennis *(Motschulsky)*

Biology and Ecology *A. glabripennis* is a large (20–35 mm long, Fig. 11.4a), stout longhorn beetle characterized by a glossy-black body with white spots on the elytra (Sauvard 2009a). This species colonizes a wide range of broadleaf trees (such as *Acer*, *Betula*, *Fraxinus*, *Populus*, *Salix* and *Ulmus*), with adults that feed on bark of small branches and larvae that live inside the wood, in tree bole or large branches (Sauvard 2009a). Eggs (from 10 to 100) are laid by females in oviposition slits in the bark of the trees from spring to late summer (Sauvard 2009a). Hatching within 10–15 days, the immature larvae tunnel under tree bark and bore into healthy hardwood trees (Faccoli et al. 2015). Depending on the date of egg laying and climate conditions, larval development lasts from 10 to 22 months (Faccoli et al. 2015). After emerging, adult beetles feed for 2 or 3 days, then mate. They remain active only during summer and early fall before perishing (Faccoli et al. 2015). Given that beetle larvae live deeply inside trees for a long time, they can easily and unintentionally be moved with firewood, live trees or fallen timber (Sauvard 2009a).

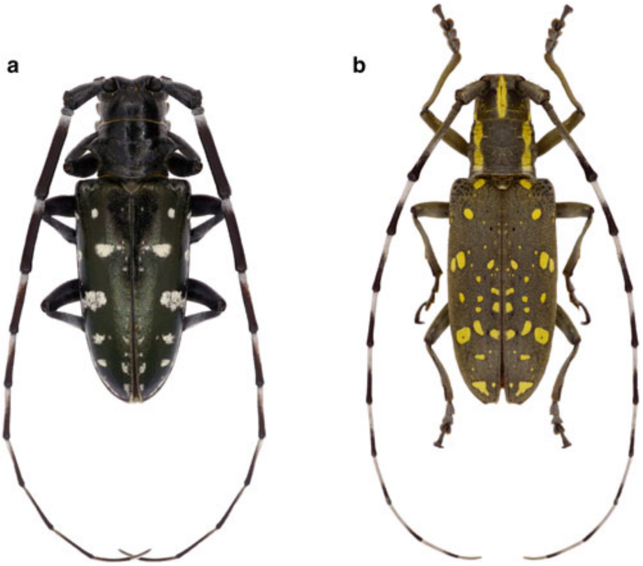

Fig. 11.4 Adults of *Anoplophora glabripennis* (**a**) and *Psacothea hilaris* (**b**) (Photos: P. Paolucci)

Possible Damage *A. glabripennis* may impact European broadleaf ecosystems both directly, killing trees and competing with native xylophagous species (Sauvard 2009a), and indirectly, causing losses due to the sanitation felling regimes adopted by the national authorities (MacLeod et al. 2002). Given that the primary introduction points are urban areas, a reduction in property prices and amenity value of street and parkland trees can be expected, causing a severe economic and social impact (MacLeod et al. 2002).

11.4.14 Anoplophora chinensis *(Förster)*

Biology and Ecology *A. chinensis* is a large (21–37 mm long) stout longhorn beetle characterized by shiny-black elytra marked with 10–12 white round spots (Sauvard 2009b). The long antennae are marked at the base with white or light blue (Sauvard 2009b). This species is highly polyphagous as it can attack over 100 species of broadleaf trees and shrubs (Sauvard 2009b). Immature larvae feed in the phloem-cambium region, whereas later instars larvae develop into the xylem (Sabbatini Peverieri and Roversi 2010). Eggs are laid by females in slits chewed at the base of host trees (Sauvard 2009b). Full development is achieved in 1 or 2 years depending on climate and egg laying date (Sauvard 2009b). This species can easily and unintentionally be moved by firewood, bonsai and fallen timber (Sauvard 2009b).

Possible Damage *A. chinensis* attacks both young and old healthy trees, and the galleries bored by the larvae cause structural weakness and disrupt the flow of water and nutrients, leading to the deterioration or death of the host tree (Sabbatini Peverieri and Roversi 2010). Larval tunnels also depreciate harvested wood (Sauvard 2009b). As for *A. glabripennis*, the impact of *A. chinensis* is expected to be greater in urban areas, which are considered as the primary points of entry (Sauvard 2009b). Killing trees in streets, as well as in private and public gardens, this beetle can have a severe social and economic impact (Sauvard 2009b).

11.4.15 Psacothea hilaris *(Pascoe)*

Biology and Ecology *P. hilaris* is a large (13–30 mm long, Fig. 11.4b) longhorn beetle that is easily recognizable for its black tegument covered by a green-greyish pubescence with yellow spots on the elytra and the abdomen, and yellow stripes on the pronotum (Lupi et al. 2013). It attacks plants belonging to the Moraceae family, in particular *Ficus* and *Morus* spp. (Lupi et al. 2013). Larvae first bore tunnels under the bark of trunks and branches of the host trees, and then complete the development in the xylem (Lupi et al. 2013). Adults feed on leaves and tender bark of smaller branches (Jucker et al. 2006). *P. hilaris* is considered as univoltine, although it has been recorded to have two generations per year or to complete the life cycle in 2 years depending on the time of egg laying and temperature (Lupi et al. 2013). Furthermore, this beetle could transport the nematode *Bursaphelenchus conicaudatus,* which is closely related to the quarantine pine wood nematode *B. xylophilus*, but its pathogenicity and economic importance remain unknown (Kanzaki and Kazuyoshi 2001).

Possible Damage Although data on the biology of this species in Europe is lacking, it is considered as a potential threat to *Morus* and *Ficus* trees growing in Mediterranean regions (Lupi et al. 2013). In particular, given the large production of figs around the Mediterranean Basin and the use of many *Ficus* spp. as ornamental trees across Europe, *P. hilaris* could become an economically important pest (Lupi et al. 2013).

11.5 Introduction Pathways

Although it is difficult to determine when wood-boring beetle invasions began, the link between this phenomenon and globalization is well recognized worldwide (Perrings et al. 2005; Meyerson and Mooney 2007; Hulme 2009). The technological advances reached by humans in the last decades have allowed organisms to pass the natural barriers which have ever limited their natural dispersal (Levine and D’Antonio 2003). Given the clear need to develop risk assessment methods as well as detection and mitigation strategies (Byers et al. 2002), a number of studies have been focused on introduction pathways of alien wood-boring beetles (Haack 2001, 2006; Work et al. 2005; Brockerhoff et al. 2006a; McCullough et al. 2006; Roques and Auger-Rozenberg 2006; Haack and Rabaglia 2013; Eschen et al. 2015), allowing to draw a picture of their arrival rate.

Wood-packaging materials, such as crating, dunnage and pallets, are recognized as the main pathway of introduction of alien wood-boring beetles (Haack 2001, 2006; Zahid et al. 2008; Colunga-Garcia et al. 2009; Haack and Rabaglia 2013; Rassati et al. 2015b). Given that these materials are always associated with international trade, and that during transport insects can find protection within the wood and escape detection at points of entry (Haack 2001; McCullough et al. 2006), they represent an optimal pathway for alien species introduction. In recognition of the threat posed by untreated wood-packaging materials, an international standard (ISPM 15) has been approved in 2002, constraining producers to treat wooden materials in order to kill pest organisms that reside in the wood (Haack and Petrice 2009). Although the rate of infested wood-packaging materials has decreased, living wood-boring beetles are still found in treated wood, indicating that the risk of biological invasions through wood pathway still exists (Haack et al. 2014).

The colonization of wood-packaging materials can occur either before or after treatments (Haack and Petrice 2009). The source material, represented by recently cut trees, resides at yard near sawmills a sufficient amount of time to be colonized by wood-boring beetles (Shore and McLean 1988). When the wood is turned into wood-packaging materials, beetles can be already present within the wood, especially as unnoticed early stages, such eggs or first-instar larvae (Cocquempot and Lindelöw 2010). At this point, given that the approved treatments are not completely able to kill all the insects (McCullough et al. 2007) and that some of them can be improperly applied (Haack and Petrice 2009), the development of insects can continue during transportation and adults can emerge weeks or months after the arrival of woody materials in a new country. The longhorn beetles *Anoplophora glabripennis* and *Psacothea hilaris,* for example, have been introduced to Mediterranean countries following this pathway (Cocquempot and Lindelöw 2010). Anyway, Haack and Petrice (2009) demonstrated that wood-boring beetles, especially bark and ambrosia beetles, can infest logs and wood-packaging materials also after treatment, especially when bark residuals are present.

A few accidental introductions are, however, linked to other introduction pathways, among which the importation of ornamental plants (McCullough et al. 2006; Liebhold et al. 2012). Two main kinds of ornamental plants are commonly imported: herbaceous plants for indoor use or destined for ornamental beddings, and woody ornamental plants, including bonsai (Liebhold et al. 2012). This has resulted in the arrival, for instance, of *Anoplophora chinensis* and *Callidiellum rufipenne* among longhorn beetles (Cocquempot 2007), *Xylosandrus morigerus* among ambrosia beetles (Kirkendall and Faccoli 2010), and *Hypocryphalus scabricollis* among bark beetles (Mifsud and Knížek 2009). Other longhorn beetles, instead, arrived within building furniture, such as *Chlorophorus annularis*, or via the importation of timber for pulp (such as *Phoracantha recurva* and *P. semipunctata*) (Cocquempot 2007).

Regardless the importation pathways, ports represent the first point of entry for alien wood-boring beetles in coastal areas, as they receive every week commodities and associated wood-packaging materials from foreign countries (Haack 2001, 2006; Brockerhoff et al. 2006a; Rassati et al. 2015a). In recent years, moreover, international cargo has been increasingly shipped in large containers, making the inspection process more difficult (Stanaway et al. 2001). Given the dark and the poor ventilation within containers, as well as the need to send commodities to their final destination on time and in suitable condition for sale, the possibilities for the inspectors to locate alien species have inevitably decreased (Stanaway et al. 2001; McCullough et al. 2006). Although the bulk of alien species are first intercepted in coastal areas, several wood-boring beetle invasions started from inland areas (Colunga-Garcia et al. 2013). In this regard, metropolitan and industrial areas experience the highest invasion pressure, representing the final destination of imported commodities (Colunga-Garcia et al. 2013). Furthermore, wood waste landfills have been identified as high-risk sites for alien species introduction (Rassati et al. 2015b). Wood-packaging materials associated with imported commodities, when not recyclable or reusable, are in fact discarded and sent to companies authorized to destroy the wood (Buehlmann et al. 2009), where they are left for longer periods than in ports. This allows beetles to complete life cycle, emerge and start the invasion process without being detected (Rassati et al. 2015b).

11.6 Establishment and Spread of Alien Wood-Boring Beetles in Mediterranean Countries: The Role of Native Forests and Human Activities

After introduction, alien species are challenged by several environmental and demographic stochastic forces that must be overcome to establish and spread (Liebhold and Tobin 2008). Establishment, in particular, represents a crucial phase as founder populations are usually small and consequently exposed to a greater risk of extinction (Liebhold and Tobin 2008). This is especially true for cerambycids and buprestids, as the number of individuals that survive transportation and escape detection at points of entry is usually low (Cocquempot 2007). Several factors, such as unsuitable climatic conditions at points of entry or Allee effects, may drive low-density populations towards extinction (Taylor and Hastings 2005; Liebhold and Tobin 2008; Brockerhoff et al. 2014). For this reason, a number of alien species fail the invasion process at this phase.

Following the experience of New Zealand, Canada and the USA, it is within the first 5–10 km zone around points of entry that first establishment of alien wood-boring beetles usually occurs (Bashford 2008; Rabaglia et al. 2008). These areas often consist of mosaics of different habitats, such as urban parks, green spaces, crop fields, or natural reserves, which can be more or less suitable for the reproduction of alien wood-boring beetles (Bashford 2008). Although there is still much debate on the effect of native and alien tree density, diversity and distribution on the invasion success of alien wood-boring species (Brockerhoff et al. 2006b; Colunga-Garcia et al. 2010), a recent study has demonstrated that a key role is played by the composition of forest stands located in the area surrounding ports (Rassati et al. 2015a). Given that the majority of alien species established in Mediterranean areas are generalist insects feeding on broadleaf trees, the presence of broadleaf-dominated forests rather than conifer-dominated ones can increase the possibilities of alien wood-boring beetle establishment (Rassati et al. 2015a). This process is, however, not influenced by the extent of the forest areas (Colunga-Garcia et al. 2009; Rassati et al. 2015a), with alien wood-boring beetles that can establish even in landscape with a very low amount of forests, such as urban areas. The latter are characterized by the presence of a large number of both native and alien trees and shrubs, located in parks, gardens and along streets, which can represent adequate hosts for the introduced alien species (Bashford 2008; Rassati et al. 2015a). In any case, if a species is able to establish a self-sustaining population, then it can start the next step of the invasion process, the spread.

The spread is estimated as an increase in range radius over time (Liebhold and Tobin 2008). This process can occur in two main forms: continuous spread or spread through long-distance dispersal. The continuous spread is the natural spread along a population front and it is strongly dependent on the flight ability of the alien species (Liebhold and Tobin 2008). The long-distance dispersal is instead usually driven by humans activities or passive dispersal (i.e. by wind), with species that are moved to disjoint sites located several kilometers from the original point of establishment (Piel et al. 2008; Hulme 2009; Colunga-Garcia et al. 2013). The most common scenario when considering wood-boring beetles is related to movement of wood and woody materials along roads, rails and canals towards the final destination of imported commodities, such as commercial and industrial areas (Colunga-Garcia et al. 2013; Rassati et al. 2015b). This explaines, for example, the presence of different populations of the same species in different and disjoined locations of the same country, as in the case of *A. glabripennis* in North East (Cornuda, Treviso) and central Italy (Fermo, Marche).

Both the establishment and spread of alien wood-boring beetles are strongly influenced by environmental, climatic and human-related variables (Marini et al. 2011). Their effect, however, can be different depending on the life history traits of alien species. This has been clearly demonstrated for the two main groups of scolytids, the bark and the ambrosia beetles (Marini et al. 2011). While the amount of import is a strong predictor of the number of established alien bark beetles, climate is the main factor influencing the establishment of alien ambrosia beetles (Marini et al. 2011). Although the latter study and similar others have been performed at the continental scale (Marini et al. 2011; Liebhold et al. 2013), similar effects might be found also at smaller spatial scale. Given that Mediterranean countries are characterized by the presence of a number of different habitats, it is reasonable to suppose that alien species which are strongly dependent on climatic variables (i.e. ambrosia beetles) will not be able to establish in forest stands located at high altitudes, where temperature might not be suitable for their development and that of their associated organisms (Lombardero et al. 2000; Hofstetter et al. 2006). These patterns are, however, still understudied and further research should be performed to gain insight into the mechanisms driving the invasion process at different spatial scales.

Finally, for certain species, establishment and spread in Mediterranean countries are strictly related to the presence of plantations of alien woody species (Sect. 11.7).

11.7 Role of Forest Plantations in Spread of Alien Wood-Boring Beetles

Tree plantations can facilitate the establishment of alien wood boring insects under two main circumstances, both of them existing in the Mediterranean Basin: (i) plantations of indigenous tree species becoming hosts of introduced exotic insect species; (ii) plantations of alien tree species followed more or less rapidly by insects from the trees' original areas. The first situation most often implies a host shift and thus concerns mainly polyphagous insect species. The second situation does not imply a host shift and mostly corresponds to monophagous or oligophagous alien insect species. In both cases, the low genetic diversity of plantations favors insect spread, especially if plantations occur over large areas. This favorable effect is, however, particularly efficient for insect species which have a narrow host range. The case of indigenous plantations invaded by an exotic polyphagous wood-boring species is illustrated by the presence of the pinhole ambrosia beetle *Megaplatypus mutatus* Chapuis (Platypodinae) on poplars in Central Italy. The invasions of *Eucalyptus* plantations by the longhorn wood-boring species of the *Phoracantha* genus perfectly illustrate the case of oligophagous insects following their host trees planted in new areas.

11.7.1 **Megaplatypus mutatus** ***Chapuis in Italy***

The first report on the presence in the Mediterranean Basin of that ambrosia beetle originating from Central and South America was in 2000, from a poplar plantation in Campania, Central Italy (Tremblay et al. 2000). After a rapid local development (450 km^2 between 2000 and 2007) (Allegro and Griffo 2008), the infestation is considered practically stabilized (Kirkendall and Faccoli 2010), although the infestation's boundary is reported to have extended on average by 5 km per year between 2008 and 2012 (Griffo et al. 2012). Even if stabilized, this situation represents a real threat for the Mediterranean Basin since *M. mutatus* is considered as a dangerous polyphagous pest for trees, being responsible for considerable damage in South America, especially in Argentina (Alfaro 2003; Giménez and Etiennot 2003; Marquina et al. 2006).

The insect usually has only one generation per year (Santoro 1965) and is xylomycetophagous. Contrary to most ambrosia beetle species which live on recently cut or dying trees, *M. mutatus* attacks standing and vigorous trees but only over 15 cm diameter (Etiennot et al. 1998; Casaubon and Fracassi 1999; Casaubon et al. 2002). The adult bores sinuous galleries where symbiotic fungi develop and serve as food for the first and second larval instars. In Argentina, the Ascomycete *Raffaellea santoroi* Von Arx has been identified in the beetle's galleries (Guerrero 1966). *M. mutatus* is able to develop on a wide range of broadleaved genera and species (Giménez and Etiennot 2003) of which many are present in the Mediterranean Basin.

In South America, it causes important damages on poplar and several other tree genera (Santoro 1962; Etiennot et al. 1998; Alfaro 2003; Giménez and Etiennot 2003; Marquina et al. 2006) and in Italy damage has been recorded on *Populus, Corylus, Malus, Pyrus, Castanea, Juglans, Prunus, Quercus* and *Eucalyptus* (Carella and Spigno 2002; OEPP/EPPO 2009). Consequently, although its extension is presently limited, *M. mutatus* needs to be carefully surveyed because of the risk it represents for a large diversity of tree species, especially for poplar plantations in the whole Mediterranean Basin.

No other adaptation of alien wood-boring beetle to indigenous plantations than that of *M. mutatus* on poplars has been reported in the Mediterranean Basin. However, a careful attention should be paid to the *Anoplophora* species already introduced in Italy and France. They are presently limited to urban trees (Herard et al. 2006, 2009) but their polyphagous habits could allow them to extend in indigenous plantations of hardwood trees, especially to poplar plantations where they would rapidly cause drastic damage, as already observed in China (Li and Wu 1993; Luo and Li 1999).

11.7.2 The Eucalyptus longhorn *Beetles*

Eucalyptus plantations presently exist in practically all countries of the Mediterranean Basin, where they are the most common plantations. Many species have been planted at least for experimental purpose to test their possibilities of local adaptation. For example in Morocco, not less than 150 species have been planted in various arboreta, of which 91 were still present in 1994 (Achhal El Kadmiri and Fechtal 1994). Finally the main species presently cultivated in plantations of the Mediterranean Basin are *Eucalyptus camaldulensis* Dehn., *E. gomphocephala* DC. and *E. globulus* Labill. In Morocco, the first two species account for 80 % of the *Eucalyptus* planted area (El Yousfi 1992). Although of minor importance in Australia, their country of origin where attacks concern damaged, stressed or newly felled trees, *Phoracantha semipunctata* (Fabricius) and *P. recurva* Newman have colonized all *Eucalyptus*-growing regions in the world after their accidental introductions with pulpwood. They are present all around the Mediterranean Sea (Cocquempot and Debreuil 2006). Table 11.3 summaries the history of their introduction or establishment in the Mediterranean Basin. Everywhere in the world and in the Mediterranean Basin, introduction of *P. semipunctata* largely preceded that of

Table 11.3 Year of first observation of *Phoracantha semipunctata* (*P. s.*) and *Phoracantha recurva* (*P. r.*) in various countries of the Mediterranean Basin

	Egypt	France	Israel	Italy	Morocco	Portugal	Spain	Tunisia	Turkey
P. s.	1950 (12)	1976[a] (5) 1986[b] (13)	1945 (4)	1969 (15)	1972 (6)	1980 (8)	1981 (8)	1962 (3)	1959 (1)
P. r.		2003 (13)	2001 (7)	1990 (11)	1994 (10)	2006 (9)	1998 (13)	1999 (2)	2002 (14)

References: (1) Acatay (1959), (2) Ben Jamâa et al. (2002), (3) Biliotti and Schoenenberger (1963), (4) Bytinski-Salz and Neumark (1952), (5) Cocquempot (2003), (6) Fraval and Haddan (1988), (7) Friedman et al. (2008), (8) Gil Sotres and Mansilla (1983), (9) Grosso-Silva (2007), (10) Haddan (personal communication), (11) Ighilesi et al. (2013), (12) Lepesme (1950), (13) Miquel (2008), (14) Özdikmen and Çaglar (2004), (15) Tassi (1969)

[a] Corsica

[b] Mainland; numbers indicate references (see footnote)

P. recurva, leading to competition between the two species. Both species have similar requirements and occupy the same ecological niche but in all cases, competition has turned into advantage for *P. recurva*. The reasons relate to effects of various factors. The egg parasitoid *Avetianella longoi* Siscaro (Encyrtidae), also accidentally introduced almost everywhere from Australia, prefers, for example, the eggs of *P. semipunctata* rather than those of *P. recurva* (Luhring et al. 2004) and the parasitoid eggs are encapsulated by *P. recurva* (Reed et al. 2007). Moreover, adult emergence occurs earlier and fecundity is higher in *P. recurva* (Bybee et al. 2004; Haddan and Lieutier 2005).

The biology of the insects is well documented in the Mediterranean Basin (Chararas 1969; Mendel 1985; Haddan et al. 1988; Fraval and Haddan 1989; Haddan 1992; Gonzales-Tirado 1992; Way et al. 1992; Maatouf et al. 2001; Dharhi and Ben Jamâa 2008). Both species lay between a dozen and more than 100 eggs (Fig. 11.5a), in bark crevices or under exfoliations of the outer bark. Larvae hatch 3–5 days later and, after some scraping on the bark external surface, they get through the bark and the phloem. They then bore galleries between the phloem and the sapwood (Fig. 11.5b, c), before entering into the sapwood. This penetration causes the stop of sap flow, generally leading to rapid tree death (Chararas 1969; Hanks et al. 1991). Everywhere, in absence of most of their natural enemies and facing *Eucalyptus* stands often in poor environmental conditions, they cause heavy damage, even on healthy trees, with significant tree mortality (Paine et al. 2011) including the Mediterranean Basin (Romano 2007; Inghilesi et al. 2013; Branco et al. 2015). For example, shortly after its introduction in Southern Spain, *P. semipunctata* caused economic losses over $ 9 million in 1983 and $ 7 million in 1984 for an area of 300 000 ha of *Eucalyptus* plantations (Gonzalez-Tirado 1986). Following introduction of *P. semipunctata* in Portugal at the same period, the annual cost of quarantine measures has been evaluated at $ 300,000, with abandonment of *Eucalyptus* plantations in marginal areas and land conversion (Kenis and Branco 2010). In Tunisia, after its introduction in 1962, *P. semipunctata* caused the death of 70–80 % of the trees in some regions in 1966 and 1967 (Dharhi, pers. comm.).

There are large variations in susceptibility to attacks among *Eucalyptus* species. For example, in a same Moroccan locality of the humid Mediterranean climate, the percentage of attacked trees was below 10 % for *E. camaldulensis*, *E. cladocalyx* F.v.M. and *E. sideroxylon* A. Cunn., while it was over 50 % for *E. gomphocephala* and *E. globulus* (El Yousfi 1992). In California, the survivorship of immature stages of *P. semipunctata* in field logs was significantly higher for *E. camaldulensis* and *E. cladocalyx* than for *E. tereticornis* Sm. (Hanks et al. 1993). Following artificial introductions in planted trees in Morocco, larval performances of *P. recurva* in the phloem were particularly high (more than 80 % larvae reaching sapwood surface) in *Eucalyptus citriodora* Hook., *E. falcata* Turcz., *E. maculata* Hook. and *E. occidentalis* Endl., and particularly low (less than 20 % larvae reaching the sapwood) in *Eucalyptus blackleyi* Maid., *E. camaldulensis*, *E. dealbata* A. Cunn. and *E. oleosa* F.v.M. (Haddan et al. 2010). In all Mediterranean regions, the main regulating factors of *Phoracantha* populations are host tree resistance, intraspecific competition and natural enemies, especially *A. longoi* (Paine et al. 2011). In the Mediterranean

Fig. 11.5 (**a**) Eggs of *Phoracantha semipunctata* with parasitoids; (**b**) *P. semipunctata* larvae; (**c**) Galleries of *P. semipunctata* larvae on the sapwood surface of a killed *Eucalyptus*; (**d**) Hypersensitive reaction induced by *P. semipunctata* larvae in the sapwood of *Eucalyptus citriodora.* (**a**) (Photo M. Haddan) (**b, c, d**) (Photos: F. Lieutier)

Basin, tree resistance appears to be due to bark characteristics, phloem thickness and sapwood hypersensitive reactions (Fig. 11.5d), and explains variations in beetle preference and attack success among tree species (Haddan et al. 2010; Paine et al. 2011). Water stressed trees are particularly susceptible, but both very low and high phloem water content have negative effects on the success of larval establishment, and can explain preference among individuals of a same tree species, as well as seasonal variations in attack success (Hanks et al. 1999; Haddan et al. 2010).

11.8 Survey and Early-Detection Protocols

Early-detection is recognized as the first step to increase the chance of eradication or control of alien wood-boring beetles, and consequently to reduce related costs and damage (Epanchin-Niell and Hastings 2010). Although the rate of infested wood-packaging materials has been reduced following the approval of ISPM 15, the risk of alien wood-boring beetle introduction is still present (Haack et al. 2014). In this context, a key role is played by inspectors at points of entry, who examine the imported commodities checking for the presence of the IPPC mark, which attests that the wood has been treated before its use in international trades, and other signs, such as entry holes or sawdust, indicating the presence of living insects within the wood (Haack 2006). However, considering the volume of commodities imported every day, the possibilities for inspectors to examine incoming wood-packaging materials is clearly limited (Haack 2001). In this regard, it has been estimated, for example, that only less than 2 % of the international cargo arriving in the USA is inspected every year (National Research Council 2002). Given that the greatest opportunities for eradication occur immediately after the insect introduction (Rabaglia et al. 2008), in the last years the USA (Rabaglia et al. 2008), Canada (Allen and Humble 2002), New Zealand (Brockerhoff et al. 2006c), and Italy (Rassati et al. 2014, 2015a) have implemented trapping and sampling strategies to enhance the detection of alien wood-boring beetles at ports of entry. Although different trap models exist for monitoring scolytids, cerambycids and buprestids (Augustin et al. 2012), the use of multi-funnel traps baited simultaneously with kairomones and pheromones (multi-lure traps), has been identified as the monitoring protocol most suitable for the interception of alien wood-boring beetles arriving in both coastal and inland areas of Mediterranean countries (Rassati et al. 2014, 2015b).

Given the limited resources that are usually available for surveillance programs, it is of utmost importance to concentrate the efforts in the most at risk sites (Epanchin-Niell et al. 2014). Recent studies suggested that the biggest ports and their surrounding broadleaf forests should be prioritized in order to enhance the early-detection in coastal areas (Rassati et al. 2015a), whereas wood-waste landfills have been identified as suitable sites for the interception of alien species in inland areas (Rassati et al. 2015b). In Italy, a such surveillance program allowed to intercept a number of species new to Mediterranean countries, among which the scolytids *A. rubricollis* (Faccoli et al. 2009) and *C. luteus* (Faccoli et al. 2012). Anyway, this approach provided also useful data on the geographical distribution of already established alien species, supporting regulatory controls and specific management programs. In 2013, for example, the scolytid *C. luteus*, which was reported only in Veneto and Friuli Venezia Giulia regions until 2012 (Faccoli et al. 2012), was trapped also in central and southern Italian regions, demonstrating how a such trapping program can also give information on the current distribution of alien species (Rassati et al. 2015b).

A second approach to improve the possibilities of alien wood-boring beetle early-detection considers the use of “sentinel trees” (Bashford 2008). These are locally important species that are planted in areas surrounding high-risk sites, such as ports (Wylie et al. 2008), or where the first detection of an alien species occurs. Such technique was used, for example, for monitoring the presence of the Asian longhorn beetles *A. glabripennis* in northern Italy (Herard et al. 2009) and can be especially useful when specific attractive lures are not available. Furthermore, Britton et al. (2010) suggested botanical gardens as sites that can provide advance warning for potential pests for every country represented in the tree collections. In 2009, for example, a large number of individuals of the alien scolytid *A. rubricollis* was found in the botanical garden of Padova (Faccoli et al. 2009), attesting the potential role that these sites can have in the early-detection of alien species.

11.9 Impact of Alien Wood-Boring Beetles on Native Ecosystems

Although the economic and ecological impacts of many alien species are minor, some of them can significantly affect the invaded environment (Kenis et al. 2009). From an ecological perspective, species that are able to kill living trees, such as *A. glabripennis*, *A. chinensis*, and some ambrosia beetles, can impact indigenous species by decreasing or increasing the distribution and abundance of certain plants, altering habitat and food supply, changing predation pressure and competing for food or space (Gandhi and Herms 2010). Looking at the communities of ambrosia beetles trapped at different locations in the USA and Italy, for example, it is possible to notice that alien species dominate ambrosia beetle communities in forested ecosystems (Miller et al. 2015; Rassati et al. 2015a). Although the effect of competition among ambrosia beetle species is still unknown (Miller et al. 2015), this trend may reflect the elimination of native species across forested lands. In any case, even less aggressive species, such as wood-boring beetles attacking only dead or dying trees, can modify the invaded natural habitats. Gandhi and Herms (2010) suggested, for example, that they can affect gap dynamics, as they generate canopy gaps that are different from those caused by gradual decline of canopy trees or abiotic disturbance events, or can alter the dynamics of snags and downed woody debris. Given that the ecological impacts of alien wood-boring beetles in Mediterranean countries is still unclear, future researches should be conducted in order to fill this gap of knowledge. Such information, in fact, are essential to develop effective management strategies and local monitoring programs (Kenis et al. 2007).

From an economic perspective, *A. glabripennis* and *A. chinensis* caused the most severe damage to urban trees in Mediterranean countries (Jucker and Lupi 2011). For the eradication of *A. chinensis* in Italy, for example, more than 18,000 plants have been removed and the cost of the eradication program has amounted to more than 12 million euros (Jucker and Lupi 2011). This has also led to a severe alteration of the landscape in many urban and suburban areas (Maspero et al. 2007). Among the other alien wood-boring beetles, the majority has not yet shown particular impacts on our environment (Jucker and Lupi 2011). Exceptions can be considered the pinehole borer *M. mutatus*, which caused serious damage on *Populus* spp. in Italy, mainly compromising the stability of plants, the scolytid *X. germanus*, which caused local damage to walnut plantations and apple orchards (Kirkendall and Faccoli 2010), and the longhorn beetles *P. recurva* and *P. semipunctata*, which caused economic losses in plantation of *Eucalyptus*. It is necessary to underline, however, that the real impact of several species is still unknown, and the risk related to their spread in the new environment is extremely high. The recently introduced scolytid *P. juglandis*, vector of the fungus *Geosmithia morbida* Kolařik, is the latest example (Montecchio and Faccoli 2014). This beetle-fungus symbiosis, responsible for the thousand cankers disease, has caused a widespread mortality of black walnut in the USA (Kolařík et al. 2011), and it is considered as a clear threat to both black and English walnut in Mediterranean countries (Montecchio and Faccoli 2014; Montecchio et al. 2014).

11.10 Biological Invasions and Climatic Change: A Global Challenge

Biological invasions and climate change are two key drivers affecting biodiversity worldwide (Vitousek 1994; Walther et al. 2009). These two elements are, however, not independent (Walther et al. 2009). There is increasing evidence that global warming has enabled alien species to expand into regions where previously they were not able to survive and reproduce (Walther et al. 2009). In particular, any increase in temperature or precipitation patterns can impact the possibilities of establishment of wood-boring beetles native to areas with a warm and wet climate, such as tropical countries (Kirkendall and Faccoli 2010). Among wood-boring beetles, ambrosia beetles are probably the most susceptible to changes in climatic conditions (Marini et al. 2011). The nutritional dependence that they have for their symbiotic fungi is recognized as one of the main limitations to their presence outside wet and warm regions (Kirkendall and Faccoli 2010; Marini et al. 2011). Although Mediterranean climate has been already demonstrated to be more suitable for alien ambrosia beetles than that of temperate regions (Kirkendall and Faccoli 2010), changes in either temperature or amount of rainfall could potentially render Mediterranean areas even more adapt to their establishment. Furthermore, such changes can reduce the thermal constraints limiting the presence of alien ambrosia species to lower altitudes, favoring insect development and winter survival in high elevation forests (Kirkendall and Faccoli 2010; Marini et al. 2011).

Climate change can also modify the impact that alien species may have in the invaded environment affecting resistance or resilience of native ecosystems (Walther et al. 2009). Changes in climate are, for example, linked to an increased frequency of extreme climatic events which are able to damage or kill trees (Kharin and Zwiers 2005). Stressed or dying plants are induced to emit a set of low molecular weight volatile compounds, such as ethanol, which are strongly attractive for secondary wood-boring beetles (Kelsey 2001), predisposing themselves to beetle attack. Furthermore, in recent years, normally secondary species have been increasingly observed to attack living trees, either as alien or in their native range (Kühnholz et al. 2003). This change of behavior can be explained partly by climate change (Kühnholz et al. 2003). Early flight of some ambrosia beetles, for example, might allow them to attack broadleaf hosts before budflush, when the tree capability to contrast attacks through induced resistance is at least weak (Kühnholz et al. 2003). Climate change, however, can also modify the activity of organisms associated with introduced alien species, enhancing, for example, the pathogenicity of some fungi (Kühnholz et al. 2003).

References

Acatay A (1959) *Phoracantha semipunctata* Fabr (Col. cerambycidae) in der Turkei. Ans Schadlingks 32:4–5

Achhal El Kadmiri A, Fechtal M (1994) Atlas des Eucalyptus du Maroc. Caisse Nationale de Crédit Agricole du Maroc, Rabat

Alfaro RI (2003) The 'grand forest borer' *Platypus mutatus* (= s*ulcatus*): an important pest of poplar culture in Argentina. A plan of action SAGPyA. Forestal 28:11–18

Alfaro RI, Humble LM, Gonzalez P et al (2007) The threat of the ambrosia beetle *Megaplatypus mutatus* (Chapuis) (=*Platypus mutatus* Chapuis) to world poplar resources. Forestry 80:471–479

Allegro G, Griffo R (2008) I rischi di diffusione di *Megaplatypus mutatus*. L'Informatore Agrario 13:73–76

Allen EA, Humble LM (2002) Nonindigenous species introduction: a threat to Canada's forests and forest economy. Can J Plant Pathol 24:103–110

Augustin S, Boonham N, De Kogel WJ et al (2012) A review of pest surveillance techniques for detecting quarantine pests in Europe. OEPP/EPPO Bull 42:515–551

Balachowsky A (1949) Coléoptères Scolytides. Faune de France 50:241–243

Bashford R (2008) The development of a port surrounds trapping system for the detection of exotic forest insect pests in Australia. In: Oteng-Amoako AA (ed) New advances and contribution to forestry research. InTech, Rijeka, pp 85–100

Beaver RA (1979) Host specificity of temperate and tropical animals. Nature 281:139–141

BenJamâa ML, Villemant C, Mnara S (2002) *Phoracantha recurva* Newman, 1840: nouveau ravageur des eucalyptyus en Tunisie (Coleoptera, Cerambycidae). Rev Fr Entomol NS 24:19–21

Biliotti E, Schoenenberger A (1963) Sur la presence in Tunisie de *Phoracantha semipunctata* Fabr (Coleóptera, Cerambycidae) ravageur de l'eucalyptus. Ann INRA Tunisie 35:97–110

Bouget C, Noblecourt T (2005) Short-term development of ambrosia and bark beetle assemblages following a windstorm in French broadleaved temperate forests. J Appl Entomol 129:300–310

Branco S, Videira N, Branco M et al (2015) A review of invasive alien species impacts on eucalypt stands and citrus orchards ecosystem services: towards an integrated management approach. J Environ Manage 149:17–26

Britton KO, White P, Kramer A et al (2010) A new approach to stopping the spread of invasive insects and pathogens: early detection and rapid response via a global network of sentinel plantings. N Z J For Sci 40:109–114

Brockerhoff EG, Bain J, Kimberley MO et al (2006a) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. Can J For Res 36:289–298

Brockerhoff EG, Liebhold AM, Jactel H (2006b) The ecology of forest insect invasions and advances in their management. Can J For Res 36:263–268

Brockerhoff EG, Jones DC, Kimberley MO et al (2006c) Nationwide survey for invasive wood-boring and bark beetles (Coleoptera) using traps with pheromones and kairomones. For Ecol Manage 228:234–240

Brockerhoff EG, Kimberley M, Liebhold AM et al (2014) Predicting how altering propagule pressure changes establishment rates of biological invaders across species pools. Ecology 95:594–601

Browne FG (1961) The biology of Malayan Scolytidae and Platypodidae. Malayan For Rec 22:1–255

Buehlmann U, Bumgardner M, Fluharty T (2009) Ban on landfilling of wooden pallets in North Carolina: an assessment of recycling and industry capacity. J Clean Prod 17:271–275

Bybee LF, Millar JG, Paine TD et al (2004) Seasonal development of *Phoracantha recurva* and *P. semipunctata* (Coleoptera: Cerambycidae) in Southern California. Environ Entomol 33:1232–1241

Byers JE, Reichard S, Randall JM et al (2002) Directing research to reduce the impacts of nonindigenous species. Conserv Biol 16:630–640

Bytinski-Salz H, Neumark S (1952) The *Eucalyptus* borer *(Phoracantha semipunctata* F.) in Israel. Trans. IXth international congress of entomology, Amsterdam 1:696–699

Carella D, Spigno P (2002) The xylophage *Platypus mutatus* (Coleoptera: Platypodidae) from poplar to fruit trees. Boll Lab Entomol Agr Filippo Silvestri 58:139–141

Casaubon E, Fracassi (1999) Comportment of clones of *Populus deltoides* confronted to the grand forest borer's attacks in the Parana Delta. Libro de resúmenes. XlX Reunión Argentina de Ecología, Tucumán

Casaubon E, Cueto G, Hodara K et al (2002) Interactions among site, plague and a trunk disease in a plantation of *Populus deltoides* cv Catfish-2 in the Low Delta of Parana River (Argentina) Investigacion Agraria. Sist y Recursos Forestales 11:29–38

Chararas C (1969) Biologie et écologie de *Phoracantha semipunctata* (Coléoptères, Cerambycidae, xylophage) ravageur des eucalyptus en Tunisie et méthodes de protection des peuplements. Ann Inst Rech For Tunisie 2:1–37

Cocquempot C (2003) L'expansion circumméditerranéenne de *Phoracantha recurva* (Newman, 1840) (Coleoptera, Cerambycidae). L'Entomologiste 59:209–214

Cocquempot C (2007) Alien longhorned beetles (Coleoptera; Cerambycidae): original interceptions and introductions in Europe, mainly in France, and notes about recently imported species. Redia 89:35–50

Cocquempot C, Debreuil M (2006) *Xylotrechus stebbingi* Gahan 1906 et *Phoracantha semipunctata* (Fabricius, 1775): historique de l'expansion française de deux envahisseurs (Coleoptera Cerambycidae). Rutilans 9:85–89

Cocquempot C, Lindelöw A (2010) Longhorn beetles (Coleoptera; Cerambycidae). BioRisk 4:193–218

Colunga-Garcia M, Haack RA, Magarey RA et al (2009) Freight transportation and the potential for invasions of exotic insects in urban and periurban forests of the United States. J Econ Entomol 102:237–246

Colunga-Garcia M, Haack RA, Magarey RA et al (2010) Modeling spatial establishment patterns of exotic insects in urban areas in relation to tree cover and propagule pressure. J Econ Entomol 103:108–118

Colunga-Garcia M, Haack RA, Magarey RD et al (2013) Understanding trade pathways to target biosecurity surveillance. NeoBiota 18:103–118

Coyle DR, Booth DC, Wallace MS (2005) Ambrosia beetle (Coleoptera: Scolytidae) species, flight, and attack on living Eastern cottonwood trees. J Econ Entomol 98:2049–2057

Dharhi S, Ben Jamâa ML (2008) Les insectes ravageurs des *Eucalyptus* en Tunisie. Actes 10ème journées scientifiques de l'INRGREF, La biodiversité dans les aires protégées, Hammamet, Tunisie, 11–13 Nov

El Yousfi M (1992) Possibilités de lutte préventive contre *Phoracantha semipunctata* (F.) par la sélection d'espèces d'*Eucalyptus*. Bol San Veg Plagas 18:735–743

Epanchin-Niell RS, Hastings A (2010) Controlling established invaders: integrating economics and spread dynamics to determine optimal management. Ecol Let 13:528–541

Epanchin-Niell R, Brockerhoff EG, Kean JM et al (2014) Designing cost-efficient surveillance for early detection and control of multiple biological invaders. Ecol Appl 24:1258–1274

Eschen R, Roques A, Santini A (2015) Taxonomic dissimilarity in patterns of interception and establishment of alien arthropods, nematodes and pathogens affecting woody plants in Europe. Divers Distrib 21:36–45

Etiennot AE, Giménez RA, Bascialli ME (1998) *Platypus sulcatus* Chapuis (Coloeptera: Platypodidae): distribution of the attack according to the Diameter at the Height of Chest (DAP) of *Populus deltoides* and efficiency evaluation of herbicides. I Simposio Argentino Canadiense de Protección Forestal, Buenos Aires

Faccoli M (1998) The North American *Gnathotrichus materiarius* (Fitch) (Coleoptera Scolytidae): an ambrosia beetle new to Italy. Redia 81:151–154

Faccoli M (2010a) *Xylosandrus crassiusculus* (Motschulsky, 1866) – Granulate Ambrosia Beetle (Coleoptera, Curculionidae, Scolytinae). In: Roques A, Kenis M, Lees D et al (eds) Alien terrestrial arthropods of Europe. Pensoft Publishers, Sofia, pp 900–901

Faccoli M (2010b) *Xylosandrus germanus* (Blandford, 1894) (= *Xyleborus germanus*) – Black stem borer (Coleoptera, Curculionidae, Scolytinae). In: Roques A, Kenis M, Lees D et al (eds) Alien terrestrial arthropods of Europe. Pensoft Publishers, Sofia, pp 902–903

Faccoli M, Frigimelica G, Mori N et al (2009) First record of *Ambrosiodmus* (Hopkins, 1915) (Coleoptera: Curculionidae, Scolytinae) in Europe. Zootaxa 2303:57–60

Faccoli M, Simonato M, Petrucco Toffolo E (2012) First record of *Cyrtogenius* Strohmeyer in Europe, with a key to the European genera of the tribe Dryocoetini (Coleoptera: Curculionidae, Scolytinae). Zootaxa 3423:27–35

Faccoli M, Favaro R, Smith MT et al (2015) Life history of the Asian longhorn beetle *Anoplophora glabripennis* (Coleoptera Cerambycidae) in southern Europe. Agr For Entomol 17:188–196

Fraval A, Haddan M (1988) *Platystasius transversus* (Hym. Platygasteridae) parasitoïde oophage de *Phoracantha semipunctata* (Col., Cerambycidae), au Maroc. Entomophaga 33:381–382

Fraval A, Haddan M (1989) *Phoracantha*. Dissertation, Doc Sci Tech, Actes Editions, Rabat

Friedman ALL, Rittner O, Chikatunov VI (2008) Five new invasive species of longhorn beetles (Coleoptera: Cerambycidae) in Israel. Phytoparasitica 36:242–246

Gandhi KJK, Herms DA (2010) Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol Inv 12:389–405

Garonna AP, Dole SA, Saracino A et al (2012) First record of the black twig borer *Xylosandrus compactus* (Eichhoff) (Coleoptera: Curculionidae, Scolytinae) from Europe. Zootaxa 3251:64–68

Garonna AP, Nugnes F, Espinosa B et al (2013) *Aromia bungii*, a new Asian worm found in Campania. Informatore Agrario 69:60–62

Gil Sotres MC, Mansilla JP (1983) Detección en España de *Phoracantha semipunctata* Fb. Sobre *Eucalyptus globulus* Labill. Anales INI A. Serie Forestal 7:171–192

Giménez RA, Etiennot AE (2003) Host range of *Platypus mutatus* (Chapuis, 1865) (Coleoptera; Platypodidae). Entomotropica 18:89–94

Gómez D, Martinez G, Beaver RG (2012) First record of *Cyrtogenius luteus* (Blandford) (Coleoptera; Curculionidae; Scolytinae) in the Americas and its distribution in Uruguay. Coleopt Bull 66:362–364

Gonzales-Tirado L (1986) *Phoracantha semipunctata* F. damages caused in the province of Huelva during 1983 and 1984. Bol San Veg Plagas 12:147–162

Gonzales-Tirado L (1992) Estudio sobre integrales térmicas de *Phoracantha semipunctata* Fab (Col : Cerambycidae), insecto perforador del género *Eucalyptus*, en Huelva (Espana). Bol San Veg Plagas 18:529–545

Grégoire JC, Piel F, De Proft M et al (2001) Spatial distribution of ambrosia beetle catches: a possibly useful knowledge to improve mass-trapping. Integr Pest Manag Rev 6:237–242

Griffo R, Pesapane G, Funes H et al (2012) Diffusione e controllo di platipo in Campania. L'Informatore Agrario 31:66–67

Grosso-Silva JM (2007) New and interesting beetle (Coleoptera) records from Portugal (5th note). Bol Soc Entomol Aragon 40:471–472

Guerrero RT (1966) Una nueva especies de hongo imperfecto asociado con el *Platypus sulcatus* Chapuis. Rev Inv Agrop 8:97–103

Haack RA (2001) Intercepted Scolytidae (Coleoptera) at US ports of entry: 1985–2000. Integr Pest Manag Rev 6:253–282

Haack RA (2006) Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can J For Res 36:269–288

Haack RA, Petrice T (2009) Bark- and wood-borer colonization of logs and lumber after heat treatment to ISPM 15 specifications: the role of residual bark. J Econ Entomol 102:1075–1084

Haack RA, Rabaglia RJ (2013) Exotic bark and ambrosia beetles in the USA: potential and current invaders. In: Peña JE (ed) Potential invasive pests of agricultural crops. CAB International, Wallingford, pp 48–74

Haack RA, Britton KO, Brockerhoff EG et al (2014) Effectiveness of the International Phytosanitary Standard ISPM No.15 on reducing wood borer infestation rates in wood packaging material entering the United States. PLoS One 9, e96611

Haddan M (1992) Variations saisinnières de la durée du cycle biologique de *Phoracantha semipunctata* (F.) (Coléoptère, Cerambycidae) ravageur xylophage des eucalyptus au Maroc. Ann Rech For Maroc 26:100–102

Haddan F, Lieutier F (2005) Comparison of the length of the life cycle, population abundance and fecundity of *Phoracantha semipunctata* Fabricius and *P. recurva* Newman, two xylophagous pests of Eucalyptus in Morocco. In: Lieutier F, Gaioule D (eds) Entomological research in Mediterranean forest ecosystems. INRA Editions, Versailles, pp 209–217

Haddan M, Fraval A, Thevenot M (1988) Ennemis naturels de *Phoracantha semimpunctata* F (Col: Cerambycidae), ravageur xylophage des eucalyptus au Maroc. Bull Instr Sci 12:167–170

Haddan M, Sauvard D, Lieutier F (2010) Tree factors in relation to success of artificial introductions of *Phoracantha recurva* larvae in various Eucalyptus species in Morocco. Redia 93:19–30

Hanks LM, Paine TD, Millar JG (1991) Mechanisms of resistance in *Eucalyptus* against larvae of the eucalyptus longhorn borer (Coleoptera: Cerambycidae). Environ Entomol 20:1583–1588

Hanks LM, Paine TD, Millar JG (1993) Host species and larval performances in the wood-boring beetle *Phoracantha semipunctata* F. Oecologia 95:22–29

Hanks LM, Paine TD, Millar JG et al (1999) Water relation of host trees and resistance to the phloem boring beetle *Phoracantha semipunctata* F (Coleoptera: Cerambycidae). Oecologia 119:400–407

Henin JM, Versteirt V (2004) Abundance and distribution of *Xylosandrus germanus* (Blandford 1894) (Coleoptera Scolytidae) in Belgium: new observations and an attempt to outline its range. J Pest Sci 77:57–63

Herard F, Ciampitti M, Maspero M et al (2006) *Anoplophora* species in Europe: infestations and management processes. OEPP/EPPO Bull 36:470–474

Herard F, Maspero M, Ramualde N et al (2009) *Anoplophora glabripennis* – eradication programme in Italy. OEPP/EPPO Bull 39:146–152

Hofstetter RW, Cronin JT, Klepzig KD et al (2006) Antagonisms, mutualisms and commensalisms affect outbreak dynamics of the southern pine beetle. Oecologia 147:679–691

Hulme PE (2009) Trade, transport and trouble: managing invasive species in an era of globalization. J Appl Ecol 46:10–18

Inghilesi AF, Cervo R, Pennacchio F et al (2013) Alien insects on *Eucalyptus* spp.: an Australian biocenosis in Tuscany. Redia 96:21–26

Jordal BH, Beaver RA, Kirkendall LR (2001) Breaking taboos in the tropics: incest promotes colonization by wood-boring beetles. Glob Ecol Biogeogr 10:345–357

Jucker C, Lupi D (2011) Exotic insects in Italy: an overview on their environmental impact. In: Pujol JL (ed) The importance of biological interactions in the study of biodiversity. InTech, Rijeka, pp 51–74

Jucker C, Tantardini A, Colombo M (2006) First record of *Psacothea hilaris* (Pascoe) in Europe (Coleoptera Cerambycidae Lamiinae Lamiini). Boll Zool Agr e Bachicoltura, Serie II 38:187–191

Kanzaki N, Kazuyoshi F (2001) Life history of *Bursaphelenchus conicaudatus* (Nematoda: Aphelenchoididae) in relation to the yellow-spotted longicorn beetle, *Psacothea hilaris* (Coleoptera: Cerambycidae). Nematology 3:473–479

Kelsey RG (2001) Chemical indicators of stress in trees : their ecological significance and implication for forestry in eastern Oregon and Washington. Northwest Sci 75:70–76

Kenis M, Branco M (2010) Impact of alien terrestrial arthropods in Europe, Chapter 5. BioRisk 4:51–71

Kenis M, Rabitsch W, Auger-Rozenberg MA et al (2007) How can alien species inventories and interception data help us prevent insect invasions? Bull Entomol Res 97:489–502

Kenis M, Auger-Rozenberg M, Roques A et al (2009) Ecological effects of invasive alien insects. Biol Invas 11:21–45

Kharin VV, Zwiers FW (2005) Estimating extremes in transient climate change simulations. J Climate 18:1156–1173

Kirkendall LR (1983) The evolution of mating systems in bark and ambrosia beetles (Coleoptera: Scolytidae and Platypodidae). Zool J Linn Soc 77:293–352

Kirkendall LR (1993) Ecology and evolution of biased sex ratios in bark and ambrosia beetles (Scolytidae). In: Wrensch DL, Ebbert MA (eds) Evolution and diversity of sex ratio: insects and mites. Chapman and Hall, New York, pp 235–345

Kirkendall LR, Faccoli M (2010) Bark beetles and pinhole borers (Curculionidae, Scolytinae, Platypodinae) alien to Europe. ZooKeys 56:227–251

Kirkendall LR, Jordal BH (2006) The bark and ambrosia beetles (Curculionidae, Scolytinae) of Cocos Island, Costa Rica and the role of mating systems in island zoogeography. Biol J Linn Soc 89:729–743

Kolařík M, Freeland E, Utley C et al (2011) *Geosmithia morbida* sp. nov., a new phytopathogenic species living in symbiosis with the walnut twig beetle (*Pityophthorus juglandis*) on *Juglans* in USA. Mycologia 103:325–332

Kovacs KF, Haight RG, McCullough DG et al (2010) Cost of potential emerald ash borer damage in U.S. communities, 2009–2019. Ecol Econ 69:569–578

Kühnholz S, Borden JH, Uzunovic A (2003) Secondary ambrosia beetles in apparently healthy trees: adaptations, potential causes and suggested research. Integr Pest Manag Rev 6:209–219

Lepesme P (1950) Sur la dispersion par l'homme et l'acclimatation de quelques «Phoracanthini». Longicornia 1:576–579

Levine JM, D'Antonio CM (2003) Forecasting biological invasions with increasing international trade. Conserv Biol 17:322–326

Li W, Wu C (1993) Integrated management of longhorn beetles damaging poplar trees. China Forestry Press, Beijing (in Chinese)

Liebhold AM, Tobin PC (2008) Population ecology of insect invasions and their management. Annu Rev Entomol 53:387–408

Liebhold AM, Brockerhoff EG, Garrett LJ et al (2012) Live plant imports: the major pathways for forest insect and pathogen invasions of the US. Front Ecol Environ 10:135–143

Liebhold AM, McCullough DG, Blackburn LM et al (2013) A highly aggregated geographical distribution of forest invasions in the USA. Divers Distrib 19:1208–1216

Lombardero MJ, Ayres MP, Ayres BD et al (2000) Cold tolerance of four species of bark beetle (Coleoptera: Scolytidae) in North America. Environ Entomol 29:421–432

Luhring KA, Millar JG, Paine TD et al (2004) Ovipositional preferences and progeny development of the egg parasitoid *Avetianella longoi*: factors mediating replacement of one species by a congener in a shared habitat. Biol Control 30:382–391

Luo Y, Li J (1999) Strategy on applied technology and basic studies on poplar longhorned beetle management. J Beijing For Univ 21:6–21 (in Chinese)

Lupi D, Jucker C, Colombo M (2013) Distribution and biology of the yellow-spotted longicorn beetle *Psacothea hilaris hilaris* (Pascoe) in Italy. OEPP/EPPO Bull 43:316–322

Maatouf N, Haddan M, Atay Kadiri Z (2001) Etude des potentialités reproductives de *Platystasius transversus* Th (Hym.: Platygasteridae), parasite oophage de *Phoracantha* spp (Col.: Cerambycidae). Ann Rech For Maroc 34:128–136

MacLeod A, Evans HF, Baker RHA (2002) An analysis of pest risk from an Asian longhorn beetle (*Anoplophora glabripennis*) to hardwood trees in the European community. Crop Protec 21:635–645

Marini L, Haack RA, Rabaglia RJ et al (2011) Exploring associations between international trade and environmental factors with establishment patterns of alien Scolytinae. Biol Invas 13:2275–2288

Marquina JL, Marlats R, Núñez Cresto N (2006) Cloning susceptibility of poplar (*Populus sp.*) when attacked by *Platypus mutatus in* Buenos Aires, Argentina. Bosque 27:92–97

Maspero M, Jucker C, Colombo M (2007) First record of *Anoplophora glabripennis* (Motschulsky) (Coleoptera, Cermabycidae Lamiinae Lamiini) in Italy. Boll Zool agr e Bachicoltura, Serie II 39:161–164

Mattson W, Vanhanen H, Veteli T et al (2007) Few immigrant phytophagous insects on woody plants in Europe: legacy of the European crucible? Biol Invas 9:957–974

McCullough DG, Work TT, Cavey JF et al (2006) Interceptions of nonindigenous plant pests at US ports of entry and border crossings over a 17-year period. Biol Invas 8:611–630

McCullough DG, Poland TM, Cappaert D et al (2007) Effects of chipping, grinding, and heat on survival of emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae), in chips. J Econ Entomol 100:1304–1315

Mendel Z (1985) Seasonal development of the *Eucalyptus* borer *Phoracantha semipunctata* in Israel. Phytoparasitica 13:58–93

Meyerson LA, Mooney HA (2007) Invasive alien species in an era of globalization. Front Ecol Environ 5:199–208

Mifsud D, Knížek M (2009) The bark beetles (Coleoptera; Scolytidae) of the Maltese Islands (Central Mediterranean). Bull Entomol Soc Malta 2:25–52

Miller DR, Doods KJ, Hoebeke ER et al (2015) Variation in effects of conophthorin on catches of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) in ethanol-baited traps in the United States. J Econ Entomol 108:183–191

Miquel ME (2008) The presence of *Phoracantha recurva* (Newman) (Coleoptera: Cerambycidae) in France and how to differentiate it from *P. semipunctata*. Br J Entomol Nat Hist 21:193–194

Montecchio L, Faccoli M (2014) First record of thousand cankers disease *Geosmithia morbida* and walnut twig beetle *Pityophthorus juglandis* on *Juglans nigra* in Europe. Plant Dis 98:696

Montecchio L, Fanchin G, Simonato M et al (2014) First record of thousand cankers disease fungal pathogen *Geosmithia morbida* and walnut twig beetle *Pityophthorus juglandis* on *Juglans regia* in Europe. Plant Dis 98:1445

Moraal LG (2010) *Phloeosinus rudis* Blandford, Japanese Thuja Bark Beetle (Coleoptera, Curculionidae, Scolytinae). In: Roques A, Kenis M, Lees D et al (eds) Alien terrestrial arthropods of Europe. Pensoft Publishers, Sofia, pp 898–899

National Research Council (2002) Predicting invasions of nonindigenous plants and plant pests. National Academy Press, Washington, DC

Newton L, Fowler G (2009) Pathway assessment: *Geosmithia* sp. and *Pityophthorus juglandis* Blackman movement from the western into the eastern United States. U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Washington, DC

Ngoan ND, Wilkinson RC, Short DE et al (1976) Biology of an introduced ambrosia beetle, *Xylosandrus compactus*, in Florida. Ann Entomol Soc Am 69:872–876

Nowak DJ, Pasek JE, Sequeira RA et al (2001) Potential effect of *Anoplophora glabripennis* (Coleoptera; Cerambycidae) on urban trees in the United States. J Econ Entomol 94:116–122

OEPP/EPPO (2009) *Megaplatypus mutatus*. OEPP/EPPO Bull 39:55–58

Oliver BJ, Mannion CM (2001) Ambrosia beetle (Coleoptera: Scolytidae) species attacking chestnut and captured in ethanol-baited traps in middle Tennessee. Environ Entomol 30:909–918

Özdikmen H, Çaglar Ü (2004) Contribution to the knowledge of longhorned beetles (Coleoptera, Cerambycidae) from Turkey Subfamilies Prioninae, Lepturinae, Spondylidinae and Cerambycinae. J Ent Res Soc 6:39–69

Paine TD, Steinbauer MJ, Lawson SA (2011) Native and exotic pests of *Eucalyptus* : a worldwide perspective. Annu Rev Entomol 56:181–201

Pennacchio F, Roversi PF, Francardi V et al (2003) *Xylosandrus crassiusculus* (Motschulsky) a bark beetle new to Europe (Coleoptera Scolytidae). Redia 86:77–80

Pennacchio F, Faggi M, Gatti E et al (2004) First record of *Phloeotribus liminaris* (Harris) from Europe (Coleoptera Scolytidae). Redia 87:85–89

Pennacchio F, Santini L, Francardi V (2012) Bioecological notes on *Xylosandrus compactus* (Eichhoff) (Coleoptera Curculionidae Scolytinae), a species recently recorded into Italy. Redia 95:67–77

Perrings C, Dehnen-Schmutz K, Touza J et al (2005) How to manage biological invasions under globalization. Trends Ecol Evol 20:212–215

Piel F, Gilbert M, De Cannière C et al (2008) Coniferous round wood imports from Russia and Baltic countries to Belgium. A pathway analysis for assessing risks of exotic pest insect introductions. Divers Distrib 14:318–328

Rabaglia RJ, Duerr D, Acciavatti RE et al (2008) Early detection and rapid response for non-native bark and ambrosia beetles. USDA For Serv, Forest Health Protection, Washington, DC

Rassati D, Petrucco Toffolo E, Roques A et al (2014) Trapping wood-boring beetles in Italian ports: a pilot study. J Pest Sci 87:61–69

Rassati D, Faccoli M, Petrucco Toffolo E et al (2015a) Improving the early detection of alien wood-boring beetes in ports and surrounding forests. J Appl Ecol 52:50–58

Rassati D, Faccoli M, Marini L et al (2015b) Exploring the role of wood-waste landfills in early-detection of non-native wood boring beetles. J Pest Sci 88:563–572

Reed DA, Luhring KA, Stafford CA et al (2007) Host defensive response against an egg parasitoid involves cellular encapsulation and melanization. Biol Control 41:214–222

Rexrode CO (1982) Bionomics of the peach bark beetle *Phloeotribus liminaris* in black cherry. J Georgia Entomol Soc 17:388–398

Roberts H (1977) Observations on the biology of some tropical rain forest Scolytidae (Coleoptera) from Fiji. II, Subfamily Ipinae – tribe Xyleborini. J Nat Hist 11:251–272

Romano M (2007) Nuovi dati sulla presenza in Sicilia di *Phoracantha recurva* Newman, 1840 (Coleoptera Cerambycidae). Nat Sicil 31:241–247

Roques A, Auger-Rozenberg MA (2006) Tentative analysis of the interceptions of non-indigenous organisms in Europe during 1995–2004. OEPP/EPPO Bull 36:490–496

Roques A, Rabitsch W, Rasplus JY et al (2009) Alien terrestrial invertebrates of Europe. In: Nentwig W, Hulme P, Pysek P, Vila M (eds) Handbook of alien species in Europe. Springer, Dordrecht, pp 63–79

Sabbatini Peverieri G, Roversi PF (2010) Feeding and oviposition of *Anoplophora chinensis* on ornamental and forest trees. Phytoparasitica 38:421–428

Santoro FH (1962) Basis for manual control of *Platypus sulcatus*. Rev Inv Forest 3:17–23

Santoro FH (1965) Description of five larval stages and of the pupal stage of *Platypus sulcatus* Chapuis (Coleoptera: Platypodidae). IDIA Suplemento Forestal 2:49–57

Sauvard D (2009a) *Anoplophora glabripennis* (Motschulsky), Asian longhorned beetles (Cerambycidae, Coleoptera). In: Roques A, Kenis M, Lees D et al (eds) Alien terrestrial arthropods of Europe. Pensoft Publishers, Sofia, pp 874–875

Sauvard D (2009b) *Anoplophora chinensis* (Förster), citrus longhorned beetle (Cerambycidae, Coleoptera). In: Roques A, Kenis M, Lees D et al (eds) Alien terrestrial arthropods of Europe. Pensoft Publishers, Sofia, pp 872–873

Sauvard D, Branco M, Lakatos F et al (2010) Weevils and bark beetles (Coleoptera, Curculionidae), Chapter 8.2. In: Roques A, Kenis M, Lees D et al (eds) Alien terrestrial arthropods of Europe. Pensoft Publishers, Sofia, pp 219–266

Shore TL, McLean JA (1988) The use of mark – recapture to evaluate a pheromone-based mass trapping program for ambrosia beetles in a sawmill. Can J For Res 18:1113–1117

Stanaway MA, Zalucki MP, Gillespies PIS et al (2001) Pest risk assessment of insects in sea cargo containers. Austral J Entomol 40:180–192

Tassi F (1969) Un longicorne australiano per la prima volta in Italia (Col. Cerambycidae). Boll Ass Romana Entomol 24:3

Taylor CM, Hastings A (2005) Allee effects in biological invasions. Ecol Lett 8:895–908

Tremblay E, Espinosa B, Mancini D et al (2000) Un coleottero provaniente dal Sudamerica minaccia i pioppi. L'informatore Agrario 48:89–90

Vitousek PM (1994) Beyond global warming: ecology and global change. Ecology 75:1862–1876

Walther GR, Roques A, Hulme PE et al (2009) Alien species in a warmer world: risks and opportunities. Trends Ecol Evol 24:686–693

Way MJ, Cammel EL, Paiva MR (1992) Studies on egg predation by ants (Hymenoptera: Formicidae) especially on eucalyptus borer *Phoracantha semipunctata* (Coleoptera: Cerambycidae) in Portugal. Bull Entomol Res 82:425–432

Weber BC, McPherson JE (1983) Life history of the ambrosia beetle *Xylosandrus germanus* (Coleoptera: Scolytidae). Ann Entomol Soc Am 76:455–462

Wermelinger B (2004) Ecology and management of the spruce bark beetle *Ips typographu*s – a review of recent research. For Ecol Manage 202:67–82

Wood SL (1982) The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Nat Mem 6:1–1359

Work TT, McCullough DG, Cavey JF et al (2005) Arrival rate of nonindigenous insect species into the United States through foreign trade. Biol Invas 7:323–332

Wylie FR, Griffiths M, King J (2008) Development of hazard site surveillance programs for forest invasive species: a case study from Brisbane, Australia. Austral For 71:229–235

Yan SP, Huang HY, Wang JB (2001) The occurrence of chestnut beetle and its control. South China Fruits 30:48

Zahid MI, Grgurinovic CA, Walsh DJ (2008) Quarantine risks associated with solid wood packaging materials receiving ISPM-15 treatments. Aust For 71:287–293

Chapter 12
The Pine Wood Nematode and Its Local Vectors in the Mediterranean Basin

Pedro Naves, Luis Bonifácio, and Edmundo de Sousa

Abstract The pine wood nematode *Bursaphelenchus xylophilus* is the causal agent of pine wilt disease, being one of the most important threats to conifer forests in the EU. This exotic nematode was detected in Southern Portugal in 1999, and has since been introduced into neighbouring Spain. In Iberia, the nematode affects mainly maritime pine, *Pinus pinaster*, but also black pine *Pinus nigra*, being its single vector the pine sawyer *Monochamus galloprovincialis*. In general, the entire Mediterranean basin presents a high risk to pine wilt disease, due to favourable climatic environments with prolonged periods of hot and dry conditions, the existence of forests with susceptible pine species such as maritime, black and scots pine, and the presence of multiple potential vectors of native species of the *Monochamus* genus, sharing similar biologies and life-histories. Besides *M. galloprovincialis*, special attention should be given to *Monochamus sutor*, a similar species with widespread distribution in Europe, and already found to be a key-vector of the related native nematode, *Bursaphelenchus mucronatus*. This chapter summarises the latest research on the ecology of European *Monochamus* and their interaction with *Bursaphelenchus* nematodes, with a natural emphasis on the PWN's vector, *M. galloprovincialis*. Also discussed are the options available to manage and control this tree health problem, which is currently responsible for significant pine mortality in Iberia's affected regions, and constitutes an immediate threat to pine ecosystems all over Europe, but particularly in the Mediterranean basin.

12.1 Introduction

Introduced alien species are a major component of global trade and environmental changes, resulting in a significant loss in the economic value, biological diversity and function of invaded ecosystems (e.g., Pimentel et al. 2001). In Europe, numerous alien species have been introduced over the last 200 years, becoming

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successfully established over large areas of the old continent (Hulme 2007). Terrestrial invertebrates represent one of the most numerous groups of introduced organisms, with over 1500 established exotic species in Europe (Roques et al. 2009). Although only 12 % of these aliens have become established in woodlands and forests, they can cause serious sanitary problems, and include bark beetles, phytophagous scales, leafhoppers and seed and cynipid gall-makers, among others (Roques et al. 2009). One of the exotic organisms affecting European forests is the pine wood nematode (PWN) *Bursaphelenchus xylophilus* (Steiner and Buhrer 1934) Nickle, the causal agent of pine wilt disease (PWD). This devastating micro-organism affects conifers, mainly pines, and is considered one of the most important threats to forests in the EU (Webster and Mota 2008) and one of the 100 most invasive alien species in Europe (Roques 2009). It is classified as a harmful organism to plants and plant products by the EU (Directive 2000/29, EEC), and an A2 type quarantine pest by the European and Mediterranean Plant Protection Organization (EPPO 2013).

Although native to North America, the PWN has been widely dispersed by human activity, and was accidentally introduced into Japan in the early 1900s, with devastating effects on native pines (Mamiya 1984, 1988). It was subsequently introduced into other East Asian countries, namely China (Cheng et al. 1986), Taiwan (Tzean and Tang 1985) and South Korea (La et al. 1999), with similar impacts. In 1979, it was also reported from wilted maritime pines, *Pinus pinaster* Aiton, on the Landes region in south-west France (Baujard et al. 1979), but subsequent studies found mixed characteristics of *B. xylophilus* and a closely related species, *Bursaphelenchus mucronatus* Mamya and Enda (de Guiran and Boulbria 1986). In 1999, *B. xylophilus* was confirmed to be established in Europe, being detected in dead maritime pines in Southern Portugal (Mota et al. 1999).

The detection of the exotic nematode in Europe prompted large-scale containment and control measures in and around the infested area, including felling and destruction of symptomatic pines and the establishment of a surrounding 20 km radius buffer zone, adjusted over the years according to the detection of new focus of the disease. In 2007, following EU Plant Health commission indication, all coniferous hosts were eliminated within a clear cut belt 3 km wide and covering over 130,000 ha, to prevent further spread (Rodrigues 2008). Nevertheless, and despite these efforts, in 2008/2009 new infestations were detected approximately 200 km northward from the original demarcated area, and the PWN is now found in many counties of Southern and Central Portugal. Subsequently, the PWN was detected in 2009 in Madeira Island (Fonseca et al. 2012) and also in neighbouring Spain, with outbreaks reported in 2008 and 2010 (Abelleira et al. 2011; Robertson et al. 2011).

In addition to the nematode and the susceptible conifer host, pine wilt disease requires the presence of an additional organism, an insect vector. The vector is necessary to carry the nematode from the dead infested host to a new healthy one within the forest, and the most important ones are cerambycid beetles of the genus *Monochamus*, commonly referred to as sawyer beetles (Kobayashi et al. 1984; Linit 1988, 1990; Kishi 1995). In Europe, the nematode's sole vector is the pine sawyer *Monochamus galloprovincialis* (Olivier) (Sousa et al. 2001, 2011b).

Wilt disease is undoubtedly one of the most serious threats to European pine forests (Webster and Mota 2008; Tomiczek and Hoyer-Tomiczek 2008; Roques 2009), and the Mediterranean basin presents a particularly high risk due to the occurrence of favourable climatic conditions for the nematode's development, the existence of extensive forests of various susceptible pine species, and the presence of multiple potential vectors. In fact, a major question for European forestry is whether other native *Monochamus* species can be effective vectors of *B. xylophilus*, and this has greatly increased the importance devoted to this genus and resulted in recent new research into the ecology of these insects and their interaction with *Bursaphelenchus* nematodes, with a natural emphasis on the PWN's sole vector, *M. galloprovincialis*.

12.2 The Pine Wood Nematode

The Genus *Bursaphelenchus* comprises around 110–120 known species (Futai 2013), many of which have been described during the last years, and with most species being fungal feeders transmitted to dead or dying trees during oviposition by insect vectors (Ryss et al. 2005; Hunt 2008). In Europe 28 conifer-inhabiting species occur (Braasch 2001), including the introduced pine wood nematode. First described in the United States as "the timber nematode" *Aphelenchoides xylophilus* by Steiner and Buhrer in 1934, the species was later transferred to the genus *Bursaphelenchus* by Nickle in 1970. Two years later, Mamiya and Kiyohara (1972) described *Bursaphelenchus lignicolus* in Japan, which was synonyzed with *B. xylophilus* by Nickle et al. (1981).

The PWN is a microscopic organism, with around 1 mm long, and can be separated from other species of the genus by the existence of a distinct vulval flap and a rounded tail terminus in the majority of the females and by the characteristic shape of the male spicules (Mamiya 1984; Braasch 2001; Penas et al. 2007). The life cycle can be extremely fast, and under favourable temperatures above 20 °C *B. xylophilus* can develop from egg to adult within just 4 or 5 days (Ishibashi and Kondo 1977; Mamiya 1984), with development requiring a minimum ambient temperature of 9.5 °C (Mamiya 1975; Aikawa 2008). Each female lays between 80 and 150 eggs during a 28-day oviposition period (Mamiya 1975; Kishi 1995). There are four juvenile instars and the adult stage (Ishibashi and Kondo 1977; Mamiya 1984). The larval development can follow either a reproductive or a dispersal pathway. The first two instars (designated as J_1 and J_2) are common to both pathways; if the conditions in the wood are favourable, the nematode continues to develop through the reproductive pathway, passing through the third and fourth juvenile instars (designated as J_3 and J_4) and moulting to the reproductive adult (Mamiya 1984). Under unfavourable conditions (low moisture, decayed wood, adverse temperatures), the nematode switches to the dispersal pathway, with the third and fourth instars designated as J_{III} and J_{IV} (Warren and Linit 1993). The J_{III} dispersal juveniles are a specialized resistance form, able to survive for long periods under unfavourable conditions, and is therefore the dominant stage during winter (Mamiya 1984). In spring, the juveniles aggregate around the pupal chambers of the insect vector and moult into J_{IV}, a non-feeding instar also known as dauer juveniles (Mamiya 1983). This non-feeding instar is morphologically and physiologically distinct from other instars and is very resistant to adverse ambient conditions, which allows it to invade an insect vector and survive until it contacts with a new suitable host plant (Wingfield and Blanchette 1983; Kobayashi et al. 1984; Mamiya 1984; Linit 1990).

Once introduced into a healthy tree, *B. xylophilus* assumes a phytophagous phase and starts feeding and reproducing in the new host. The exact mechanisms of how the nematode kills its host are still debatable (Futai 2013), although apparently it diffuses through the resin canals and feeds on living parenchyma and epithelial cells, causing a rapid reduction and resulting on the complete cessation of the resin flow. The destruction of cells leads to a runaway embolism of the tracheids, decreasing in the water potential, causing the abrupt cavitation in the whole xylem area and the appearance of the first wilting symptoms on the canopy, before the tree's death (Dropkin et al. 1981; Malek and Appleby 1984; Kuroda 1991).

Within a few weeks, a widespread fungal contamination of the dead wood occurs (Fig. 12.1), and the PWN switches to its mycetophagous phase which allows it to feed on this new and abundant food resource (Mamiya 1983, 1984). Although *B. xylophilus* can feed on several wood-inhabiting fungi, the blue-stain fungi of the genus *Ophiostoma* and *Ceratocystis* are clearly preferred (Maehara 2008). These fungi are transported and inoculated into the host by the phloeophagous bark and

Fig. 12.1 Detail of *Pinus pinaster* wood with blue-stain fungi, a valuable food resource for the mycetophagous phase of *Bursaphelenchus xylophilus*

wood-boring insects attracted to the decaying pines, and help weaken the tree and make it more suitable for colonization and development of the offspring (e.g., Kirisits 2004; Lieutier et al. 2009; Jankowiak 2013). Although bark beetles are the main vectors of blue-stain fungi, *Monochamus* adults can also carry spores between hosts, as it has been found for *Monochamus urussovi* (Fischer von Waldheim) in Russia (Jacobs et al. 2000), and *M. galloprovincialis* (Jankowiak and Rossa 2007; Jankowiak et al. 2007) and *Monochamus sutor* (L.) (Jankowiak 2010) in Poland.

To detect the PWN in the wood it is necessary to collect samples to analyse in the laboratory. Nematodes are extracted from the wood by keeping small pieces in water for 48 h, forcing them to leave into the aqueous medium where they can be sieved with a fine mesh, in order to be extracted and identified. The use of morphological identification keys allows for the identification of the PWN to species level (Tarjan and Baéza-Aragon 1982; Ryss et al. 2005; Gu et al. 2011; EPPO 2013; Sarniguet et al. 2013), although this can be difficulted by the presence of similar species cohabiting with *B. xylophilus* in the wilt-affected trees, either of the *Bursaphelenchus* genus or of other genera (Penas et al. 2004), and therefore the use of molecular tools may be required (Hoyer et al. 1998; Burgermeister et al. 2005, 2009; Castagnone et al. 2005; François et al. 2007; Gu et al. 2011; Aikawa et al 2013). Moreover, recent developments have been made on a reverse transcription loop-mediated isothermal amplification (RT-LAMP) kit, which allows to detect the PWN in wood samples and clarifies whether it originates from live or dead individuals, being more sensitive, faster and less dependent on expensive laboratory equipment than classical PCR methods (Leal et al. 2015).

12.3 The Hosts

Pines (*Pinus* spp.) are the most important hosts of the PWN worldwide (Dwinell 1997), although it has also been found in conifers of the genera *Cedrus, Larix* and *Picea* (Wingfield et al. 1982). In its native North America the PWD appears to be confined largely to stressed exotic pines, especially *Pinus sylvestris* L. in the eastern United States. Most native pines appear to be resistant (Dropkin et al. 1981; Burnes et al. 1985; Dwinell 1985). In eastern Asia, the introduced pathogen causes significant mortality to native red pine (*Pinus densiflora* Sieb. and Zucc.) and black pine, *Pinus thunbergii* Parl. (Mamiya 1983, 1984, 1988; Kobayashi 1988; Kishi 1995). In Europe, until now the main host is maritime pine, *P. pinaster* (Mota et al. 1999; Rodrigues 2008; Sousa et al. 2011b), although recently it has also been found killing *Pinus nigra* Arnold in Central Portugal (Inácio et al. 2015). Other pines inhabiting Europe are also thought to be susceptible to the PWN, including the widespread scots pine *P. sylvestris* (Futai and Furuno 1979; Evans et al. 1996; Fielding and Evans 1996; Daub 2008). Inversely, a few native pines may be resistant or tolerant to wilt disease, namely *Pinus halepensis* Mill. and *Pinus pinea* L., which have never been found affected by PWD in Portugal, even in locations with heavy incidence of this pathogen for several years (Sousa et al. 2011b).

After infestation by the PWN, susceptible trees stop oleoresin exudation, decrease sap flow and begin to show external wilting symptoms within a month (Takeuchi 2008; Bonifácio and Sousa 2011), although these symptoms are not specific to *B. xylophilus* infestation, and other biotic and abiotic agents can cause similar decline and wilting on adult pines (Rodrigues 2008; Sousa et al. 2011b). Although variable, the whole process of tree dying takes 3–6 weeks in the United States (Malek and Appleby 1984), while in Japan, it extends for 5–8 weeks or more (Mamiya 1984). In Portugal, studies made in adult *P. pinaster* forests found that the oleoresin flow ceases in less than 1 month, and the first visual wilting symptoms on the canopy appear 4–8 weeks later (Bonifácio and Sousa 2011) (Fig. 12.2). In North America and Japan it has been reported that infested trees may remain asymptomatic and express wilt only several months or even years after the nematode's infestation (Bergdahl and Halik 1998; Futai 2003; Takeuchi 2008). In Portugal, late infections can result on wilting symptoms only in the following spring, but trees

Fig. 12.2 Maritime pine (*Pinus pinaster*) tree killed by the pine wood nematode in coastal Alentejo, Portugal. Wilted and dead trees are preferred breeding hosts for *Monochamus* spp. and bark-beetles (Scolitinae)

infested with *B. xylophilus* and remaining asymptomatic for consecutive years have not been yet recorded (Bonifácio and Sousa 2011).

Besides host susceptibility, environmental factors such as ambient temperatures and water deficit modify the vulnerability and expression of wilt disease on trees, and condition its intensification and spread (Enda 1976; Mamiya 1984; Rutherford and Webster 1987). Ambient temperature is a crucial factor conditioning the risk of wilt disease, and only in locations where the mean air temperatures exceeds 20 °C for prolonged periods will susceptible hosts experience epidemic wilting, which can be aggravated if a dry season occurs simultaneously (Rutherford and Webster 1987; Rutherford et al. 1990; Evans et al. 2008). In Japan, the greatest damage is observed in locations with low rainfall and temperatures above 25 °C for 2 months (Takeshita et al. 1975). Such conditions are common in Southern Europe during the summer months, resulting in highest risk of wilt expression for the Mediterranean basin. Furthermore, the beginning of the dry season is a crucial parameter for the evolution of wilting in infested trees, according to an evapo-transpiration model recently developed by the EU-funded project REPHRAME and which simulates pine wilt using a range of environmental and tree host parameters (Evans et al. 2008; Gruffudd et al. 2013).

In Central and Northern Europe a different pattern may be expected, with the lower ambient temperatures and higher water soil content eventually deterring the impact of wilt disease (Evans et al. 2008; Pukkala et al. 2014), although future climate changes may deteriorate this scenario (Pérez et al. 2008; Sturrock 2012; Pukkala et al. 2014). Nevertheless, even in the absence of direct mortality, the simple presence of this quarantine nematode in the forests would still lead to serious economic impacts, due to loss of export markets and the necessity to disinfest wood destined for exportation (Robinet et al. 2011).

Besides the existence of favourable climatic conditions and the presence of suitable conifer hosts, the risk for Europe in general and the Mediterranean basin in particular is further aggravated by the presence of effective and potential insect vectors, these being native species of the *Monochamus* genus.

12.4 The Vectors

The insect vector is a fundamental component of wilt disease, and only in its presence can the nematode leave a dead host and colonize new and healthy pines. This association is obligatory for the nematode but facultative for the insect; *B. xylophilus* needs the insect to be dispersed but the insect is perfectly able to survive in the nematode's absence.

Worldwide, cerambycid beetles of the *Monochamus* genus are the most important vectors of the PWN, with seven species found to be effective vectors in field and laboratory observations and a few more reported as nematode carriers (Evans et al. 1996; Akbulut and Stamps 2012). In North America the most important vector is *Monochamus carolinensis* (Olivier) (Linit 1987, 1988), while in South-east Asia

Monochamus alternatus Hope has this role (Mamiya and Enda 1972; Kobayashi et al. 1984; Mamiya 1984; Kishi 1995). In Europe, the sole vector is *M. galloprovincialis* (Sousa et al. 2001; Penas et al. 2006), this being the only species of its genus found in the Iberian locations where the PWN occurs.

The *M. galloprovincialis* – *B. xylophilus* association established after the nematode was introduced in to Portugal has been the subject of several studies over the years. These confirm that the stimuli regulating this interaction are extremely effective and consistent, regardless of the *Monochamus* species involved. In Europe, Asia and North America, the most important aspects of the nematode-vector interaction (namely the association of the nematode with the insect's immature stages and the transmission to new hosts) are surprisingly similar for *M. galloprovincialis*, *M. alternatus* and *M. carolinensis.* This similarity across species in their association with the nematodes is one of the most interesting aspects of wilt disease worldwide (Akbulut and Stamps 2012).

Insect Infestation For the three main vectors, the nematodes inside the wood begin to aggregate around the insect's pupal chambers in early spring, in response to the moulting of the *Monochamus* larvae to pupae and adults (Mamiya 1972; Linit 1988; Naves et al. 2006a). Using the fungi filaments which cover the interior of the pupal chamber (Aikawa 2008), the nematodes eventually contact with the unsclerotised teneral adult beetle a few days before it emerges, and enter the spiracles of the thoracic segments. Studies made with recently-emerged *M. galloprovincialis* found nematodes to be present on all body segments, although with much higher abundance in the thoracic spiracles, contrasting with very low numbers on the antennae, legs, head and elytra (Naves et al. 2006a).

The infestation rates and number of nematodes transported by the adult *Monochamus* will vary according to diverse biotic and abiotic factors, including the ambient temperature and the water content of the wood, with extremely dry or saturated wood resulting in insects carrying fewer nematodes (Mamiya 1984; Togashi 1989; Fukushige 1990; Warren and Linit 1992). Wood moisture is crucial as it regulates the abundance and diversity of fungi, which are the main food source of *B. xylophilus* during its mycophagous phase and have a direct effect on the its abundance (Wingfield and Blanchette 1983; Fukushige 1990; Warren et al. 1995; Maehara and Futai 1996, 1997).

Infestation rates of vector insects show a wide variation, ranging from 13 % to 54 % or even higher for *M. galloprovincialis* sampled in Portugal, although it is also common to find insects emerging from *B. xylophilus*-infested wood carrying no nematodes (Sousa et al. 2001, 2002). The mean number of nematodes (nematode load) is also quite variable between individual insects, with most *M. galloprovincialis* carrying only a few hundred or a few thousand nematodes (Sousa et al. 2001), although higher values can occur and a maximum of approximately 72,000 *B. xylophilus* was found for one insect (Sousa et al. 2002). Likewise, for *M. alternatus* and *M. carolinensis* means of a few thousand nematodes are usually reported (Linit et al. 1983; Malek and Appleby 1984; Kim et al. 2009), with a maximum record of 289,000 nematodes for a single *M. alternatus* (Kobayashi et al. 1984), although such high number is exceptional. Apparently, low nematode loads have no negative effect on the vector insect, while high loads can reduce the flight capacity of adults (Humphry and Linit 1989; Akbulut and Linit 1999) and the fecundity of females (Arakawa and Togashi 2004). Moreover, very high nematode loads of several thousand individuals have been found to slightly decrease the longevity of *M. alternatus* (Togashi and Sekizuka 1982; Togashi 1985; Kishi 1995), although this particular aspect of the nematode-vector interaction has not yet been studied for *M. galloprovincialis*.

The size of the beetles is important, as there is a positive correlation between the insect's dimension and their nematode load, with larger insects carrying more nematodes (Linit et al. 1983; Humphry and Linit 1989). The sex of the vector does not affect the nematode load (Linit et al. 1983; Wingfield 1983; Wingfield and Blanchette 1983; Sousa et al. 2001).

Transmission to Tree Another important aspect which does not vary significantly between the most important *Monochamus* vectors in the three continents is the inoculation of *B. xylophilus* into a new tree host. Inoculation can occur by two pathways: (i) the maturation feeding; and (ii) the oviposition activity of the adult beetles (Linit 1988; Kishi 1995). Both are well documented for the vectors of North America and Asia, and have also been studied in Portugal for *M. galloprovincialis* (Naves et al. 2007a, b).

Transmission by maturation feeding occurs when adult *Monochamus* feed on the tender bark of stems or shoots after emergence, which can be made on the same species of host where they developed as larvae (Linsley 1959; Hanks 1999) or on different hosts (Naves et al. 2006b). It is during this period of feeding on healthy conifer trees, which extends for the entire life span of the beetle, that J_{IV} nematodes leave the insect's spiracles and move to the abdominal tip of the body, entering the host through the feeding wounds (Kobayashi et al. 1984). Studies made with *M. galloprovincialis* under laboratory conditions found that all infested beetles transmitted the nematodes to pine branches during several consecutive weeks, independently of sex or longevity (Naves et al. 2007a). Nematode transmission was more frequent from the second to the sixth week after emergence, decreasing subsequently in a pattern which is surprisingly similar to what has been described for other vectors such as *M. alternatus* (Togashi and Sekizuka 1982; Togashi 1985; Kishi 1995; Kim et al. 2009) and *Monochamus saltuarius* (Gebler) (Kim et al. 2009).

Transmission by maturation feeding is especially important in regions where the PWN was introduced, like Europe (Naves et al. 2007a) and Asia (Kishi 1995; Li et al. 2007), due to the presence of nematode-susceptible pines. In North America, most of the native pines are resistant to the nematode and do not experience wilt even if the beetles feed on them, and therefore the most important pathway for transmission is through the oviposition (Wingfield and Blanchette 1983; Linit 1989). In this pathway the female insect chooses dead or weakened trees (or recently-cut wood) to lay its eggs, and while excavating the bark with the mandibles the nematodes leave its body and enter the host through the egg-pit wounds (Wingfield and

Blanchette 1983; Linit 1989). Although unfrequently, *M. galloprovincialis* can also transmit the PWN through oviposition, even if only 37 % of the pines with eggs became infested with *B. xylophilus* and with low nematode numbers (Naves et al. 2007b). These results confirm that infestation of wood by the vector's oviposition is a secondary component of the pine wilt disease epidemiology in both Europe and Eastern Asia (Kishi 1995), although it allows *B. xylophilus* populations to be maintained in the forests without killing living pines.

Relation with Other Nematodes European *Monochamus* can carry other species of *Bursaphelenchus*, namely *B. mucronatus*, a widespread nematode found in North America, Asia and Europe (Tomminen et al. 1989; Kulinich et al. 1994). Although it can also be found in the Mediterranean region, *B. mucronatus* is apparently more common in the North and Centre of the continent (Schroeder and Magnusson 1992; Braasch 2001). Its main local vectors are *M. galloprovincialis* (Tomminen et al. 1989; Palmisano et al. 1994; Meyer 2002; Vincent et al. 2008b) and *M. sutor* (Tomminen et al. 1989; Schroeder and Magnusson 1992; Braasch et al. 1999; Abelleira et al. 2015). Despite the two nematode species being morphologically and biologically very similar, an important difference is that *B. Mucronatus* is usually considered to be non-pathogenic to healthy adult pines, unlike *B. xylophilus* (Mamiya and Enda 1979; Cheng et al. 2009).

The interaction between the two species was studied under controlled conditions, and it was found that *B. xylophilus* was competitively dominant over *B. mucronatus* on growth rates and on its ability to board the vector *M. galloprovincialis* (Vincent et al. 2008a). Similar results were described by Cheng et al. (2009) and Niu et al. (2013), who found a higher phenotypic plasticity of reproductive traits in *B. xylophilus* resulting in competitive advantage against *B. mucronatus*, and concluded the exotic invasive nematode could eventually exclude the native one from its original niche in European pine forests.

Overall, experience from Portugal confirms that new functional nematode-vector associations can be established whenever susceptible conifer hosts and vector insects coexist, as in Europe. European *Monochamus* share similar life history patterns, biological characteristics and comparable interactions with their hosts, suggesting they can eventually be effective vectors of *B. xylophilus* (Evans et al. 1996; Hoyer-Tomiczek and Tomiczek 2005; Akbulut and Stamps 2012), if the nematode further spreads from Iberia.

12.5 Biology and Ecology of European *Monochamus*

12.5.1 Species Diversity and Geographic Distribution

The genus *Monochamus* belongs to the subfamily Lamiinae within the coleopteran Cerambycidae (Dillon and Dillon 1941; Hellrigl 1971; Cherepanov 1990). It is composed of more than 100 species, distributed mainly in the Northern hemisphere and Central Africa where the diversity is highest and a few species are important pests of coffee and cocoa (Hellrigl 1971; Schoeman et al. 1998; Hillocks et al. 1999; Hillocks 2001). In Western and Central Europe, four species occur exclusively associated with conifers: *M. galloprovincialis*, *M. sutor*, *Monochamus sartor* (Fabricius) and *M. saltuarius*. Another member of the genus, *Monochamus impluviatus* (Motschulsky), is found in Europe only in the Ural mountains of Russia (Cherepanov 1990), while *Monochamus urussovi* was considered a valid species for many years but has been revised as a subspecies of *M. sartor,* and is now classified as *M. sartor urussovi* (Cesari et al. 2005; Wallin et al. 2013).

The European species have widespread distributions in the continent, although they are absent from some large Islands such as Britain (Twinn and Harding 1999) and Cyprus (Hellrigl 1971). *Monochamus galloprovincialis* is undoubtedly the most abundant species in southern Europe and the Mediterranean basin, being common in Turkey, Greece, Italy, France, Spain and Portugal (Francardi and Pennacchio 1996; Vives 2000; Brustel et al. 2002; González et al. 2007; Koutroumpa 2007). Furthermore, it is also the only species of its genus found in Northern Africa, namely in Morocco, Algeria and Tunisia (Villiers 1946; Kerris and Guerroudj 1991; Mejri et al. 2014). Outside Europe and Africa, its wide range extends into Russia, Iraq, Kazakhstan, Kyrgyzstan and Mongolia (Hellrigl 1971; Cherepanov 1990; Danilevskaya et al. 2009; Danilevsky 2012; Özdikmen and Ali 2012). Also widespread, *M. sutor* is found from Scandinavia (where it is the most abundant species) to the Alps and Pyrenees, its only location in the Iberian Peninsula (Hellrigl 1971; Vives 2000; González et al. 2007; Wallin et al. 2013). Further East, it can be found in Russia, Northern Caucasus, Kazakhstan, Northern Mongolia, Northern China, Korea and Japan (Hellrigl 1971; Cherepanov 1990; Chu et al. 1990; Cesari et al. 2005).

The remaining *Monochamus* species have smaller European ranges, and are, in general, rare or absent from the Mediterranean basin. *Monochamus sartor* is an exclusively European species, found in Central and Eastern Europe, from the Southern Alps of France, Italy, Switzerland, Germany and Austria into Scandinavia in the North, and from Eastern France in the West into Ukraine in the East (Hellrigl 1971; Meyer 2002; Cesari et al. 2005; Halbig 2013). *Monochamus saltuarius* is adapted to mountain forests of Central, Eastern and Northern Europe, extending from Finland through the taiga zone of Russia into Kazakhstan, Northern Mongolia, Northern China, Korea and Japan (Hellrigl 1971; Cherepanov 1990; Danilevskaya et al. 2009). Being mainly an Asian species, *M. impluviatus* occurs in Northern Mongolia, Northeast China, North Korea and Northern Russia, from the Pacific coast to the Ural Mountains, this being its only location in Europe (Cherepanov 1990).

European *Monochamus* are medium-sized insects, with a body length (without antennae) of 13–19 mm for *M. saltuarius* (the smaller species) and 18–37 mm for *M. sartor*, the largest. The head and pronotum have a grey or brownish hairy pubescence, and the pronotum has a lateral pair of conically extended tubercles. The elytra have several irregular, faint, bronze or gold colored markings, which vary between individuals. Despite their size, the discrete and cryptic nature of the adult beetles and their camouflage coloration makes direct observation of adults in the field difficult, even in locations with high population densities. The two sexes can be easily distinguished by the coloration and size of the antennae, as adult females have smaller antennae with a band of white strips while males have proportionally bigger antennae and entirely black. In general, females are bigger than males (Hellrigl 1971; Wallin et al. 2013).

Because European *Monochamus* have similar morphological features, the different species can be difficult to identify (Fig. 12.3). Among the most distinctive characters are the size, body pubescence, coloration and punctuation, shape and size of reproductive organs, number of larval instars and host preference. Adult *M. galloprovincialis* and *M. sutor*, for instance, are morphologically very similar, and can only be distinguished by variations on the pubescence of the elytra and scutellum and the shape of the male's reproductive organ (Tomminen and Leppänen 1991; Koutroumpa et al. 2013; Wallin et al. 2013). The widespread range of all species generates extreme variability in the morphological features, leading to subdivisions into multiple subspecies. For *M. galloprovincialis* two subspecies are described for Western and Central Europe, namely *M. galloprovincialis galloprovincialis* and *M. galloprovincialis pistor* (Hellrigl 1971; Koutroumpa et al. 2013). These can be sepa-

Fig. 12.3 *Monochamus* species from Europe. From *left* to *right*, first row: *M. galloprovincialis*, *M. sutor*. Second row: *M. sartor*, *M. saltuarius*. All insects are females, except for *M. saltuarius*

rated by morphological characters (different coloration of the antennae and legs), geographic distribution (low-altitudes of Mediterranean and South-Western Europe versus mountains of Central-Eastern Europe) and host preference (*P. pinaster* and *P. halepensis* versus *P. sylvestris* and *P. nigra*) (Hellrigl 1971; Koutroumpa et al. 2013). Nevertheless, recent morphological, chromosomal and mitochondrial studies failed to validate the existence of these sub-species, with the occurrence of multiple intermediate morphological forms and significant gene flow among the widespread populations (Cesari et al. 2005; Sláma 2006; Koutroumpa 2007; Koutroumpa et al. 2013; Wallin et al. 2013).

12.5.2 Hosts

European *Monochamus* are associated with conifers (Hellrigl 1971) (Table 12.1). In its vast distribution range, *M. galloprovincialis* develops in spruce and pines, mainly *P. nigra*, *P. halepensis* and *P. pinaster*, although *P. sylvestris* is undoubtedly its most common host in Central and Northern Europe and Russia (Hellrigl 1971; Agafonov and Kuklin 1979; Cherepanov 1990; Evans et al. 1996; Meyer 2002; Koutroumpa et al. 2009). Even Portuguese populations of *M. galloprovincialis* emerging from *P. pinaster* preferred to feed and lay eggs on scots pine on studies made under laboratory conditions (Naves et al. 2006b). Akbulut (2009) described a higher reproductive performance when eggs were laid in *P. sylvestris,* which suggests a strong ecological association between the insect and this particular host. Other hosts include *Pinus brutia* Ten., *Pinus peuce* Griseb. and *Pinus mugo* Turra (Hellrigl 1971; Georgiev et al. 2005a, b; Behalová 2006; Alexandrov and Andonovski 2011; Koutroumpa et al. 2013), and, very occasionally, *P. pinea*, *Pinus radiata* D. Don. and *Picea orientalis* (L.) Link (Yüksel 1998; Cesari et al. 2005; Mejri et al. 2014).

In all of these hosts the most limiting factor for colonization is the bark thickness, due to limitations of the females to dig the egg pits and insert their relatively small ovipositor in bark with more than 5 mm (Francardi and Pennacchio 1996; Francardi et al. 1998; Bonifácio 2009). In general, pine sections with bark suitable for *M. galloprovincialis* egg-laying are the upper trunk and branches (Hellrigl 1971; Markalas 1997; Ehnström and Axelsson 2002; Foit 2010), corresponding to a preferred diameter between 2 and 20 cm for adult maritime pines (Pennacchio et al. 2006; Bonifácio 2009).

While *M. galloprovincialis* colonizes almost exclusively pines, the remaining European members of the genus prefer other conifers such as spruces (*Picea*), firs (*Abies*) and larch (*Larix*) (Hellrigl 1971; Jurc et al. 2012b). In Central and Northern Europe, *M. sutor* can be found in the tree tops and lower stems of spruce and pines (Hellrigl 1971; Ehnström and Axelsson 2002; Halbig 2013). The main host of *M. sartor* in mountainous areas of central Europe is old spruce of large diameters, whereas pines and firs are rarely colonized (Hellrigl 1971; Halbig 2013). Similar habits are found for *M. saltuarius*, which prefers to colonize the thinner branches and tops of old spruce trees, its main host (Hellrigl 1971; Izhevsky et al. 2005;

Table 12.1 Most important hosts of *Monochamus* spp. in European and North African countries

	Pinus					Picea		Abies		
	P. pinaster	*P. halepensis*	*P. nigra*	*P. sylvestris*	*Pinus sp.*	*P. abies*	*Picea sp.*	*Abies alba*	*Abies sp.*	Larix sp.
M. galloprovincialis	CR FR IT PT SP TU	AG BH CR FR GR IT MR PT SL SP TU	AL CZ FR HU IT GR PT SL TR	AU BU BY CZ FR GE HU FI IT LT NR PL RO RS SK SL SP SV SZ TR	BE EN GO LA MC MD NL SB UK	AU BU FI FR GE GR IT LA NR PL RS SK SL SV	BE BY CZ EN HU LT NL RO SB SZ UK	BU PL	BY HU LA LT NE RO SK UK	RS
M. sutor	SP	CR SL	FR GR RS	AU BU FR LT NR SP SV	HU LA NL RO RS SB SK	AU BU BY FR GE GR NR PL RS SK SL SV	BE BY CZ EN HU LA LT RO UK	PL	EN LA LT RO UK	BH RS
M. sartor			SL	AU	EN HU RO RS SK UK	AU BU FI GE IT LA RS SK SV	BE BY CZ EN HU LT NL RO SB UK	PL	BY EN HU LA LT RO RS SK UK	RS

M. saltuarius		EN SL	AU LA PL RS	BY CZ EN GE IT LT SL SZ UK		EN BY RS	
M. impluviatus				RS			RS

References: Abelleira et al. 2015; Adlbauer 2010; Aistleitner and Aistleitner 1997; Akbulut and Stamps 2012; Akbulut et al. 2008; Akhmatovich and Kotlyarskii 2009; Alekseev 2007; Alexandrov and Andonovski 2011; Anonymous 2005; Audisio et al. 2008; Averenskiy and Isaev 2011; Averkiev 1984; Baranchikov 1997; Behalová 2006; Berkvens et al. 2013; Brelih et al. 2006; Ciesla 2011; Cocquempot and Lindelöw 2010; CSCF-karch 2015; Danilevsky 2014; Donis et al. 2009; Evans et al. 2004; Foit 2010; Francardi et al. 2003; Georgebits 1974; Georgiev et al. 2005a, b; 2006; Gutowski et al. 2011; Halbig et al. 2014; Hoskovec 2010; Hoyer-Tomiczek and Tomiczek 2005; Ibeas et al. 2008; Ilic and Curcic 2013; Inácio et al. 2015; Izhevsky et al. 2005; Jankowiak et al. 2007; Hjältén et al. 2007; Jurc et al. 2003, 2012a, b; Kobzar 2009; Komonen 2007; Kopinga et al. 2010; Korma 2009; Koutroumpa et al. 2009, 2013; Kovács 1997; Kovács et al 1999; López and Goldarazena 2012; Magnusson and Schroeder 1989; Magnusson et al. 2007; Markalas 1997; Masutti et al. 2005; McNamara and Stoen 1988; Mejri et al. 2014; Migliaccio et al 2004; Mihajlovic 2008; Mikaia et al. 2010; Novotný et al. 2012; Pajares et al. 2010; Pernek com pess; Pernek et al. 2012; Petersen-Silva et al. 2014a; Piletskis and Yakaitis 1981; Rapuzzi and Sama 2012; Rassati et al. 2012; Rusin 2009; Ryss 2008; Sama 2008; Schönfeld 2006; Schroeder and Magnusson 1992; Schroeder et al. 1999; Serafim 2004; Sousa et al. 2001; Starzyk 1996; Starzyk and Hilszczanski 1997; Sushko 2014; Svihra 1972; Telnov et al. 2005, 2007; Tomminen and Leppänen 1991; Tozlu 2001; Tsankov et al. 1996; Villiers 1946; Vincent 2007; Wallin et al. 2013; Witrylak 2008; Zamoroka et al. 2012

Country codes: *AG* Algeria, *AL* Albania, *AU* Austria, *BE* Belgium, *BH* Bosnia and Herzegovina, *BU* Bulgaria, *BY* Belorussiya, *CR* Croatia, *CZ* Czechia, *EN* Estonia, *FI* Finland, *FR* France, *GE* Germany, *GO* Georgia, *GR* Greece, *HU* Hungary, *IT* Italy, *LA* Latvia, *LT* Lithuania, *MC* Macedonia, *MD* Moldova, *MR* Morocco, *NL* Netherlands, *NR* Norway, *PL* Poland, *PT* Portugal, *RO* Romania, *RS* Russia, *SB* Serbia, *SK* Slovakia, *SL* Slovenia, *SP* Spain, *SV* Sweden, *SZ* Switzerland, *TR* Turkey, *TU* Tunisia, *UK* Ukraine (Based on Danilevsky 2012, 2014)

Adlbauer 2010). In the East, *M. impluviatus* inhabits preferentially in larch forests (Cherepanov 1990; Averenskiy and Isaev 2011).

In general, European *Monochamus* breed in weakened or recently-dead conifers, being dependent of other biotic and abiotic agents that damage or kill the trees (Ehnström and Axelsson 2002; Pennacchio et al. 2006; Akbulut and Stamps 2012). Most European species appear to be pyrophilous ("fire loving"), being attracted to scorched and superficially burned trees after forest fires (Hellrigl 1971; Agafonov and Kuklin 1979; Cherepanov 1990; Chu et al. 1990; Zhang et al. 1990; Markalas 1997; Meyer 2002). This behavior is also described for many North American members of the genus (Rose 1957; Wilson 1962; Saint-Germain et al. 2004; Boulanger et al. 2010, 2013). After eggs are laid in the weakened or dead host, the larval activity can cause significant timber degradation (technical damage) and economic losses, with heavy damage being reported for *M. sutor* and *M. sartor* during periodic outbreaks in Romania (Evans et al. 2004).

Besides the economic loses, *Monochamus* spp. can occasionally demonstrate aggressive behavior as a result of outbreaks with very high population levels (Hellrigl 1971). Most reports come from Russia, where *M. sartor urussovi* (identified as *M. urussovi*) periodically behaves as a primary pest affecting hundreds of thousands of hectares of mature Siberian spruce and fir, being responsible for significant tree mortality (Hellrigl 1971; Isaev and Krivosheina 1976; Isaev 1995; Vetrova et al. 1998). During these outbreaks in the boreal forests, the maturation feeding by millions of insects cause branch dieback and heavy defoliation results in severe crown damage, leading to irreversible tree weakening which predispose the trees to subsequent attacks by other pests (Gavrikov and Vetrova 1991).

When locating suitable hosts for breeding, adult *Monochamus* mainly respond to volatiles emitted by the stressed or dead conifers, being attracted to conifer monoterpenes (Erbilgin and Raffa 2000; Allison et al. 2004; Fan et al. 2007; Miller et al. 2011; Bonifácio et al. 2012) and to pheromones emitted by bark and wood-boring beetles, in a pheromone-mediated aggregation (Allison et al. 2001, 2003, 2004; Pajares et al. 2004; Francardi et al. 2009; Miller et al. 2011; Ryall et al. 2015). This is the case for *M. galloprovincialis*, which is highly attracted to trees previously attacked by bark beetles of the *Ips* genus (Pajares et al. 2004; Bonifácio et al. 2012). Once they arrive on the host, the males produce a short-range pheromone (2-undecyloxy-1-ethanol, or "monochamol") which attracts mature females to the oviposition site (Pajares et al. 2010). Monochamol also appears to be a component of the male-produced aggregation pheromone of *M. sutor* (Pajares et al. 2013), *M. sartor urussovi* (Ryall et al. 2015) and other members of the genus from North America and Asia (Teale et al. 2011; Allison et al. 2012; Macias-Samano et al. 2012; Fierke et al. 2012). The pheromone is now available as a commercial kit (pheromone plus kairomonal lure) which has proven its efficiency in trapping European *Monochamus* (Jurc et al. 2012b; Rassati et al. 2012).

12.5.3 Reproduction and Larval Development

12.5.3.1 Mating and Oviposition

Upon emergence, *Monochamus* beetles are sexually immature and unable to breed. They fly to nearby healthy host trees to feed on the thin bark and phloem tissues of living branches to mature their reproductive organs (Hellrigl 1971; Cherepanov 1990; Allison et al. 2004; Akbulut and Stamps 2012). This obligatory period of nutrition, called maturation feeding, extends for the first 15–20 days after emergence of *M. galloprovincialis* (Naves et al. 2006c), although adults will continue feeding on conifer tissues throughout their lives (Naves et al. 2007a; Tomiczek and Hoyer-Tomiczek 2008).

When sexually mature, both sexes aggregate on the surface of a host selected for breeding, and use their long antennae to recognize the other sex and mate (Linit 1988; Kishi 1995; Hanks 1999). Males and females copulate with several mates throughout their lifespan, suggesting a polygynous mating system (Fauziah et al. 1987). When two males meet, they interact with their antennae and the larger one usually repels the smaller individual and prevents it from breeding, a behavior observed in various species of *Monochamus* (Hughes 1981; Edwards and Linit 1991; Kobayashi et al. 2003).

The selection of the egg-laying site is made by the female, based on characteristics of the host such as bark thickness and moisture content of the sapwood. Females use the mandibles to gnaw small niches on the bark, creating “egg-pits” which are flat and slit-like when the bark is thin and assume a pit-like structure for thicker barks. The egg is inserted under the bark on the cambium/sapwood interface. The oviposition scar is plugged with a gelatinous substance that protects the egg from desiccation and natural enemies and signals to other females that an egg has been laid in that location (Anbutsu and Togashi 1997a, 2000, 2001). In outbreaks of *M. sartor urussovi* in Siberia, very high colonization density of up to seven eggs per 1 sq/dm was observed on Siberian fir (Gavrikov and Vetrova 1991).

In general, *Monochamus* eggs are laid singly (Evans et al. 2004; Koutroumpa et al. 2008), as for most members of the Lamiinae (Cherepanov 1990), although two or three eggs in the same egg-pit have been occasionally reported for *M. galloprovincialis* (Naves et al. 2006c). The eggs are elongate, slightly rounded at the poles, and the chorion has a fine, faint reticulate sculpture, being in general 4.0 mm long by 1.2 mm wide. Being initially white and matte, they acquire a light-brownish coloration over time.

In their first weeks after emergence, *M. galloprovincialis* females lay an average of two eggs per day, although this rate gradually decreases over time. Some variability has been described for the reproductive parameters of populations studied under laboratory conditions, with a mean of 67 eggs/female described for Portugal (Naves et al. 2006c) and 138 eggs/female in France (Koutroumpa et al. 2008). Occasionally, adults with prolonged longevities can lay higher number of eggs, with a female being reported to lay 359 eggs in a study made in Turkey (Akbulut 2009).

Comparable mean fecundities have been reported for the other European species, with 50–80 eggs for *M. saltuarius* and 80–120 eggs for *M. sartor*, according to Hellrigl (1971).

The eggs of *M. galloprovincialis* require 6–11 days to incubate, depending on ambient temperatures (Francardi and Pennacchio 1996). In colder locations of northern Russia, *Monochamus* eggs can take up 4 weeks incubating (Cherepanov 1990).

12.5.3.2 Larval Development and Pupation

Monochamus larvae are robust, legless, and have a white and opaque coloration with small black and red hairs through the body. The head capsule is amber-black, with well developed chewing mouthparts. Four larval instars (L1–L4) are reported for *M. galloprovincialis* (Koutroumpa et al. 2008), while for *M. sutor* four or five instars have been described (Bakke and Kvamme 1992; Starzyk and Hilszczanski 1997). The first instars make sinuous galleries under the bark while consuming tissues on the inner bark, cambium and outer sapwood (Hellrigl 1971; Bakke and Kvamme 1992; Naves et al. 2008). While feeding, *Monochamus* larvae may ingest larvae of other insects (such as bark beetles) colonizing the same host, which may be beneficial in a diet poor in essential nutrients such as nitrogen (Hellrigl 1971; Miller 1985; Dodds et al. 2001; Schoeller 2011).

The asymmetrical galleries increase in size with larval development and may end up having lengths of 15 cm or more, becoming obstructed by frass and excrements with time (Hellrigl 1971). Under favorable ambient temperatures larval development is very fast, and in warmer locations of Southern Portugal last instar larvae of *M. galloprovincialis* can be found after only 40 or 50 days during the summer months. Besides temperature, other factors such as moisture content of the sapwood and nutritional quality of the host also appear to exert some influence on larval development (Akbulut et al. 2008; Koutroumpa et al. 2008). Recently, a laboratory rearing protocol including an artificial diet which allows completing the whole cycle has been developed for *M. galloprovincialis*, and can be adapted for other European members of the genus (Petersen-Silva et al. 2014b).

The mature larvae eventually cease feeding on the phloem and external sapwood and begin tunneling into the xylem through an oval hole, making an internal gallery where they spend winter protected by a plug of coarse and fibrous frass and excrements (Cherepanov 1990; Starzyk and Hilszczanski 1997; Koutroumpa et al. 2008). For *M. galloprovincialis*, these heartwood galleries are usually about 8–10 cm long, although dimensions vary in face of location and larval density. Their shape also varies, and while most are "U" shaped, others can be "S" shaped or have intermediate forms (Hellrigl 1971; Koutroumpa et al. 2008). At the end of the gallery the larvae construct an enlarged pupal chamber, around 6 cm by 1 cm and located close (usually within less than 20 mm) to the surface of the wood (Fig. 12.4). Pupal chambers of *M. alternatus* tend to have a greater distance to the wood surface in regions of colder climate, in a strategy to provide higher thermal isolation during periods of cold temperatures (Kishi 1995).

Fig. 12.4 Mature larvae of *Monochamus galloprovincialis* inside the gallery and pupal chamber

The last-instar larvae endure winter in a state of dormancy (diapause), experiencing visible physiological and morphological modifications such as a change in body coloration from milky white with fecal material (active larvae) to a vivid yellowing without fecal material (dormant larvae), while ceasing feeding. Dormancy allows larvae to survive negative temperatures during the winter months and to synchronize emergencies of insects with 1 and 2-year cycles (Naves et al. 2007c). Being a common feature to the European and Asian species of the genus (Hellrigl 1971; Togashi 1991; Togashi et al. 1994; Akbulut and Stamps 2012), an obligatory dormancy appears to be absent from some North American species, such as *M. carolinensis* (Alya and Hain 1985; Linit 1985; Pershing and Linit 1986).

After winter the larvae resume development and molt into pupa, which usually occurs from May onwards. This developmental stage resembles the adult insect superficially, with the mouthparts, legs, antennae and wings projected externally from the body. Within 2 or 3 weeks, depending on the ambient temperature, the fully sclerotised adult emerges through a perfectly round hole at the surface of the wood, with about 4–12 mm in diameter (Fig. 12.5). Although conspicuous, the round hole of *Monochamus* emergence can be confused with similar emergence

Fig. 12.5 Emergence of *Monochamus galloprovincialis*

orifices of other wood-inhabiting insects, such as *Sirex* spp. wood-wasps and *Xilocopa* spp. carpenter bees.

12.5.4 Emergence and Flight Activity

Populations of *M. galloprovincialis* in Mediterranean countries share similar phenology and are typically univoltine, completing their life cycles in 1 year (Hellrigl 1971; Francardi and Pennacchio 1996; Koutroumpa et al. 2008; Naves et al. 2008; Mejri et al. 2014). Nevertheless, 2-year life cycles also occur and have been described for 5 % of the population in southern Portugal (Naves et al. 2008), 8 % in France (Koutroumpa et al. 2008) and 90 % in southern Finland (Tomminen 1993). The 2-year life cycle also appears to predominate in mountainous regions of Central Europe (Hellrigl 1971). This suggests a latitudinal and altitudinal influence on the frequency of insects with 1 or 2 year cycles, which is related to variations in mean annual temperatures. Similar phenologies have been reported for other members of the genus, such as *M. sutor*: In Sweden, this species requires 1 year to develop in the South and 2 years in the Center and North (Ehnström and Holmer 2007), while in Norway 60 % of the population has annual generations in Center of the country, while in inland and mountainous regions with colder climates a 2-year cycle is more frequent (Bakke and Kvamme 1992).

Ambient temperatures are crucial for the development of *Monochamus* and, inside defined tolerance intervals, the temperature needs to exceed a certain threshold for development to occur, based on an accumulation of daily thermal energy or degree-days (DD). These parameters have been studied for *M. galloprovincialis*, establishing extreme temperature thresholds of 12.2 °C and 32 °C for pos-dormancy larvae, with thermal requirements of 822 DD at 50 % emergence date (Naves and Sousa 2009). No similar studies have been conducted on other European *Monochamus*, but lower thermal requirements are reported for *M. alternatus* in Japan and Korea (Kobayashi 1988; Park et al. 2014a).

Emergence of European *Monochamus* spp. tends to occur from late spring to late summer, extending for up to 5 months. The emergence of *M. galloprovincialis* has been studied in detail in wilt-affected forests of continental Portugal, with adults exiting the wood during late spring/early summer. During a 4-year study in coastal Alentejo province, the first individuals emerged in early-May and the last insects in late August or early September (Fig. 12.6). The emergence peak occurred in June and July, despite small annual discrepancies caused by variations in ambient temperatures. The flight activity is obviously related with emergence, and flying beetles were caught in traps from May to late October, being most abundant in June, July and August (Naves et al. 2008).

The emergence and flight period are extremely uniform throughout *M. galloprovincialis'* vast distribution range: In Austria, emergence takes place from May to September with a peak in June and July (Tomiczek and Hoyer-Tomiczek 2008), while in Tunisia it occurs from May to August with a peak in June (Mejri et al. 2014), which is similar to Italy (Francardi and Pennacchio 1996) and southern Finland (Tomminen 1993). As for the flight period, in Turkey it extends from May to late September (Canakçıoğlu and Mol 1998). In Spain, flying insects are captured from May to October (Saldaña 2012) or early November (Hernández et al. 2011), and in Northern Italy from July to September (Rassati et al. 2012). In Siberia beetles are found throughout the summer months until early October (Cherepanov 1990).

Similar emergence and flight patterns are found for the other European members of the genus. In the Austrian Alps, *M. sartor* emerges in June (Halbig 2013) and in the Caucasus in June and July (Averkiev 1984). As for *M. sutor*, adults in Sweden can be found from the middle of May to the end of August (Ehnström and Holmer 2007), and in Norway from June to September (Bakke and Kvamme 1992). In Central Europe and Northern Russia, both *M. sutor* and *M. saltuarius* flight from June to mid-September, with maximum activity in June and July (Hellrigl 1971; Cherepanov 1990).

12.5.5 Adult Dispersal

Adult *Monochamus* appear to have age-related variations on their flight activity. Soon after emergence, *M. galloprovincialis* make dispersive flights of around 150–300 m in search of suitable hosts for maturation feeding (Bonifácio 2009). In Spain, mark-recapture trails found that lifetime adult dispersal was 107–122 m on average,

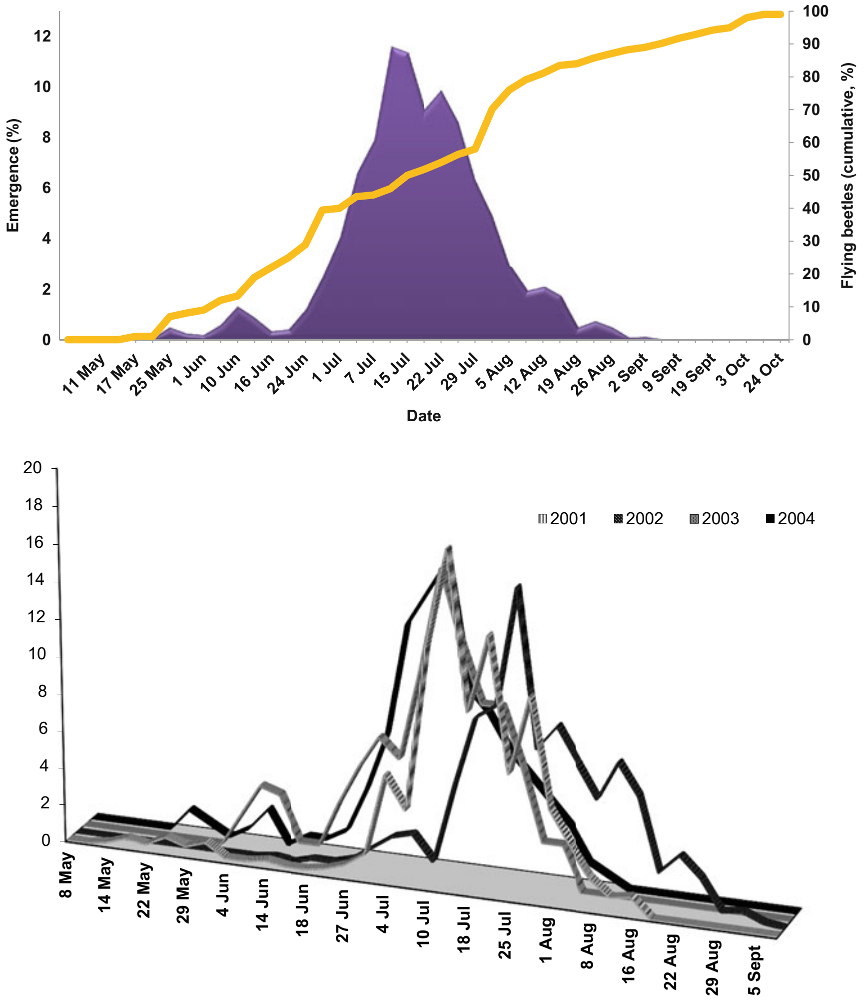

Fig. 12.6 Mean emergence pattern (area in top Figure, lower Figure) and mean capture in traps (line in top Figure) of flying adult *Monochamus galloprovincialis* in southern Portugal during 2001–2004

with a maximum dispersal of 464 m (Torres-Vila et al. 2015). Similar observations were made in Norway and Sweden with *M. sutor*, which flew an average of 157 m from clear cut areas in search of branches to feed (Okland et al. 2010). Once the initial sexual maturation is completed, the beetle's mobility drops substantially in the presence of suitable breeding hosts. In field trails made in Portugal, sexually mature *M. galloprovincialis* made consecutive daily flights of around 4 m/day, with a third of the insects remaining on the same tree for up to three consecutive days (Bonifácio 2009). Similar patterns of age-conditioned flying activity were reported on field studies with *M. alternatus* in Japan (Togashi 1990). Nevertheless, when studied under laboratory conditions in a flight mill, the flight distance of *M. galloprovincialis* increased with age in both sexes (David 2014), and therefore additional studies are needed to clarify the contradictory observations between field and laboratory experiments for *M. galloprovincialis*.

Despite the low dispersal exhibited by adults in field trials, it has been proven that *Monochamus* beetles can make substantially longer flights if necessary, using the prevailing winds to detect odors of suitable hosts. In Spain, 2 % of the *M. galloprovincialis* from a marked-release experiment were recaptured in traps distant 8 and 13 km from the release point (Gallego et al. 2012; Mas et al 2013). Laboratory studies with a flight mill showed that insects can fly 15–16 km over their life span, this being the sum of successive smaller flights of around 2 km (David et al. 2014). According to these authors, *M. galloprovincialis* has the physiological capacity to perform cumulative flights of up to 40–60 km during its life span. In Japan, the annual natural dispersion of wilt disease, resulting exclusively from the flight of the local vector *M. alternatus*, was estimated to average 6 km, with maximum of 15 km per year (Togashi and Shigesada 2006).

Adverse weather conditions, such as precipitation or strong winds, can affect the flight behavior of the *Monochamus* insects (Naves et al. 2008; Halbig 2013). Ambient temperatures are also important for beetle activity, and when daily values fall below 20 °C the captures of *M. galloprovincialis* are much reduced or even null, indicating reduced flight activity (Hernández et al. 2011; Saldaña 2012). Similar observations were made for *M. sartor* and *M. sutor* in the Austrian Alps, with flight activity being directly influenced by air temperatures (Halbig 2013).

12.5.6 Sex Ratio and Adult Longevity

The sex ratio is generally well balanced for *Monochamus* (Hellrigl 1971; Francardi and Pennacchio 1996), with a slight predominance of males described for *M. galloprovincialis* (Koutroumpa et al. 2008; Naves et al. 2008), while for *M. saltuarius* the inverse pattern was recorded, with females slightly dominant (Han et al. 2007).

The longevity of both sexes is similar, with mean life spans of 61.2 ± 6.5 days for *M. galloprovincialis* males and 64.0 ± 6.3 days for females studied in Portugal under laboratory conditions (Naves et al. 2006c). Similar studies made under natural conditions in France, with ca. 17 °C of average ambient temperature, resulted in a much higher mean longevity of 126 ± 1 days (David 2014), and its not uncommon for individuals under laboratory conditions to survive more than 4 months (Naves et al. 2006c; Akbulut 2009).

Comparable longevities are described for the other European species of the genus (Tomiczek and Hoyer-Tomiczek 2008), with *M. sartor, M. sutor* and *M. saltuarius* reported to live up to 2 or 3 months (Hellrigl 1971; Cherepanov 1990).

The dimensions of the adults affect their fecundity and longevity, with bigger individuals of *M. galloprovincialis* living longer and laying more eggs (Naves et al. 2006c; Akbulut et al. 2008), similarly to species from Asia (Jikumaru et al. 1994) and North America (Walsh and Linit 1985; Togashi et al. 2009). Size also affects the flight capacity, and according to David (2014) the distance flown by both sexes of *M. galloprovincialis* increases for beetles with higher weight at emergence.

12.5.7 Mortality Factors

The *Monochamus* larvae are very aggressive, and to avoid cannibalism produce chirping sounds by the contact of the mandibles with the gallery walls, in order to keep other individuals away (Togashi 1989; Izumi et al. 1990; Victorsson and Wikars 1996). If this fails and two individuals meet, the bigger larvae usually kills and feeds upon the smaller one (Victorsson and Wikars 1996; Anbutsu and Togashi 1997b). In fact, only around 53 % of the *M. galloprovincialis* larvae complete their development, with high mortality caused mainly by intra-specific competition and cannibalism (Naves et al. 2008).

Other biotic and abiotic agents can affect the immature stages of *Monochamus*. Eggs and larvae in small branches are more exposed to attacks by natural enemies and to adverse environmental conditions (extreme temperatures and humidity), resulting in higher mortality in thinner wood than in larger sections of the trunk and branches (Naves et al. 2008). The most important mortality agents are the entomopathogenic fungus *Beauveria bassiana* (Balsamo) Vuillemin and hymenoptera parasitic wasps. *Cyanopterus flavator* (Fabricius) (Hymenoptera: Braconidae) is the most abundant parasitoid associated with *M. galloprovincialis* larvae in Portugal (Naves et al. 2005, 2008; Petersen-Silva et al. 2012, 2014a). A critical review of parasitoids associated with *Monochamus* spp. in Europe, East Asia and North America can be found in Naves et al. (2005), while Petersen-Silva et al. (2012) provide a taxonomical key for determination of the ichneumonoid parasitoid complex associated with *M. galloprovincialis* larvae in the Palaearctic region.

12.6 Other Insects Associated with the PWN

Conifer trees killed by the PWN are frequently colonised by a diverse community of bark and wood boring insects, including cerambycids, scolytids, curculionids and buprestids, among others. In South-East Asia and North America, some of the species emerging from wilted trees were found carrying *B. xylophilus* (Table 12.2), although usually with low nematode loads and without evidence of being effective vectors (Wingfield and Blanchette 1983; Kobayashi et al. 1984; Linit 1988).

Many of the genera or species found transporting the PWN (Table 12.2) also occur in Europe, including *Arhopalus* spp., *Acanthocinus griseus* (F.), *Spondylis buprestoides* (L.), *Chrysobothris* spp., *Tomicus piniperda* (L.), *Hylobius* spp. and *Pissodes* spp., among others. To study possible European vectors of the PWN, Tomminen and Akar (1990) evaluated the native species *Rhagium inquisitor* (L.), *Asemum striatum* (L.) (both Cerambycidae) and *Hylobius abietis* (L.) (Curculionidae), under artificial conditions. Although these authors were able to infest these beetles with the PWN in laboratory, the nematode loads were extremely low, and each infested insect only carried a few nematodes at maximum (Tomminen and Akar 1990).

Table 12.2 Insects (other than *Monochamus*) found associated with *Bursaphelenchus xylophilus* in Asia and North America

Family/species	Location	Reference
Cerambycidae		
Acanthocinus griseus	Japan	Mamiya and Enda 1972; Linit 1988; Kishi 1995
A. gundaiensis	China	Togashi 2008
Amniscus sexguttatus	USA	Linit et al. 1983; Wingfield and Blanchette 1983; Linit 1988
Arhopalus rusticus	Japan	Mamiya and Enda 1972; Linit et al. 1983; Linit 1988
Aromia bungii	China	Togashi 2008
Asemum striatum	USA	Linit et al. 1983; Linit 1988
Corymbya succedanea	Japan	Mamiya and Enda 1972; Linit 1988; Kishi 1995
Neacanthocinus obsoletus	USA	Carling 1984; Togashi 2008
N. pusilus	USA	Wingfield and Blanchette 1983; Linit 1988
Spondylis buprestoides	Japan	Linit 1988; Kishi 1995
Uraecha bimaculata	Japan	Linit 1988; Kishi 1995
Xylotrechus sagittatus	USA	Wingfield and Blanchette 1983; Linit 1988
Buprestidae		
Chrysobothris spp.	USA	Linit et al. 1983; Linit 1988; Wingfield and Blanchette 1983
Curculionidae		
Hylobius pales	USA	Linit et al. 1983; Linit 1988
Pissodes approximatus	USA	Linit et al. 1983; Linit 1988
Scolitinae		
Tomicus piniperda	China	Togashi 2008
Termitidae		
Odontotermes formosanus	China	Togashi 2008

In the maritime pine forests in Portugal, trees killed by the PWN are usually colonized by a diverse guild of bark and wood boring beetles, including some of the species mentioned in Table 12.2 (Sousa et al. 2000). To detect possible new vectors of the PWN, insects emerging from PWN-infested trees have been periodically sampled over the years, with 21 species analyzed (Table 12.3).

None of the sampled insects were found transporting *B. xylophilus*, although most bark beetles carried other species of the genus such as *Bursaphelenchus hellenicus* Skarmoutsos, Braasch and Michalopoulou, *Bursaphelenchus sexdentati* Rühm and *Bursaphelenchus teratospicularis* Kakuliya, among others (Sousa et al. 2001, 2002; Penas et al. 2006). Besides Scolitinae, *Bursaphelenchus* species can be transported by insects of the families Curculionidae, Lucanidae, Nitidulidae,

Table 12.3 Insects sampled for *Bursaphelenchus xylophilus* when emerging from nematode-infested pines in Portugal (Adapted and updated from Sousa et al. 2002)

Order/family/species	Number of individuals sampled (n)
Coleoptera	
Cerambycidae	
Arhopalus ferus	108
A. syriacus	101
Pogonocherus perroudi	57
Acanthocinus griseus	86
Spondylis buprestoides	32
Rhagium inquisitor	3
Ergates faber	3
Scolytinae	
Orthotomicus erosus	899
Tomicus piniperda / destruens	168
Ips sexdentatus	312
Hylurgus ligniperda	557
Pityogenes sp.	175
Hylastes spp.	34
Buprestidae	
Crysobothris solieri	53
Calcophora mariana	18
Phaenops cyanea	3
Curculionidae	
Pissodes castaneus	191
Eremotes porcatus	50
Hylobius sp.	62
Elateridae	
Unidentified sp.	10
Hymenoptera	
Siricidae	
Sirex noctilio	5

Antophoridae, Halictidae and Sesiidae (e.g., Fuchs 1937; Rühm 1956; Massey 1974; Giblin-Davis et al. 1984, 1993; Giblin-Davis 1993; Giblin-Davis et al. 2006; Braasch 2001; Ryss et al. 2005; Kanzaki et al. 2011, 2012).

All insects able to transfer nematodes between trees, particularly species of *Bursaphelenchus*, can be considered potential vectors of the PWN (Jurc et al. 2012b). In Europe, several bark and wood boring beetles are vectors of *Bursaphelenchus* spp. (e.g., Braasch et al. 2001; Ryss et al. 2005; Penas et al. 2006), and therefore can be considered potential vectors of the PWN. Nevertheless, field observations in the three continents where the PWN occurs confirm that *Monochamus* are the only effective vectors of the nematode (Akbulut and Stamps 2012; Futai 2013), as a result of extremely specific and precise chemical signals regulating the nematode-vector association (Zhao et al. 2013, 2014). All these observations suggest that the risk of *B. xylophilus* becoming associated with insects of the European fauna, other than *Monochamus*, appears to be low, although it cannot be totally excluded.

12.7 Management and Control of Pine Wilt Disease

The tactics and strategies developed to manage wilt disease rely on the control of the nematode and the insect vector, with complementary approaches designed to reduce the impact of both organisms. There are some important constrains to achieve this; *B. xylophilus* is a microscopic organism that is difficult to identify and does not cause specific symptoms in infested hosts, while the *Monochamus* vectors develop under the bark and inside the wood of infested conifers, making external chemical control problematic. Adults are able to make long-distance flights if necessary and are poorly controlled by their natural enemies.

Over the years, several options to manage wilt disease have been developed mainly in Eastern Asia, although much progress has also been made recently in Europe. Control options include silvicultural management, trapping of vector, chemical control and biological control, among others.

12.7.1 Silvicultural Management

In well managed forests with few dead trees, the pine sawyers are usually dependent on silvicultural and logging practices to supply suitable host materials for their survival. Therefore, high levels of forest hygiene can be used preventively to manage the populations of these beetles, by keeping breeding substrate at low amounts during the flight period and leaving the minimum of suitable host material in the forest. In addition, gathering and storing of logs for long periods in the forest and saw mills in forested areas should be avoided, as should the transport of infested logs to other areas (Evans et al. 1996).

Fig. 12.7 Gathering of branches and wood debris from wilted maritime pine trees in Tróia, Portugal. This small-dimension wood material has very high risk of wilt disease due to the presence of *M. galloprovincialis* immature stages and PWN, and needs to be removed from the forest or locally processed / destroyed

In wilt-affected zones, cultural practices need to include the removal of dead or dying trees from the forest, in order to avert emergence of *Monochamus* carrying the nematode, preventing further infection. In Portugal this is done on a yearly basis and relies on the survey of symptomatic and wilted pines during the autumn and winter, which are marked and geo-referentiated to be felled during the winter months, when both the nematode and the vector larvae are inside the pine wood (Rodrigues 2008). Special attention needs to be given to the removal of the upper trunk and branches of all dimensions, which can harbour *M. galloprovincialis* galleries and should not be left in the stands (Fig. 12.7). The removal and destruction of this cut-waste wood is expensive and time consuming.

12.7.2 Trapping of Vector

The arrival of *B. xylophilus* in Portugal has resulted in substantial improvements in the monitoring and management of *M. galloprovincialis* during the flight period. In the last years, a lot of research has been carried out on the chemical ecology of the adults and the development and testing of efficient traps and baits for monitoring and control (Pajares et al. 2004; Ibeas et al. 2007, 2008; Francardi et al. 2009; Bonifácio 2009; Bonifácio et al. 2012; Jurc et al. 2012a, b; Torres-Vila et al. 2015).

Overall, studies concluded that the best traps to capture *M. galloprovincialis* are the multi-funnel model (12 or 16 elements) (Bonifácio et al. 2012) and the transparent cross vane model (Francardi et al. 2009). The best lure is composed of host tree volatiles (ethanol and alpha-pinene), bark beetles pheromones (Ipsdienol and Methyl-buthenol) and the short range specific pheromone (2-undecyloxy-1-etanol, or "monochamol") (Pajares et al. 2010; Bonifácio et al. 2012; Álvarez et al. 2014). Attraction distance of lured traps averages between 50 m (Torres-Vila et al. 2015) and 150 m (Bonifácio 2009). Unpublished observations made in Portugal found that traps placed hanging on the lower branches of adult pines, at canopy height, had higher captures, as this is where *M. galloprovincialis* flies and lands to feed and lay its eggs.

The use of traps for monitoring and control can be optimized with the predictive degree-day model used by Naves and Sousa (2009), which allows to estimate dates of *M. galloprovincialis* seasonal emergence and can be tested and adapted for other European *Monochamus* species. The model can be a useful component of management and control strategies when employed to temporize the felling of the wilted and nematode-infested trees, and to optimize the placement of traps with attractants to capture flying insects during the spring and summer months.

When applied timely and with rigor, the combination of trapping and forest hygiene has proven efficient in some locations, namely in Tróia peninsula in southern Portugal, where yearly pine mortality has been reduced to less than one tree/hectare and wilt disease is nowadays responsible for only 10–20 % of annual pine mortality (Sousa et al. 2011b). Nevertheless, as Torres-Vila et al. (2015) conclude, the lures and traps currently available are highly effective for monitoring, but their implementation in mass trapping strategies still requires substantial improving.

12.7.3 Chemical Control

Nematicides and insecticides have been used to prevent the introduction and spread of the nematode and vector by the international transport of wood packaging materials. Wood originating from wilt-affected countries must comply with international standards for phytosanitary measures – ISPM 15 (IPPC 2002, 2013) and needs to be heat-treated or fumigated (Dwinell 1990, 1997; Webster 1999; Haack et al. 2014). The phasing out of methyl bromide has created an urgent need for alternative treatments of packaging materials, and the effect of sulfuryl fluoride (SF), a broad-spectrum fumigant, was successfully tested in pine boards naturally infested by PWN (Bonifácio et al. 2014). This fumigant is currently under evaluation by International Phytosanitary Authorities for inclusion in ISPM n°15, and should become a future alternative to disinfest commodity wood destined for the international trade. Other alternatives include ethanedinitrile recently found to have great potential to treat, at low temperatures, pine wood infested with *M. alternatus* and *B. xylophilus* (Park et al. 2014b).

In forests, insecticides have been used to control adult pine sawyers in Asian countries like Japan, China and Korea, with aerial spraying during the flight period of the local vectors (Mamiya 1984; Kobayashi 1988; Kamata 2008). However, widespread chemical control has also caused negative effects on the biodiversity of pine forests and to human activities. The public has become critical or even opposed to aerial spraying of pesticides (Togashi 1990; La et al. 1999; Kosaka et al. 2001), with more environmentally friendly control methods being demanded. In Europe, aerial spraying of insecticides to control the pine sawyers in nematode-infested areas has never been conducted, although insecticides are used in Portugal to prevent the spread of the vector by the transport of infested wood, which needs to be treated or covered with an insecticide-net during transport in trucks (Sousa et al. 2011b).

Preventive trunk injection of a nematicide/insecticide is an alternative method to control PWD if performed before trees are infested with the nematode. These preventive methods have been tested with success in Japan (Kazuya et al. 1999; Takai et al. 2003a) and the United States (James et al. 2006) and have the advantage of being target-specific and environmentally friendly (Takai et al. 2003b). In Europe, preventive trunk injection with emamectin benzoate has recently been tested, and found to effectively protect healthy pines against wilt disease and bark beetle attacks for several consecutive years (Sousa et al. 2013). Nevertheless, despite being a new option for wilt disease management in Europe, trunk injection is also labor consuming and expensive, being suitable mainly for small groups of trees in urban and recreational areas, and in the vicinity of high-risk areas such as commercial ports and sawmills.

12.7.4 Biological Control

In 2004, Kenis and Hilszczanski stated that "very little is known of the natural enemies of this pine feeding species", referring specifically to *M. galloprovincialis* and to European *Monochamus* in general. Since then, however, several surveys and samplings have been done mainly in Portugal, with *M. galloprovincialis* being subject of target studies with natural enemies which greatly increased our knowledge on this aspect. We now know a total of 14 species of parasitoids (6 Ichneumonidae and 8 Braconidae), associated with *M. galloprovincialis* worldwide. All the parasitoid species are generalists attacking a vast array of Cerambycidae and other coleopteran insects living in dead and dying trees, and therefore their use as biological control agents could be ineffective (Petersen-Silva et al. 2012). A similar pattern occurs with other European *Monochamus*, with *M. sartor* and *M. sutor* sharing basically the same (or related) parasitoids found on *M. galloprovincialis* (Kenis and Hilszczanski 2004). As for egg parasitoids, they appear to be quite rare for *Monochamus* in general, although a species new to science has recently been described in China associated with the eggs of *M. alternatus* (Yang et al. 2014).

Entomoparasitic fungi such as *Beauveria* spp. are frequently collected from dead and moribund *Monochamus* larvae, and have been tested under artificial conditions in controlling larvae and adults of different species (Shimazu et al. 1995; Francardi et al. 2003; Shimazu and Sato 2003; Shimazu 2008). A well-known entomophatogenic fungus, *B. bassiana*, has been tested under controlled conditions against *M. galloprovincialis* larvae and adults, causing rapid mortality (within 5 days) of nearly 50 % of adults (Petersen-Silva et al. 2015). Nevertheless, additional studies are needed, as *B. bassiana* is not a specific natural enemy and can infect at least 100 different insect species (Wegensteiner 2004). Furthermore, it can be difficult to apply against the target insects in the field (Petersen-Silva et al. 2015).

12.7.5 Other Techniques

Other alternative techniques and strategies have recently been developed. Latest experiments tested the elimination of *B. xylophilus* by exposing pine wood to high pressure processing (HPP), and found the nematode could be successfully eliminated at 30 MPa for 5 min, demonstrating this technology has potential to be used as a phytosanitary treatment at an industrial level (Fonseca et al. 2014).

Breeding for resistance of pine trees is being done for almost 40 years in Japan, with *P. thunbergii* and *P. densiflora* selected as key-species for these programs (Nose and Shiraishi 2008). A resistance breeding program has also been initiated in Portugal, with 504 adult *P. pinaster* trees phenotypically selected as candidate trees from an area with high incidence of wilt disease. It is hoped that even in this susceptible host pine there will always be resistant or tolerant individuals, which can form the basis of a breeding program to develop populations of genetically diverse and resistant trees. This new program will clone, test and analyze progenies of the selected trees for tolerance and resistance to PWD, although these are long-term studies which will require several years to, eventually, provide the desired plants (Ribeiro et al. 2012).

12.8 Conclusions

In the last decade of the twentieth century, pest risk analysis discussed the possible introduction and establishment of the pine wilt disease in Europe (Evans et al. 1996; Fielding and Evans 1996), concluding that *B. xylophilus* would undoubtedly survive in the continent and tree mortality would more likely occur in warmer Southern countries around the Mediterranean basin. Time proved this analysis to be correct, and only a few years later the PWN was detected in Portugal (Mota et al. 1999), where it has been causing significant mortality to maritime pine forests, resulting in significant economic and ecological impacts (Mota et al. 2009; Sousa et al. 2011b). The PWN was probably introduced into Europe by transport of wood or derivates (sawn wood, round wood, chips, packaging material) contaminated with both the nematode and vector beetles, this being the most important pathway for dissemination of wilt disease (Tomminen and Nuorteva 1992; Braasch et al. 2001; Sousa et al.

2011a; Tomiczek et al. 2003). It is possible, and even likely, that a an exotic *Monochamus* vector was introduced into Portugal along with *B. xylophilus*, which is not surprising considering that both nematode and vector can easily be transported alive in untreated wood packaging material through the international trade (e.g., Dwinell and Nickle 1989; Evans et al. 1996; Cocquempot 2006; Gu et al. 2006; Kvamme and Magnusson 2006; Evans 2007; Sousa et al. 2011a). Although the exotic vector was never detected and did not establish long-term viable breeding populations, the newly-arrived *B. xylophilus* took advantage of the presence of native *M. galloprovincialis* inhabiting the region, and established a successful nematode-vector association which allowed it to endure in Europe.

The new association proved successful. The vector, *M. galloprovincialis*, was relatively scarce in well-managed pine forests before the introduction of the PWN. The vector was limited by the shortage and unpredictability of suitable hosts for breeding, as it still occurs outside the PWD-outbreak areas in Portugal (Petersen-Silva et al. 2014a). The accidental introduction of *B. xylophilus* changed all this, and the pine sawyer ceased to be a passive, secondary forest insect depending on the irregular and random appearance of pine trees weakened by biotic or abiotic agents, such as bark beetle attacks or forest fires. Now, the infested insects play an active role in the creation of an abundant supply of suitable hosts for their own reproduction, leading to an increase on their population and to even more pine hosts killed, in an unstable positive feedback system which, uncontrolled, can compromise the sustainability of susceptible pine forest ecosystems.

The nematode's presence has also resulted in unexpected collateral-effect: the appearance of a large number of dead and decaying pines has promoted outbreaks of native bark beetles, such as *Orthotomicus erosus* (Wollaston), *Ips sexdentatus* (Börner) and *Tomicus* spp., which now benefit from the abundant supply of wilted pines to increase their populations and further contribute to the sanitary degradation of the pine forests (Sousa et al. 2011b). However, it is important to note that, in Europe, *B. xylophilus* has not interacted with any of these native wood-boring insects colonizing wilted pines. It is possible that the strong bonds which make the *B. xylophilus*- *Monochamus* spp. association so successful may also inhibit the nematode from becoming associated with insects of other genera, although careful monitoring of other possible vectors should continue over the next years.

The presence of the PWN in Iberia represents a significant new threat for European coniferous forests. Experience from Asia and Portugal show that once established into a new territory, the eradication of *B. xylophilus* is virtually impossible (Futai 2008; Shin 2008; Zhao 2008; Mota et al. 2009), and in the absence of efficient methods to control the PWN or its vectors (Dwinell 1997; Mota et al. 2009; Sousa et al. 2011b), focus should be made on preventing further spread from its current range in the Iberian Peninsula. Nematode dispersal can occur on short-distance by the active flight of the vector beetles or on long-distance due to human-mediated transport of untreated and infested wood (Tomiczek and Hoyer-Tomiczek 2008; Økland et al. 2010; Robinet et al. 2011). Human-mediated transport is the most important dispersal pathway, as has been proven in Japan (Kawai et al. 2006), China (Robinet et al. 2009) and Portugal, with the appearance of new outbreaks hundred of kilometers away from the original sources (Sousa et al. 2011b).

High risk areas include major ports from which the nematode can rapidly spread across Europe, mainly in Eastern and Northern Europe (Robinet et al. 2011). Nevertheless, the Mediterranean basin is undoubtedly the zone with the highest risk, due to the presence of widespread vectors [the confirmed *M. galloprovincialis* and the probable *M. sutor*, already found to be a key-vector of the related *B. mucronatus* (Magnusson and Schroeder 1989; Tomminen et al. 1989; Schroeder and Magnusson 1992; Braasch 2001)], various susceptible hosts (widespread forests and plantations of *P. pinaster*, *P. nigra* and *P. sylvestris*, among others), and favorable climatic conditions (prolonged periods of high temperatures and moisture deficit). According to Soliman et al. (2012), highest timber loses and economic impacts are expected in Portugal, Spain, Italy and France, if the PWN further spreads on Europe. Overall, if containment of the current Iberian outbreaks fails, we can conclude that pine ecosystems all over Europe, but especially in the Mediterranean basin, will be at very high risk from the negative impacts of pine wilt disease, one of the most serious threats to conifer forests worldwide.

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References

Abelleira A, Picoaga A, Mansilla JP et al (2011) Detection of *Bursaphelenchus xylophilus*, causal agent of pine wilt disease on *Pinus pinaster* in Northwestern Spain. Plant Dis 95:776

Abelleira A, Ibarra N, Aguín O et al (2015) First report of *Bursaphelenchus mucronatus kolymensis* (Nematoda: Aphelenchoididae) on *Monochamus sutor* (Coleoptera: Cerambycidae) in Spain. For Pathol 45:82–85

Adlbauer K (2010) Die Bockkäfer des Nationalparks Gesäuse. Joannea Zoologie 11:51–95

Agafonov A, Kuklin L (1979) Stem pests on Scots pine on burns (In Russian). Lesnoe-Khozyaistvo 10:55–57

Aikawa T (2008) Transmission biology of *Bursaphelenchus xylophilus* in relation to its insect vector. In: Zhao BG, Futai K, Sutherland JR et al (eds) Pine wilt disease. Springer, Tokyo, pp 123–138

Aikawa T, Kanzaki N, Maehara N (2013) ITS-RFLP pattern of *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae) does not reflect nematode virulence. J For Res 18:384–388

Aistleitner E, Aistleitner U (1997) Fragmenta entomofaunistica III. Daten zur Verbreitung und Phaenologie der Bockkäfer in Vorarlberg (Austria occ.) und Liechtenstein, sowie Streudaten aus dem Ost- und Südalpenraum (Coleoptera: Cerambycidae). Vorarlberger Naturschau 3:191–216

Akbulut S (2009) Comparison of the reproductive potential of *Monochamus galloprovincialis* Olivier (Coleoptera: Cerambycidae) on two pine species under laboratory conditions. Phytoparasitica 37:125–135

Akbulut S, Linit MJ (1999) Flight performance of *Monochamus carolinensis* (Coleoptera: Cerambycidae) with respect to nematodephoresis and beetle characteristics. Environ Entomol 28:1014–1020

Akbulut S, Stamps WT (2012) Insect vectors of the pinewood nematode: a review of the biology and ecology of *Monochamus* species. For Pathol 42:89–99

Akbulut S, Baysal I, Keten A et al (2008) Effect of log seasonality on reproductive potential of *Monochamus galloprovincialis* Olivier (Coleoptera: Cerambycidae) reared in Scots pine logs under laboratory conditions. Phytoparasitica 36:187–198

Akhmatovich NA, Kotlyarskii OB (2009) Potential wood carriers of pathogenic nematodes. J For Eng Acad St Petersburg 187:25–30

Alekseev VI (2007) Longhorn beetles (Coleoptera: Cerambycidae) of Kaliningrad region. Acta Biol Univ Daugavp 7:7–62

Alexandrov AH, Andonovski V (2011) *EUFORGEN*, Technical guidelines for genetic conservation and use of Macedonian pine (Pinus peuce). Biodiversity International, Rome

Allison JD, Borden JH, McIntosh RL et al (2001) Kairomonal responses by four *Monochamus* species (Coleoptera: Cerambycidae) to bark beetle pheromones. J Chem Ecol 27:633–646

Allison JD, Morewood WD, Borden JH et al (2003) Differential bio-activity of *Ips* and *Dendroctonus* (Coleoptera: Scolytidae) pheromone components for *Monochamus clamator* and *M. scutellatus* (Coleoptera: Cerambycidae). Environ Entomol 32:23–30

Allison JD, Borden JH, Seybold SJ (2004) A review of the chemical ecology of the Cerambycidae (Coleoptera). Chemoecology 14:123–150

Allison JD, McKenney JL, Millar JG et al (2012) Response of the woodborers *Monochamus carolinensis* and *Monochamus titillator* to known cerambycid pheromones in the presence and absence of the host plant volatile alpha-pinene. Environ Entomol 41:1587–1596

Álvarez G, Etxebeste I, Gallego D et al (2014) Optimization of traps for live trapping of pine wood nematode vector *Monochamus galloprovincialis*. J Appl Entomol. doi:10.1111/jen.12186

Alya AB, Hain FP (1985) Life histories of *M. carolinensis* and *M. titillator* (Coleoptera: Cerambycidae) in the piedmont of North Carolina. J Entomol Sci 20:390–397

Anbutsu H, Togashi K (1997a) Oviposition behavior and response to the oviposition scars occupied by eggs in *Monochamus saltuarius*. Appl Entomol Zool 32:541–549

Anbutsu H, Togashi K (1997b) Effects of spatio-temporal intervals between newly-hatched larvae on larval survival and development in *Monochamus alternatus* (Coleoptera: Cerambycidae). Res Popul Ecol 39:181–189

Anbutsu H, Togashi K (2000) Deterrent oviposition response of *Monochamus alternatus* (Coleoptera: Cerambycidae) to oviposition scars occupied by eggs. Agric For Entomol 2:217–223

Anbutsu H, Togashi K (2001) Oviposition deterrent by female reproductive gland secretion in Japanese Pine Sawyer. J Chem Ecol 27:1151–1161

Anonymous (2005) Forest pests on the territories of the former USSR. https://www.eppo.int/QUARANTINE/special_topics/forestry_project/forestry.htm. Consulted on 30 Mar 2015

Arakawa Y, Togashi K (2004) Presence of the pine wood nematode, *Bursaphelenchus xylophilus*, in the spermatheca of the female *Monochamus alternatus*. Nematology 6:157–159

Audisio P, Cornacchia P, Fattorini L et al (2008) Selected beetle families in natural forests and Norway spruce stands at Vincheto di Celarda Nature Reserve and the effects of conservation actions (Coleoptera). Quaderni Conservazione Habitat 5:195–217

Averenskiy AI, Isaev AP (2011) Development of xylophagous groups in pesthole areas of *Dendrolimus superans sibiricus* Tschetv. in Central Yakutia forests. J Ecol Povolzhskaya 1:3–13

Averkiev I (1984) Atlas of forest insect pests, 2nd edn. Lesnaya Promyshlennost, Moscow

Bakke A, Kvamme T (1992) The pine sawyer (*Monochamus sutor*): distribution and life history in South Norway. Meddel Skogforsk 44:1–16

Baranchikov YN (1997) Siberian forest insects: ready for export. In: Britton KO (ed) Proceedings, exotic pests eastern forests, Nashville, pp 85–91

Baujard P, Boulbria A, Ham R et al (1979) Premières données sur la nématofaune associée aux dépérissements du pin maritime dans l'Ouest de la France. Ann Sci For 36:331–339

Behalová M (2006) Recent surveys for *Bursaphelenchus xylophilus* in the Czech Republic. EPPO Bull 36:467–469

Bergdahl DR, Halik S (1998) Inoculated *Pinus sylvestris* serve as longterm hosts for *Bursaphelenchus xylophilus*. In: Futai K, Togashi K, Ikeda T (eds) Proceedings IUFRO meeting on sustainability of pine forests in relation to pine wilt and decline. Shokado, Kyoto, pp 73–78

Berkvens N, Pasteels H, Damme N et al (2013) *Bursaphelenchus xylophilus* does not occur in Belgium, but what about its vectors, the *Monochamus* spp.? In: Schroder T (ed) Proceedings of the pine wilt disease conference, vol 169. Berichte aus dem Julius Kühn-Institut, pp 116–117

Bonifácio L (2009) Impacte e Evolução da Doença da Murchidão dos Pinheiros (Pine Wilt Disease) na Zona Afectada a Sul do Rio Tejo. PhD thesis in Ecology, Science Faculty of Lisbon University, Braunschweig

Bonifácio L, Sousa E (2011) Early detection methods for the detection of pine wood nematode infections in standing maritime pines, in Portugal. Silva Lusitana 19:49–60

Bonifácio L, Praias F, Sousa E (2012) Trapping *Monochamus galloprovincialis* (Coleoptera: Cerambycidae), vector of the pine wood nematode, with pine allelochemicals, in Portugal. Silva Lusitana 20:39–53

Bonifácio L, Sousa E, Naves P et al (2014) Efficacy of sulfuryl fluoride against the pine wood nematode, *Bursaphelenchus xylophilus* (Nematoda: Aphelenchidae), in maritime pine boards. Pest Manage Sci 70:6–13

Boulanger Y, Sirois L, Hébert C (2010) Distribution of saproxylic beetles in a recently burnt landscape of the northern boreal forest of Quebec. For Ecol Manage 260:1114–1123

Boulanger Y, Sirois L, Hebert C (2013) Distribution patterns of three long-horned beetles (Coleoptera: Cerambycidae) shortly after fire in boreal forest: adults colonizing stands versus progeny emerging from trees. Environ Entomol 42:17–28

Braasch H (2001) *Bursaphelenchus* species in conifers in Europe: distribution and morphological relationships. EPPO Bull 31:127–142

Braasch H, Metge K, Burgermeister W (1999) *Bursaphelenchus* species in conifer woods in Germany and their ITS-RFLP patterns. Nachr Dtsch Pflanzenschutzd 51:312–320

Braasch H, Tomiczek C, Metge K et al (2001) Records of *Bursaphelenchus* spp. (Nematoda: Parasitaphelenchidae) in coniferous timber imported from the Asian part of Russia. For Pathol 31:129–140

Brelih S, Drovenik B, Pirnat A (2006) Material for the beetle fauna (Coleoptera) of Slovenia. Scopolia 58:1–442

Brustel H, Berger P, Cocquempot C (2002) Catalogue des Vesperidae et des Cerambycidae de la faune de France (Coleoptera). Ann Soc Entomol Fr 38:443–461

Burgermeister W, Metge K, Braasch H et al (2005) ITS– RFLP patterns for differentiation of 26 *Bursaphelenchus* species (Nematoda: Parasitaphelenchidae) and observations on their distribution. Russ J Nematol 13:29–42

Burgermeister W, Braasch H, Metge K et al (2009) ITS-RFLP analysis, an efficient tool for identification of *Bursaphelenchus* species. Nematology 11:649–668

Burnes T, Wingfield M, Baker K et al (1985) The pine wood nematode in jack pine infected with Dwarf mistletoe. Forest Sci 31:866–870

Canakçıoğlu H, Mol T (1998) Forest entomology: harmful and beneficial insects. Istanbul University Publ, Istanbul

Carling DE (1984) Some insect associates of the pinewood nematode in eastern Virginia. Can J For Res 14:826–829

Castagnone C, Abad P, Castagnone-Sereno P (2005) Satellite DNA based species specific identification of single individuals of the pinewood nematode *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae). Eur J Plant Pathol 112:191–193

Cesari M, Marescalchi O, Franchardi V et al (2005) Taxonomy and phylogeny of European *Monochamus* species: first molecular and karyological data. J Zool Syst Evol Res 43:1–7

Cheng HR, Lin MS, Qian RJ (1986) A study on morphological diagnosis and pathogenicity of the pine wood nematode. J Nanjing Agric Univ 2:55–59

Cheng XY, Xie PZ, Cheng FX et al (2009) Competitive displacement of the native species *Bursaphelenchus mucronatus* by an alien species *Bursaphelenchus xylophilus* (Nematoda: Aphelenchida: Aphelenchoididae): a case of successful invasion. Biol Invasions 11:205–213

Cherepanov AI (1990) Cerambycidae of northern Asia, vol 3, Lamiinae, Part 1. Amerind Publishing, New Delhi

Chu D, Liu ZF, Zhang QH (1990) A study on the regularity of diffusion and extension of *Monochamus sutor* L. in the burned areas of the Great Xinghan Mountains. J Beijing For Univ 12:49–53

Ciesla WM (2011) Forest entomology. A global perspective. Wiley, Chichester

Cocquempot C (2006) Alien longhorned beetles (Coleoptera Cerambycidae): original interceptions and introductions in Europe, mainly in France, and notes about recently imported species. Redia 89:35–50

Cocquempot C, Lindelöw A (2010) Longhorn beetles (Coleoptera: Cerambycidae). BioRisk 4:193–218

CSCF-karch (2015) http://lepus.unine.ch/carto/index.php. Consulted on 1 Mar 2015

Danilevskaya GB, Danilevsky ML, Hadulla K et al (2009) Cerambycidae collected in North-East Kazakhstan by an international collecting trip 2005 (Coleoptera). Entomol Z (Stuttgart) 119:171–178

Danilevsky ML (2012) Additions and corrections to the new Catalogue of Palaearctic Cerambycidae (Coleoptera) edited by I. Löbl and A. Smetana, 2010. Part. III. Munis Entomol Zool 7:109–173

Danilevsky ML (2014) A check-list of Longicorn beetles (Coleoptera, Cerambycoidea) of Europe. www.cerambycidae.narod.ru. Updated 20 Aug 2014

Daub M (2008) Investigations on pathogenicity, invasion biology and population dynamics of the pine wood nematode Bursaphelenchus xylophilus (Steiner & Buhrer 1934) Nickle 1970 in European conifers. PhD thesis, Rheinischen Friedrich-Wilhelms University

David G (2014) Etude des capacités de dispersion de Monochamus galloprovincialis vecteur du nématode du pin *Bursaphelenchus xylophilus.* Thèse Doctorat, Université de Bordeaux

David G, Giffard B, Piou D et al (2014) Dispersal capacity of *Monochamus galloprovincialis*, the European vector of the pine wood nematode, on flight mills. J Appl Entomol 138:566–576

de Guiran G, Boulbria A (1986) Le nématode des pins. Caractéristiques de la souche française et risque d'introduction et d'extension de Bursaphelenchus xylophilus en Europe. EPPO Bull 16:445–452

Dillon ES, Dillon LS (1941) The tribe Monochamini in the Western Hemisphere (Coleoptera: Cerambycidae), vol 1, Reading Public Museum and Art Gallery Scientific Publication. Reading Public Museum and Art Gallery, Reading

Dodds KJ, Graber C, Stephen FM (2001) Facultative intraguild predation by larval cerambycide on bark beetle larvae. Environ Entomol 30:17–22

Donis J, Zdors L, Snepsts G et al (2009) Modeling survival of trees after forest fires in Latvia. In: Proceeding from the SNS meeting, Kokkola

Dropkin VH, Foudin A, Kondo E et al (1981) Pinewood nematode: a threat to U.S. forests? Plant Dis 65:1022–1027

Dwinell LD (1985) Relative susceptibilities of five pine species to three populations of the pinewood nematode. Plant Dis 69:440–442

Dwinell LD (1990) Heat-treating and drying southern pine lumber infested with pinewood nematodes. For Prod J 40:53–56

Dwinell LD (1997) Pinewood nematode: regulation and mitigation. Annu Rev Phytopathol 35:153–166

Dwinell LD, Nickle WR (1989) An overview of the pine wood nematode ban in North America, General technical report SE-55. USDA Forest Service, Southeastern Forest Experiment Station, Asheville

Edwards OR, Linit MJ (1991) Oviposition behaviour of *Monochamus carolinensis* (Coleoptera: Cerambycidae) infested with the pinewood nematode. Ann Entomol Soc Am 84:319–323

Ehnström B, Axelsson R (2002) Insektgnag i bark och ved. ArtDatabanken, SLU, Uppsala

Ehnström B, Holmer M (2007) Nationalnyckeln till Sveriges flora och fauna. Skalbaggar: Långhorningar. Coleoptera. ArtDatabanken, SLU, Uppsala

Enda N (1976) Life history of *Monochamus alternatus* (Coleoptera: Cerambycidae). Shinrin-boeki 25:182–185

EPPO (2013) EPPO standard PM 7/4 (3) *Bursaphelenchus xylophilus*. EPPO Bull 43:105–118

Erbilgin N, Raffa KF (2000) Opposing effects of host monoterpenes on responses by two sympatric species of bark beetles to their aggregation pheromone. J Chem Ecol 26:2527–2548

Evans HF (2007) ISPM 15 treatments and residual bark: how much bark matters in relation to founder populations of bark and wood boring beetles. In: Evans H, Oszako T (eds) Alien invasive species and international trade. Forest Research Institute, Warsaw, pp 149–155

Evans HF, McNamara DG, Braasch H et al (1996) Pest risk analysis (PRA) for the territories of the European Union (as PRA area) on *Bursaphelenchus xylophilus* and its vectors in the genus *Monochamus*. OEPP Bull 26:199–249

Evans HF, Moraal LG, Pajares JA (2004) Biology, ecology and economic importance of Buprestidae and Cerambycidae. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Dordrecht, pp 447–474

Evans S, Evans HF, Ikegami M (2008) Modelling PWN-induced wilt expression: a mechanistic approach. In: Mota M, Vieira P (eds) Pine wilt disease: a worldwide threat to forest ecosystems. Springer, London, pp 259–278

Fan JT, Sun JH, Shi J (2007) Attraction of the Japanese pine sawyer, *Monochamus alternatus*, to volatiles from stressed host in China. Ann For Sci 64:67–71

Fauziah BA, Hidaka T, Tabata K (1987) The reproductive behavior of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae). Appl Entomol Zool 22:272–285

Fielding NJ, Evans HF (1996) The pine wood nematode *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickle (= *B. lignicolus* Mamiya and Kiyohara): an assessment of the current position. Forestry 69:35–46

Fierke MK, Skabeikis DD, Millar JG et al (2012) Identification of a male-produced aggregation pheromone for *Monochamus scutellatus* scutellatus and an attractant for the congener *Monochamus notatus* (Coleoptera: Cerambycidae). J Econ Entomol 105:2029–2034

Foit J (2010) Distribution of early-arriving saproxylic beetles on standing dead Scots pine trees. Agric For Entomol 12:133–141

Fonseca L, Cardoso JMS, Lopes A et al (2012) The pinewood nematode, *Bursaphelenchus xylophilus*, in Madeira Island. Helminthologia 49:96–103

Fonseca L, Santos M, Queirós R et al (2014) Laboratory tests on the elimination of the pinewood nematode (*Bursaphelenchus xylophilus*) in *Pinus pinaster* wood by high pressure. Eur J Wood Prod 72:825–827

Francardi V, Pennacchio F (1996) Note sulla bioecologia di *Monochamus galloprovincialis* (Oliver) in Toscana e in Ligúria (Coleoptera; Cerambycidae). Redia 79:153–169

Francardi V, Pennacchio F, de Silva J (1998) Attack distribution on maritime pine bole by longhorn beetles in Tuscany (Coleoptera Cerambycidae). Redia 81:135–142

Francardi V, Rumine P, de Silva J (2003) On microbial control of *Monochamus galloprovincialis* (Olivier) (Coleoptera Cerambycidae) by means of *Beauveria bassiana* (Bals.) Vuillemin (Deuteromycotina Hyphomycetes). Redia 86:129–132

Francardi V, Silva J, Pennacchio F et al (2009) Pine volatiles and terpenoid compounds attractive to European xylophagous species, vectors of *Bursaphelenchus* spp. nematodes. Phytoparasitica 37:295–302

François C, Castagnone C, Boonham N et al (2007) Satellite DNA as a target for TaqMan real-time PCR detection of the pinewood nematode, *Bursaphelenchus xylophilus*. Mol Plant Pathol 8:803–809

Fuchs AG (1937) Neue parasitische und halbparasitische Nematoden bei Borkenkafern und einige andere Nematoden. I. Teil. Zool Jahrb, Abteil Syst, Okol Geogr Tiere 70:291–380

Fukushige H (1990) The number of *Bursaphelenchus xylophilus* carried by *Monochamus alternatus* and some possible factors regulating the number. Jpn J Nematol 20:18–24

Futai K (2008) Pine wilt in Japan: from first incidence to the present. In: Zhao BG, Futai K, Sutherland JR et al (eds) Pine wilt disease. Springer, Tokyo

Futai K (2013) Pine wood nematode, *Bursaphelenchus xylophilus*. Annu Rev Phytopathol 51:61–83. doi:10.1146/annurev-phyto-081211-172910

Futai K, Furuno T (1979) The variety of resistances among pine species to pinewood nematode, *Bursaphelenchus lignicolus*. Bull Kyoto Univ For 51:23–26

Gallego D, Sánchez-Garcia FD, Mas H et al (2012) Estudio de la capacidad de vuelo a larga distancia de *Monochamus galloprovincialis* (Olivier 1795) (Coleoptera: Cerambycidae) en un moisaco agro-forestal. Bol San Veg Plagas 38:109–123

Gavrikov V, Vetrova V (1991) Effects of Fir Sawyer Beetle on spatial structure of Siberian Fir stands. In: Baranchikov YN, Mattson WJ, Hain FP et al (eds) Forest insect guilds: patterns of interaction with host trees. Proc Joint IUFRO working party symp, Abakan, Siberia. USDA For Serv Gen Tech Rep NE-153, pp 385–388

Georgebits RP (1974) Wood- and bark-eating insects on *Pinus halepensis* in Attica (observations made in 1967–1971). Institouton Dasikon Ereunon Upourgeion Georgias 60:1–47

Georgiev G, Simov N, Stojanova A et al (2005a) New and interesting records of longhorn beetles (Coleoptera: Cerambycidae) in some Bulgarian mountains. Acta Zool Bulgarica 57:131–138

Georgiev G, Doychev D, Migliaccio E (2005b) Studies on cerambycid fauna (Coleoptera: Cerambycidae) in Western Rhodopes in Bulgaria. For Sci 2:81–90

Georgiev G, Migliaccio E, Doychev D (2006) Longhorn beetles (Coleoptera: Cerambycidae) in Western Rhodopes (Bulgaria). In: Beron P (ed) Biodiversity of Bulgaria. 2. Biodiversity of Western Rhodopes (Bulgaria and Greece). Pensoft/National Museum of Natural History, Sofia, pp 347–360

Giblin-Davis RM (1993) Interactions of nematodes with insects. In: Khan MW (ed) Nematode interactions. Chapman and Hall, London, pp 302–344

Giblin-Davis RM, Swan JL, Kaya HK (1984) *Bursaphelenchus kevini* n. sp. (Aphelenchida: Aphelenchoididae), an associate of bees in the genus *Halictus* (Hymenoptera: Halictidae). Rev Nématol 7:177–187

Giblin-Davis RM, Mundo-Ocampo M, Baldwin JG et al (1993) Description of *Bursaphelenchus abruptus* n. sp. (Nemata: Aphelenchoididae), an associate to a digger bee. J Nematol 25:161–172

Giblin-Davis RM, Kanzaki N, Ye W et al (2006) Morphology and description of *Bursaphelenchus platzeri* n. sp (Nematoda: Parasitaphelenchidae), an associate of nitidulid beetles. J Nematol 38:150–157

González CF, Vives E, Zuzarte AS (2007) Nuevo catálogo de los Cerambycidae (Coleoptera) de la Península Ibérica, islas Baleares e islas atlánticas: Canarias, Açores y Madeira. Monografías SEA 12, Sociedad Entomológica Aragonesa, Zaragoza

Gruffudd H, Evans HF, Jenkins T (2013) Using an evapo-transpiration model to predict the current and future range and severity of pine wilt disease caused by pine wood nematode, *Bursaphelenchus xylophilus* in Europe. In: Schroder T (ed) Proceedings of the pine wilt disease conference, vol 169. Berichte aus dem Julius Kühn-Institut, pp 82–88

Gu J, Braasch HM, Burgermeister W et al (2006) Records of *Bursaphelenchus* spp. intercepted in importing packaging wood at Ningbo, China. For Pathol 36:323–333

Gu J, Wang J, Braasch H et al (2011) Morphological and molecular characterization of mucronate isolates (‘M’ form) of *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae). Russ J Nematol 19:103–120

Gutowski JM, Zielinski S, Biwo T (2011) Longhorn beetles (Coleoptera: Cerambycidae) of Romincka forest. Opole Sci Soc Nat J 44:145–171

Haack RA, Britton KO, Brockerhoff EG et al (2014) Effectiveness of the International Phytosanitary Standard ISPM No. 15 on reducing wood borer infestation rates in wood packaging material entering the United States. PLoS One 9, e96611. doi:10.1371/journal.pone.0096611

Halbig P (2013) Flight activity of longhorn beetles Monochamus sartor and M. sutor: attractiveness and tree produced volatiles. Thesis, Diplom-Ingenieurin in Phytomedizin, University of Natural Resources and Life Sciences, Vienna

Halbig P, Menschhorn P, Krehan H et al (2014) Flugaktivität der Bockkäfer *Monochamus sartor* und *Monochamus sutor*: Attraktivität insekten- und baumbürtiger volatiler Substanzen. Silva Fera 3:53–59

Han JH, Yoon CH, Shin SC et al (2007) Seasonal occurrence and morphological measurements of pine sawyer, *Monochamus saltuarius* adults (Coleoptera: Cerambycidae). J Asia-Pac Entomol 10:63–67

Hanks LM (1999) Influence of the larval host plant on reproductive strategies of cerambycid beetles. Annu Rev Entomol 44:483–505

Hellrigl KG (1971) Die bionomie der Europaischen *Monochamus*–arten (Coleopt., Cerambycid.) und ihre bedeutung fur die forst- und holzwirtschaft. Redia 52:367–509

Hernández R, Ortiz A, Pérez V et al (2011) *Monochamus galloprovincialis* (Olivier, 1795) (Coleoptera: Cerambycidae), comportamiento y distancias de vuelo. Bol San Veg Plagas 37:79–96

Hillocks RJ (2001) Coffee: is it still a viable cash crop for smallholders in Africa? Outlook Agric 30:205–212

Hillocks RJ, Phiri NA, Overfield D (1999) Coffee pest and disease management options for smallholders in Malawi. Crop Prot 18:99–206

Hjältén J, Johansson T, Alinvi O et al (2007) The importance of substrate type, shading and scorching for the attractiveness of dead wood to saproxylic beetles. Basic Appl Ecol 8:364–376

Hoskovec M (2010) A check-list of Longhorn beetles (Coleoptera, Cerambycidae) of the Czech Republic and the Slovak Republic. http://www.cerambyx.uochb.cz/. Last changes in 30 May 2010, consulted on 30 Mar 2015

Hoyer U, Burgermeister W, Braasch H (1998) Identification of *Bursaphelenchus* species (Nematoda, Aphelenchoididae) on the basis of amplified ribosomal DNA (ITS–RFLP). Nachr Deut Pflanzenschutzd 50:273–277

Hoyer-Tomiczek U, Tomiczek C (2005) PHRAME project. How dangerous is the pinewood nematode for Europe? Forstschutz Aktuell 34:21–24

Hughes AL (1981) Differential male mating success in the white spotted sawyer *Monochamus scutellatus* (Coleoptera: Cerambycidae). Ann Entomol Soc Am 74:180–184

Hulme PE (2007) Biological invasions in Europe: drivers, pressures, states, impacts and responses. In: Hester R, Harrison RM (eds) Biodiversity under threat, vol 25, Issues in environmental science and technology. Royal Society of Chemistry, Cambridge, pp 56–80

Humphry SJ, Linit MJ (1989) Effect of pinewood nematode density on tethered flight of *Monochamus carolinensis* (Coleoptera: Cerambycidae). Environ Entomol 18:670–673

Hunt DJ (2008) A checklist of the Aphelenchoidea (Nematoda: Tylenchina). J Nematode Morphol Syst 10:99–135

Ibeas F, Gallego D, Diez JJ et al (2007) An operative kairomonal lure for managing pine sawyer beetle *Monochamus galloprovincialis* (Coleoptera: Cerambycidae). J Appl Entomol 131:13–20

Ibeas F, Diez JJ, Pajares J (2008) Olfactory sex attraction and mating behaviour in the pine sawyer *Monochamus galloprovincialis* (Coleoptera: Cerambycidae). J Insect Behav 21:101–110

Ilic N, Curcic S (2013) The long-horn beetles (Coleoptera: Cerambycidae) of Rtanj mountains (Serbia). Acta Entomol Serbica 18:69–94

Inácio ML, Nóbrega F, Vieira P et al (2015) First detection of *Bursaphelenchus xylophilus* associated with *Pinus nigra* in Portugal and in Europe. For Pathol. doi:10.1111/efp.12162

IPPC (International Plant Protection Convention) (2002) International standards for phytosanitary measures: guidelines for regulating wood packaging material in international trade, Publication No 15. Food and Agriculture Organization of the United Nations, Rome

IPPC (International Plant Protection Convention) (2013) International standards for phytosanitary measures: revision of ISPM 15, Regulation of wood packaging material in international trade (2009). Food and Agriculture Organization of the United Nations, Rome

Isaev AS (1995) The principles and methods of integrated protection of Siberian forests from destructive insect. In: Hain FP, Salom SM, Ravlin WF et al (eds) Behavior, population dynamics and control of forest insects: proceedings of a joint IUFRO conference work part S2.07-05 and S2.07-06. IUFRO, Maui, pp 628–634

Isaev A, Krivosheina N (1976) The principles and methods of the integrated protection of Siberian forests from destructive insects. In: Tamm CO (ed) Man and the boreal forest. Ecol Bull 21:121–124

Ishibashi N, Kondo E (1977) Occurrence and survival of the dispersal forms of pine wood nematode, *Bursaphelenchus lignicolus* Mamiya and Kiyohara. Appl Entomol Zool 12:293–302

Izhevsky SS, Nikita NB, Volkov OG et al (2005) Illustrated guide to xylophagous pests of forests and timber of Russia. Grif K, Tula

Izumi S, Ichikawa T, Okamoto H (1990) The character of larval sounds of the Japanese pine sawyer, *Monochamus alternatus* Hope. Jpn J Appl Entomol Zool 34:15–19

Jacobs K, Wingfield MJ, Pashenova NV et al (2000) A new *Leptographium* species from Russia. Mycol Res 104:1524–1539

James R, Tisserat N, Todd T (2006) Prevention of pine wilt of scots pine (*Pinus sylvestris*) with systemic abamectin injections. Arboricult Urban For 32:195–201

Jankowiak R (2010) Grzyby z grupy *Ophiostoma* sensu lato związane z kózkowatymi *Monochamus sutor* (L.) i *Rhagium inquisitor* (L.) w południowej Polsce. Sylwan 154:381–387

Jankowiak R (2013) Assessing the virulence of ophiostomatoid fungi associated with the pine-infesting weevils to scots pine *Pinus sylvestris* L. seedlings. Acta Agrobot 66:85–94

Jankowiak R, Rossa R (2007) Filamentous fungi associated with *Monochamus galloprovincialis* and *Acanthocinus aedilis* (Coleoptera: Cerambycidae) in Scots pine. Pol Bot J 52:143–149

Jankowiak R, Rossa R, Bilański P (2007) Contribution to pathogenicity of three blue-stain fungi associated with the pine sawyer beetle *Monochamus galloprovincialis* (Coleoptera: cerambycidae) to Scots pine in Poland. Phytopathol Pol 46:37–46

Jikumaru S, Togashi K, Taketsune A et al (1994) Oviposition biology of *Monochamus saltuarius* (Coleoptera: Cerambycidae) at a constant temperature. Appl Entomol Zool 29:555–561

Jurc M, Urek G, Širca S et al (2003) Pine wood nematode, *Bursaphelenchus xylophilus* (Steiner & Buhrer, 1934) Nickle, 1970 – a new threat to forests in Slovenia? Zb gozd lesar 72:121–156

Jurc M, Bojovic S, Pavlin R et al (2012a) Biodiversity of saproxylic beetles of pine forests in Slovenia with emphasis on *Monochamus* species. In: Jurc M (ed) Saproxylic beetles in Europe: monitoring, biology and conservation. Slovenian Forestry Institute, Ljubljana, pp 23–32

Jurc M, Bojovic S, Fernández MF et al (2012b) The attraction of cerambycids and other xylophagous beetles, potential vectors of *Bursaphelenchus xylophilus*, to semiochemicals in Slovenia. Phytoparasitica 40:337–349

Kamata N (2008) Integrated pest management of pine wilt disease in Japan: tactics and strategies. In: Zhao BG, Futai K, Sutherland JR et al (eds) Pine wilt disease. Springer, Tokyo, pp 304–322

Kanzaki N, Taki H, Masuya H et al (2011) Diversity of stag beetle-associated nematodes in Japan. Environ Entomol 40:281–288

Kanzaki N, Taki H, Masuya H et al (2012) *Bursaphelenchus tadamiensis* n. sp. (Nematoda: Aphelenchoididae), isolated from a stag beetle, *Dorcus striatipennis* (Coleoptera: Lucanidae), from Japan. Nematology 14:223–233

Kawai M, Shoda-Kagaya E, Maehara T et al (2006) Genetic structure of pine sawyer *Monochamus alternatus* populations in northeast Asia consequences of the spread of pine wilt disease. Environ Entomol 35:569–579

Kazuya T, Soejima T, Suzuki T et al (1999) Studies on development of a novel trunk-injection agent against the pine wilt disease. Pest Manag Sci 56:10

Kenis M, Hilszczanski J (2004) Natural enemies of Cerambycidae and Buprestidae infesting living trees. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Dordrecht, pp 475–498

Kerris T, Guerroudj A (1991) Note Technique sur le Dépérissements des pinèdes: diagnostic et méthodes de lutte. Doc Int INRFI:1–3

Kim DS, Lee SM, Huh HS et al (2009) Escape of pine wood nematode, *Bursaphelenchus xylophilus*, through feeding and oviposition behavior of *Monochamus alternatus* and *M. saltuarius* (Coleoptera: Cerambycidae) adults. Korean J Appl Entomol 48. doi:10.5656/KSAE.2009.48.4.527

Kirisits T (2004) Fungal associates of European bark beetles with special emphasis on the Ophiostomatoid fungi. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Dordrecht, pp 181–235

Kishi Y (1995) Pine wood nematode and the Japanese pine sawyer. Thomas, Tokyo

Kobayashi F (1988) The Japanese pine sawyer. In: Berryman AA (ed) Dynamics of forest insect populations: patterns, causes, implications. Plenum Press, New York, pp 431–454

Kobayashi F, Yamane A, Ikeda T (1984) The Japanese pine sawyer beetle as the vector of pine wilt disease. Annu Rev Entomol 29:115–135

Kobayashi H, Yamane A, Iwata R (2003) Mating behavior of the pine sawyer, *Monochamus saltuarius* (Coleoptera: Cerambycidae). Appl Entomol Zool 38:141–148

Kobzar VF (2009) Forecast of breeding stem insects. J For Eng Acad St Petersburg 187:151–161

Komonen A (2007) Are we conserving peripheral populations? An analysis of range structure of longhorn beetles (Coleoptera: Cerambycidae) in Finland. J Insect Conserv 11:281–285

Kopinga J, Moraal LG, Verwer CC et al (2010) Phytosanitary risks of wood chips. Alterra report 2059, Wageningen

Korma OM (2009) Komplek nematod derevyny sosny zvychaynoyi (*Pinus sylvestris* L.) Polissya Ukrayiny ta metody yikh monitorynhu. Natsionalnyy Universytet Bioresursiv i Pyrodokorystuvannya Ukrayiny

Kosaka H, Aikawa T, Ogura N et al (2001) Pine wilt disease caused by the pine wood nematode: the induced resistance of pine trees by the avirulent isolates of nematode. Eur J Plant Pathol 107:667–675

Koutroumpa FA (2007) Biologie et phylogeographie de *Monochamus galloprovincialis* (Coleoptera, Cerambycidae) vecteur du nematode du pin en Europe. PhD thesis, Université Orleans

Koutroumpa FA, Vincent B, Roux-Morabito G et al (2008) Fecundity and larval development of *Monochamus galloprovincialis* (Coleoptera Cerambycidae) in experimental breeding. Ann For Sci 65:707

Koutroumpa F, Salle A, Lieutier F et al (2009) Feeding and oviposition preferences of *Monochamus galloprovincialis* on its main hosts *Pinus sylvestris* and *Pinus pinaster*. Entomol Hell 18:35–46

Koutroumpa F, Rougon D, Bertheau C et al (2013) Evolutionary relationships within European *Monochamus* (Coleoptera: Cerambycidae) highlight the role of altitude in species delineation. Biol J Linn Soc 109:354–376

Kovács T (1997) Magyarországi cincérek tápnövény- és lelõhelyadatai II. (Coleoptera: Cerambycidae). Folia Historico Naturalia Musei Matraensis 22:247–255

Kovács T, Hegyessy G, Medvegy M (1999) Foodplant data of longhorn beetles from Europe (Coleoptera: Cerambycidae). Folia Historico Naturalia Musei Matraensis 23:333–339

Kulinich OA, Kruglic L, Eroshenko AS et al (1994) Occurrence and distribution of the nematode *Bursaphelenchus mucronatus* in the Russian Far East. Russ J Nematol 2:113–119

Kuroda K (1991) Mechanism of cavitation development in the pine wilt disease. Eur J For Pathol 21:82–89

Kvamme T, Magnusson C (2006) Furuvednematoden – like aktuell trussel mot skogen. Norsk Skogbruk 52:24–25

La YJ, Moon YS, Yeo WH et al (1999) Recent status of pine wilt disease in Korea. In: Futai K, Togashi K, Ikeda T (eds) Sustainability of pine forests in relation to pine wilt and decline. Proceedings international symposium. Shokado, Tokyo, pp 141–149

Leal I, Allen E, Foord B et al (2015) Detection of living *Bursaphelenchus xylophilus* in wood, using reverse transcriptase loop-mediated isothermal amplification (RT-LAMP). For Pathol 45:134–148

Li H, Shen P, Fu P et al (2007) Characteristics of the emergence of *Monochamus alternatus*, the vector of *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae), from *Pinus thunbergii* logs in Nanjing, China, and of the transmission of the nematodes through feeding wounds. Nematology 9:807–816

Lieutier F, Yart A, Salle A (2009) Stimulation of tree defenses by Ophiostomatoid fungi can explain attack success of bark beetles on conifers. Ann For Sci 66:801 (22 p)

Linit MJ (1985) Continuous laboratory culture of *Monochamus carolinensis* with notes on larval development. Ann Entomol Soc Am 78:212–213

Linit MJ (1987) The insect component of the pine wilt disease in the United States. In: Wingfield M (ed) Pathogenicity of the pine wood nematode. APS Press, Saint Paul, pp 26–39

Linit MJ (1988) Nematode-vector relationships in the pine wilt disease system. J Nematol 20:227–235

Linit MJ (1989) Temporal pattern of pinewood nematode exit from the insect vector *Monochamus carolinensis*. J Nematol 21:105–107

Linit MJ (1990) Transmission of pinewood nematode through feeding wounds of *Monochamus carolinensis* (Coleoptera: Cerambycidae). J Nematol 22:231–236

Linit MJ, Kondo E, Smith MT (1983) Insects associated with the pinewood nematode *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoidae), in Missouri. Environ Entomol 12:467–470

Linsley EG (1959) Ecology of cerambycidae. Annu Rev Entomol 4:99–138

López S, Goldarazena A (2012) Flight dynamics and abundance of *Ips sexdentatus* (Coleoptera: Curculionidae: Scolytinae) in different sawmills from Northern Spain: differences between local *Pinus radiata* (Pinales: Pinaceae) and Southern France incoming *P. pinaster* timber. Psyche 2012, ID 145930:1–6. doi:10.1155/2012/145930

Macias-Samano JE, Wakarchuk D, Millar JG et al (2012) 2-Undecyloxy-1-ethanol in combination with other semiochemicals attracts three *Monochamus* species (Coleoptera: Cerambycidae) in British Columbia, Canada. Can Entomol 144:821–825

Maehara N (2008) Reduction of *Bursaphelenchus xylophilus* (Nematoda: Parasitaphelenchidae) population by inoculating *Trichoderma* spp. into pine wilt-killed trees. Biol Control 44:61–66

Maehara N, Futai K (1996) Factors affecting both the numbers of the pinewood nematode, *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae), carried by the Japanese pine sawyer, *Monochamus alternatus* (Coleoptera: Cerambycidae), and the nematode's life history. Appl Entomol Zool 31:443–452

Maehara N, Futai K (1997) Effect of fungal interactions on the numbers of the pinewood nematode, *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae), carried by the Japanese pine sawyer, *Monochamus alternatus* (Coleoptera: Cerambycidae). Fundam Appl Nematol 20:611–617

Magnusson C, Schroeder LM (1989) First record of a *Bursaphelenchus*-species (Nematoda) in *Monochamus* beetles in Scandinavia. Anz Schaedlingsk Pflanz Umweitschutz 62:53–54

Magnusson C, Thunes KH, Nyeggen H et al (2007) Surveillance of pine wood nematode (PWN) *Bursaphelenchus xylophilus*. Norwegian surveys 2000–2006. Bioforsk Report 2:1–29

Malek RB, Appleby JE (1984) Epidemiology of pine wilt in Illinois. Plant Dis 68:180–186

Mamiya Y (1972) Pine wood nematode, *Bursaphelenchus lignicolus* Mamiya and Kiyohara, as a causal agent of pine wilting disease. Rev Plant Prot Res 5:46–60

Mamiya Y (1975) The life history of the pine wood nematode, *Bursaphelenchus lignicolus*. Jpn J Nematol 5:16–25

Mamiya Y (1983) Pathology of the pine wilt disease caused by *Bursaphelenchus xylophilus*. Annu Rev Phytopathol 21:201–220

Mamiya Y (1984) The pine wood nematode. In: Nickle WR (ed) Plant and insect nematoda. Marcel Dekker, New York, pp 589–626

Mamiya Y (1988) History of pine wilt disease in Japan. J Nematol 20:219–226

Mamiya Y, Enda N (1972) Transmission of *Bursaphelenchus lignicolus* (Nematoda: Aphelenchoididae) by *Monochamus alternatus* (Coleoptera: Cerambycidae). Nematologica 18:159–162

Mamiya Y, Enda N (1979) *Bursaphelenchus mucronatus* n. sp. (Nematoda: Aphelenchoididae) from pine wood and its biology and pathogenicity to pine trees. Nematologica 25:353–361

Mamiya Y, Kiyohara T (1972) Description of *Bursaphelenchus lignicolus* n. sp. (Nematoda: Aphelenchoididae) from pine wood and histopathology of nematode infested trees. Nematologica 18:120–124

Markalas S (1997) Frequency and distribution of insect species on trunks in burnt pine forests of Greece. Mitteil Schweizerisch Entomol Gesell 70:57–61

Mas H, Hernandez R, Villaroya M et al (2013) Comportamiento de dispersión y capacidad de vuelo a larga distancia de *Monochamus galloprovincialis* (Olivier 1795). 6 Congreso forestall español. 6CFE01-393, 13p

Massey CL (1974) Biology and taxonomy of nematodes parasites and associates of bark beetles in the United States. Agriculture Handbook No 446. USDA, Fort Serv Agric, Washington

Masutti L, Battisti A, Faccoli M (2005) Insect fauna of the *Pinus nigra* group in Italy. In: Lieutier F, Ghaioule D (eds) Entomological research in Mediterranean forest ecosystems. INRA, Versailles, pp 79–87

McNamara DG, Stoen M (1988) A survey for *Bursaphelenchus* spp. in pine forests in Norway. Bull OEPP 18:353–363

Mejri M, Naves P, Sousa E et al (2014) Distribution and hosts of *Monochamus galloprovincialis* in Tunisia. Tunis J Plant Prot 9:171–176

Meyer M (2002) Untersuchungen zur Verbreitung der Langhornböcke (Monochamus spp.) in Deutschland und zu deren Bedeutung als Vektoren für holzbewohnende Nematoden als Beitrag zu einer Risikoanalyse für *Bursaphelenchus xylophilus* (Steiner & Buhrer, 1934) Nickle 1970. Diploma thesis, Faculty of Forest-, Geo- and Hydro-Sciences, Technical University, Dresden

Migliaccio E, Georgiev G, Mirchev P (2004) Studies on cerambycid fauna (Coleoptera: Cerambycidae) of the Vitosha mountain, Bulgaria. Acta Zool Bulg 56:137–144

Mihajlovic L (2008) The most important insect pest species on pine, spruce and fir in Serbia. Sumarstvo 60:65–81

Mikaia N, Devdariani T, Gninenko Y (2010) Representatives of nematodes of the genus *Bursaphelenchus* (Aphelenchida, Parasitophelenchidae) in Georgia. Bull Georg Natl Acad Sci 4:146–151

Miller MC (1985) The effect of *Monochamus tittilator* (F.) (Col., Cerambycidae) foraging on the emergence of *Ips calligraphus* (Germ.) (Col., Scolytidae) insect associates. J Appl Entomol 100:189–197

Miller DR, Asaro C, Crowe C et al (2011) Bark beetle pheromones and pine volatiles: attractant kairomone lure blend for longhorn beetles (Cerambycidae) in pine stands of the Southeastern United States. J Econ Entomol 104:1245–1257

Mota MM, Braasch H, Bravo MA et al (1999) First report of *Bursaphelenchus xylophilus* in Portugal and in Europe. Nematology 1:727–734

Mota M, Futai K, Vieira P (2009) Pine wilt disease and the pinewood nematode, *Bursaphelenchus xylophilus*. In: Ciancio A, Mukerji KG (eds) Integrated management fruit crops and forest nematodes. Springer, Dordrecht, pp 253–274

Naves P, Sousa E (2009) Threshold temperatures and degree-day estimates for development of post-dormancy larvae of *Monochamus galloprovincialis* (Coleoptera: Cerambycidae). J Pest Sci 82:1–6

Naves P, Kenis M, Sousa E (2005) Parasitoids associated with *Monochamus galloprovincialis* (Oliv.) (Coleoptera: Cerambycidae) within the pine wilt nematode-affected zone in Portugal. J Pest Sci 78:57–62

Naves P, Camacho S, Sousa E et al (2006a) Entrance and distribution of the pinewood nematode, *Bursaphelenchus xylophilus*, on the body of its vector in Portugal, *Monochamus galloprovincialis* (Coleoptera: Cerambycidae). Entomol Generali 29:71–80

Naves P, Sousa E, Quartau J (2006b) Feeding and oviposition preferences of *Monochamus galloprovincialis* for some conifers under laboratory conditions. Entomol Exp Appl 120:99–104

Naves P, Sousa E, Quartau J (2006c) Reproductive traits of *Monochamus galloprovincialis* (Coleoptera; Cerambycidae) under laboratory conditions. Bull Entomol Res 96:289–294

Naves P, Camacho S, Sousa E et al (2007a) Transmission of the pine wood nematode *Bursaphelenchus xylophilus* through feeding activity of *Monochamus galloprovincialis* (Coleoptera; Cerambycidae). J Appl Entomol 131:21–25

Naves P, Camacho S, Sousa E et al (2007b) Transmission of the pine wood nematode *Bursaphelenchus xylophilus* through oviposition activity of *Monochamus galloprovincialis* (Coleoptera: Cerambycidae). Entomol Fenn 18:193–198

Naves P, Sousa E, Quartau J (2007c) Winter dormancy of the pine sawyer *Monochamus galloprovincialis* (Col., Cerambycidae) in Portugal. J Appl Entomol 131:669–673

Naves P, Sousa E, Rodrigues JM (2008) Biology of *Monochamus galloprovincialis* (Coleoptera, Cerambycidae) in the pine wilt disease affected zone, Southern Portugal. Silva Lusitana 16:132–147

Nickle WR (1970) A taxonomic review of the genera of the Aphelenchoidea (Fuchs, 1937) Thorne, 1949 (Nematoda: Tylenchida). J Nematol 2:375–392

Nickle WR, Golden AM, Mamiya Y et al (1981) On the taxonomy and morphology of the pine wood nematode, *Bursaphelenchus xylophilus* (Steiner & Buhrer 1934) Nickle 1970. J Nematol 13:385–392

Niu H, Zhao L, Sun J (2013) Phenotypic plasticity of reproductive traits in response to food availability in invasive and native species of nematode. Biol Invasions 15:1407–1415

Nose M, Shiraishi S (2008) Breeding for resistance to pine wilt disease. In: Zhao BG, Futai K, Sutherland JR et al (eds) Pine wilt disease. Springer, Tokyo, pp 334–350

Novotný P, Modlinger R, Peskova V et al (2012) Evaluation of growth and health status of European black pine (*Pinus nigra* Arnold) provenances in central Bohemia at the age of 41 years. Zprávy Lesnického Výzkumu 57:266–273

Okland B, Skarpaas O, Schroeder M et al (2010) Is eradication of the pinewood nematode (*Bursaphelenchus xylophilus*) likely? An evaluation of current contigency plans. Risk Anal 30(9):1424–1439

Özdikmen H, Ali MA (2012) A preliminary list for longhorned beetles fauna of Iraq with additions to the Palaearctic Catalogue of Löbl and Smetana (2010) (Coleoptera: Cerambycidae). Munis Entomol Zool 7:174–183

Pajares JA, Ibeas F, Díez JJ et al (2004) Attractive responses by *Monochamus galloprovincialis* (Col., Cerambycidae) to host and bark beetle semiochemicals. J Appl Entomol 128:633–638

Pajares JA, Álvarez G, Ibeas F et al (2010) Identification and field activity of a male-produced pheromone in the pine sawyer beetle, *Monochamus galloprovincialis*. J Chem Ecol 36:570–583

Pajares JA, Álvarez G, Hall DR et al (2013) 2-(Undecyloxy)-ethanol is a major component of the male-produced aggregation pheromone of *Monochamus sutor*. Entomol Exp Appl 149:118–127

Palmisano AM, Ambrogioni L, Caroppo S (1994) First record of a *Bursaphelenchus* species from *Pinus pinaster* in Italy. Bull OEPP 24:467–474

Park C, Kim D, Lee S et al (2014a) A forecasting model for the adult emergence of overwintered M*onochamus alternatus* (Coleoptera: Cerambycidae) larvae based on degree-days in Korea. Appl Entomol Zool 49:35–42

Park CG, Son JK, Lee BH et al (2014b) Comparison of ethanedinitrile (C2N2) and metam sodium for control of *Bursaphelenchus xylophilus* (Nematoda: Aphelenchidae) and *Monochamus alternatus* (Coleoptera: Cerambycidae) in naturally infested logs at low temperatures. J Econ Entomol 107:2055–2060

Penas AC, Correia P, Bravo MA et al (2004) Species of *Bursaphelenchus* Fuchs, 1937 (Nematoda: Parasitaphelenchidae) associated with maritime pine in Portugal. Nematology 6:437–453

Penas AC, Bravo MA, Naves P et al (2006) Species of *Bursaphelenchus* Fuchs, 1937 (Nematoda: Parasitaphelenchidae) and other nematode genera associated with insects from *Pinus pinaster* from Portugal. Ann Appl Biol 148:121–131

Penas AC, Bravo MA, Valadas V et al (2007) Detailed morphobiometric studies of *Bursaphelenchus xylophilus* and characterisation of other *Bursaphelenchus* species (Nematoda: Parasitaphelenchidae) associated with *Pinus pinaster* in Portugal. J Nematode Morphol Syst 10:137–163

Pennacchio F, Covassi MV, Roversi PF et al (2006) Xylophagous insects of maritime pine stands attacked by *Matsucoccus feytaudi* Duc. In Liguria and Toscana (I) (Homoptera Margarodidae). Redia 88:1–7

Pérez G, Díez JJ, Ibeas F et al (2008) Assessing pine wilt disease risk under a climate change scenario in northwestern Spain. In: Bravo F, LeMay V, Jandl RK et al (eds) Managing forest ecosystems: the challenge of climate change. Springer, Dordrecht, pp 269–282

Pernek M, Agbaba SN, Lackovic N et al (2012) The role of biotic factors on pine (*Pinus* spp.) decline in north Dalmatia. Sumarski List 5–6:343–354

Pershing JC, Linit MJ (1986) Biology of *Monochamus carolinensis* (Coleoptera: Cerambycidae) on Scotch pine in Missouri. J Kansas Entomol Soc 59:706–711

Petersen-Silva R, Pujade-Villar J, Naves P et al (2012) Parasitoids of *Monochamus galloprovincialis* (Coleoptera, Cerambycidae), vector of the pine wood nematode, with identification key for the Palaearctic region. ZooKeys 251:29–48

Petersen-Silva R, Naves P, Godinho P et al (2014a) Distribution, hosts and parasitoids of *Monochamus galloprovincialis* (Coleoptera: Cerambycidae) in Portugal Mainland. Silva Lusitana 22:67–82

Petersen-Silva R, Naves P, Sousa E et al (2014b) Rearing the pine sawyer *Monochamus galloprovincialis* (Olivier, 1795) (Coleoptera: Cerambycidae) on artificial diets. J Entomol Res Soc 16:61–70

Petersen-Silva R, Inácio L, Henriques J et al (2015) Susceptibility of larvae and adults of *Monochamus galloprovincialis* to entomopathogenic fungi under controlled conditions. Int J Pest Manag. doi:10.1080/09670874.2015.1016472

Piletskis SA, Yakaitis BY (1981) Five new and two very rare species of Coleoptera for the Lithuanian SSR, found in 1975–1980. In: Petrauskas V, Ionaitis V (eds) Novye i redkie dlya Litovskoi SSR vidy nasekomykh, Soobshcheniya i opisaniya. Institut Zoologii i Parazitologii Akademii Nauk Litovskoi SSR, Vilnius, USSR, pp 31–36

Pimentel D, McNair S, Janecka J et al (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. Agric Ecosyst Environ 84:1–20

Pukkala T, Möykkynen T, Robinet C (2014) Comparison of the potential spread of pinewood nematode (*Bursaphelenchus xylophilus*) in Finland and Iberia simulated with a cellular automaton model. For Pathol 44:341–352

Rapuzzi P, Sama G (2012) Contributo alla conoscenza dei cerambycidae de Albania (Coleoptera: Cerambycidae). Atti Museo Civ Storia Naturalle Trieste 55:181–234

Rassati D, Toffolo EP, Battisti A et al (2012) Monitoring of the pine sawyer beetle *Monochamus galloprovincialis* by pheromone traps in Italy. Phytoparasitica 40:329–336

Ribeiro B, Espada M, Vu T et al (2012) Pine wilt disease: detection of the pinewood nematode (*Bursaphelenchus xylophilus*) as a tool for a pine breeding programme. For Pathol 42:521–525

Robertson L, Cobacho Arcos S, Escuer M et al (2011) Incidence of the pinewood nematode *Bursaphelenchus xylophilus* Steiner & Buhrer, 1934 (Nickle, 1970) in Spain. Nematology 13:755–757

Robinet C, Roques A, Pan HY et al (2009) Role of human mediated dispersal in the spread of the pinewood nematode in China. PLoS One 4(2), e4646

Robinet C, Opstal NV, Baker R et al (2011) Applying a spread model to identify the entry points from which the pinewood nematode, the vector of pine wilt disease, would spread most rapidly across Europe. Biol Invasions 13:2981–2995

Rodrigues JM (2008) National eradication programme for the pinewood nematode. In: Mota MM, Vieira PR (eds) Pine wilt disease: a worldwide threat to forest. Springer, Dordrecht, pp 5–14

Roques A (2009) Species accounts of 100 of the most invasive alien species in Europe: *Bursaphelenchus xylophilus* (Steiner & Bührer), pine wood nematode (Parasitaphelenchidae, Nematoda). In: Drake JA (ed) DAISIE, handbook of alien species in Europe. Springer, Dordrecht, pp 269–275

Roques A, Rabitsch W, Rasplus JY et al (2009) Alien terrestrial invertebrates of Europe. In: Drake JA (ed) DAISIE, handbook of alien species in Europe. Springer, Dordrecht, pp 63–81

Rose AH (1957) Some notes on the biology of *Monochams scutellatus* (Say) (Coleoptera: Cerambycidade). Can Entomol 89:547–553

Rühm W (1956) Die Nematoden der lpiden. Parasitol Schrift 6:1–436

Rusin EV (2009) Pathologic assessment of Black taiga, South Kemerovo region. In: Proceedings of the IX inter-regional conference of students, Tomsk State University, Tomsk, pp 22–27

Rutherford TA, Webster JM (1987) Distribution of pine wilt disease with respect to temperature in North America, Japan, and Europe. Can J Forest Res 17:1050–1059

Rutherford TA, Mamiya Y, Webster JM (1990) Nematode induced pine wilt disease: factors influencing its occurrence and distribution. For Sci 36:145–155

Ryall K, Fidgen J, Silk P et al (2015) Further evidence that monochamol is attractive to *Monochamus* (Coleoptera: Cerambycidae) species, with attraction synergised by host plant volatiles and bark beetle (Coleoptera: Curculionidae) pheromones. Can Entomol 147:564–579

Ryss AY (2008) Entomophilic juveniles of the nematode *Bursaphelenchus mucronatus* (Nematoda, Aphelenchida, Parasitaphelenchidae) obtained from the cerambycid vector *Monochamus urussovi* (Coleoptera, Cerambycidae) under experimental conditions. Entomol Rev 88:108–114

Ryss AY, Vieira P, Mota MM et al (2005) A synopsis of the genus *Bursaphelenchus* Fuchs, 1937 (Aphelenchida: Parasitaphelenchidae) with keys to species. Nematology 7:393–458

Saint-Germain M, Drapeau P, Hébert C (2004) Landscape-scale habitat selection patterns of *Monochamus scutellatus* (Say) (Coleoptera: Cerambycidae) in a recently burned black spruce forest. Environ Entomol 33:1703–1717

Saldaña JM (2012) Biología y métodos de control para Monochamus galloprovincialis, Olivier 1775 (Coleoptera: Cerambycidae) en la Sierra de Gredos Abulense. Thesis, Univ. Politécnica Madrid/Esc.Univ Ing Técn Forestal, Madrid

Sama G (2008) Preliminary note on the Cerambycid fauna of North Africa with the description of new taxa (Insecta Coleoptera Cerambycidae). Quad Studi Nat Romagna 27:217–245

Sarniguet C, Buisson A, Anthoine G (2013) Validation of morphological keys for identification of *Bursaphelenchus xylophilus* (Nematoda, Parasitaphelenchidae) to group and species level. EPPO Bull 43:255–261

Schoeller EN (2011) Characterization of the subcortical interactions between larvae of the Southern pine sawyer, Monochamus titillator (F.) and the larvae of the Southern pine beetle guild using molecular gut analysis. MSc thesis, Faculty of Louisiana State University, Department of Entomology, Whitewater

Schoeman PS, van Hamburg H, Pasques BP (1998) The morphology and phenology of the white coffe stem borer, *Monochamus leuconotus* (Pascoe) (Coleoptera: Cerambycidae), a pest of Arabica coffe. Afr Entomol 6:83–89

Schönfeld U (2006) Investigation of *Pinus sylvestris* bait logs for hatching beetles and wood-inhabiting nematodes of the genus *Bursaphelenchus* (Nematoda: Parasitaphelenchidae). Nachrichtenblatt Deutsch Pflanzenschutzdienstes 58:122–126

Schroeder LM, Magnusson C (1992) Transmission of *Bursaphelenchus mucronatus* (Nematoda) to branches and bolts of *Pinus sylvestris* and *Picea abies* by the cerambycid beetle *Monochamus sutor*. Scand J For Res 7:107–112

Schroeder LM, Weslien J, Lindelow A et al (1999) Attacks by bark- and wood-boring Coleoptera on mechanically created high stumps of Norway spruce in the two years following cutting. For Ecol Manage 123:21–30

Serafim R (2004) Cerambycidae (Coleoptera) from Maramures and Tibles mountains (Romania). Trav Mus Nat Hist Nat Grigore Antipa 46:121–127

Shimazu M (2008) Biological control of the Japanese pine sawyer beetle, *Monochamus alternatus*. In: Zhao BG, Futai K, Sutherland JR et al (eds) Pine wilt disease. Springer, Tokyo, pp 351–370

Shimazu M, Sato H (2003) Effects of larval age on mortality of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae) after application of nonwoven fabric strips with *Beauveria bassiana*. Appl Entomol Zool 38:1–5

Shimazu M, Tsuchiya D, Sato H et al (1995) Microbial control of *Monochamus alternatus* Hope (Coleoptera: Cerambycidae) by application of nonwoven fabric strips with *Beauveria bassiana* (Deuteromycotina: Hyphomycetes) on infested tree trunks. Appl Entomol Zool 30:207–213

Shin SC (2008) Pine wilt disease in Korea. In: Zhao BG, Futai K, Sutherland JR et al (eds) Pine wilt disease. Springer, Tokyo, pp 26–32

Sláma M (2006) Icones Insectorum Europae Centralis: Coleoptera, Cerambycidae. Folia Heyrovskyana, Series B 4:1–40

Soliman T, Mourits MCM, van der Werf W et al (2012) Framework for modelling economic impacts of invasive species, applied to pine wood nematode in Europe. PLoS One 7(9), e45505

Sousa E, Naves P, Bonifácio L (2000) Distribution of bark and wood-boring insects in maritime pine trees infected with *Bursaphelenchus xylophilus* in Portugal. In: Proceedings of the XXI International Congress of Entomology, Foz do Iguaçú, Brazil, p 498

Sousa E, Bravo MA, Pires J et al (2001) *Bursaphelenchus xylophilus* (Nematoda; Aphelenchoididae) associated with *Monochamus galloprovincialis* (Coleoptera; Cerambycidae) in Portugal. Nematology 3:89–91

Sousa E, Naves P, Bonifácio L et al (2002) Preliminary survey for insects associated with the pine wood nematode *Bursaphelenchus xylophilus* in Portugal. EPPO Bull 32:499–502

Sousa E, Naves P, Bonifácio L et al (2011a) Survival of *Bursaphelenchus xylophilus* and *Monochamus galloprovincialis* in pine branches and wood packaging material. EPPO Bull 41:203–207

Sousa E, Rodrigues J, Bonifácio L et al (2011b) Management and control of the pine wood nematode, *Bursaphelenchus xylophilus*, in Portugal. In: Boeri F, Chung J (eds) Nematodes: morphology, functions and management strategies. Nova Science Publishers, Hauppauge. ISBN 13: 978–1614707844

Sousa E, Naves P, Vieira M (2013) Prevention of pine wilt disease induced by *Bursaphelenchus xylophilus* and *Monochamus galloprovincialis* by trunk injection of emamectin benzoate. Phytoparasitica 41:143–148

Starzyk JR (1996) Bionomics, ecology and economic importance of the fir weevil, *Pissodes piceae* (Ill.) (Col., Curculionidae) in mountain forests. J Appl Entomol 120:65–75

Starzyk JR, Hilszczanski J (1997) Bionomics, ecology, and economic importance of *Monochamus sutor* (L.) (Coleoptera, Cerambycidae) in mountain stands of *Picea abies* (L.) Karst Zesz Nauk. AR w Krakowie 326:121–145

Steiner G, Buhrer EM (1934) *Aphelenchoides xylophilus* n. sp., a nematode associated with bluestain and other fungi in timber. J Agric Res 48:949–951

Sturrock RN (2012) Climate change and forest diseases: using today's knowledge to address future challenges. For Syst 21:329–336

Sushko GG (2014) The zoogeographical composition of the insect fauna (Odonata, Coleoptera, Macrolepidoptera) in the raides bogs of the Bielorusian lakeland. Entomol Rev 94:40–48

Svihra P (1972) Survey of the seasonal flight pattern of *Ips typographus* L. with an attractant trap in Slovakia. Z Angew Entomol 72:80–92

Takai K, Suzuki T, Kawazu K (2003a) Development and preventative effect against pine wilt disease of a novel liquid formulation of emamectin benzoate. Pest Manag Sci 59:365–370

Takai K, Suzuki T, Kawazu K (2003b) Distribution and persistence of emamectin benzoate at efficacious concentrations in pine tissues after injection of a liquid formulation. Pest Manag Sci 60:42–48

Takeshita K, Hagihara Y, Ogawa S (1975) Environmental analysis to pine damage in Western Japan. Bull Fukuoka For Exp Stn 24:1–45

Takeuchi Y (2008) Host fate following infection by the pine wood nematode. In: Zhao BG, Futai K, Sutherland JR et al (eds) Pine wilt disease. Springer, Tokyo, pp 235–249

Tarjan A, Baéza-Aragon C (1982) An analysis of the genus *Bursaphelenchus* Fuchs, 1937. Nematropica 12:121–135

Teale SA, Wickham JD, Zhang F et al (2011) A male produced aggregation pheromone of *Monochamus alternatus* (Coleoptera: Cerambycidae), a major vector of pine wood nematode. J Econ Entomol 104:1592–1598

Telnov D, Gailis J, Kalnins M et al (2005) Contributions to the knowledge of the diversity of Latvian Coleoptera, 4. Latvijas Entomol 42:18–47

Telnov D, Bukejs A, Gailis J et al (2007) Contributions to the knowledge of the diversity of Latvian Coleoptera, 6. Latvijas Entomol 44:45–52

Togashi K (1985) Transmission curves of *Bursaphelenchus xylophilus* (Nematoda: Aphelenchoididae) from its vector, *Monochamus alternatus* (Coleoptera: Cerambycidae), to pine trees with reference to population performance. Appl Entomol Zool 20:246–251

Togashi K (1989) Variation in external symptom development of pine wilt disease in field grown *Pinus thunbergii*. J Jpn For Soc 71:442–448

Togashi K (1990) Change in the activity of adult *Monochamus alternatus* Hope (Coleoptera: Cerambycidae) in relation to age. Appl Entomol Zool 25:153–159

Togashi K (1991) Larval diapause termination of *Monochamus alternatus* (Coleoptera: Cerambycidae) under natural conditions. Appl Entomol Zool 26:381–386

Togashi K (2008) Vector-nematode relationships and epidemiology in pine wilt disease. In: Zhao BG, Futai K, Sutherland JR et al (eds) Pine wilt disease. Springer, Tokyo, pp 162–183

Togashi K, Sekizuka H (1982) Influence of the pine wood nematode, *Bursaphelenchus lignicolus* (Nematoda: Aphelenchoididae), on longevity of its vector, *Monochamus alternatus* (Coleoptera: Cerambycidae). Appl Entomol Zool 17:160–165

Togashi K, Shigesada N (2006) Spread of the pinewood nematode vectored by the Japanese sawyer: modeling and analytical approaches. Popul Ecol 48:271–283

Togashi K, Jikumaru S, Taketsune A et al (1994) Termination of larval diapause in *Monochamus saltuarius* (Coleoptera: Cerambycidae) under natural conditions. J Jpn For Soc 76:30–34

Togashi K, Appleby JE, Oloumi-Sadeghi H et al (2009) Age-specific survival rate and fecundity of adult *Monochamus carolinensis* (Coleoptera: Cerambycidae) under field conditions. Appl Entomol Zool 44:249–256

Tomiczek C, Hoyer-Tomiczek U (2008) Biology studies relevant to the vector role of *Monochamus* species for pinewood nematode. In: Mota M, Vieira P (eds) Pine wilt disease: a worldwide threat to forest ecosystems. Springer, London, pp 215–220

Tomiczek C, Braasch H, Burgermeister W et al (2003) Identification of *Bursaphelenchus* spp. isolated from Chinese packaging wood imported to Austria. Nematology 5:573–581

Tomminen J (1993) Development of *Monochamus galloprovincialis* Olivier (Coleoptera, Cerambycidae) in cut trees of young pines (*Pinus sylvestris* L.) and log bolts in southern Finland. Entomol Fenn 4:137–142

Tomminen J, Akar H (1990) Infestation of four coleopteran species by the pine wood nematode *Bursaphelenchus xylophilus* (Nematoda, Aphelenchoididae) living in wood chips. Entomol Fenn 1:171–174

Tomminen J, Leppänen P (1991) The male genitalia of *Monochamus sutor* (L.), *M. galloprovincialis* (Olivier) and *M. urussovi* (Fischer von Waldheim) (Coleoptera, Cerambycidae). Entomol Fenn 2:49–51

Tomminen J, Nuorteva M (1992) Pinewood nematode, *Bursaphelenchus xylophilus*, in commercial sawn wood and its control by kiln-heating. Scand J For Res 7:113–120

Tomminen J, Nuorteva M, Pulkkinen M et al (1989) Occurrence of the nematode *Bursaphelenchus mucronatus* in Finland. Silva Fennica 23:271–277

Torres-Vila L, Zugasti C, de Juan J et al (2015) Mark-recapture of *Monochamus galloprovincialis* with semiochemical-baited traps: population density, attraction distance, flight behaviour and mass trapping efficiency. Forestry 88:224–236

Tozlu G (2001) Studies of the pest species belonging to the familkies Elateridae, Buprestidea, Cerambycidae, Curculionidae (Coleoptera) and Diprionidae (Hymenoptera) in Scotch Pine (*Pinus sylvestris* L.) forests of Sarikamis (Kars) Turkey. Turk Entomol Derg 25:193–204

Tsankov G, Georgiev G, Naydenov Y (1996) Health status of a Scots pine provenance test experiment near Belogradchik. In: Proceedings of the 2nd Balkan Scientific conference: study, conservation and utilisation of forest resources, vol 2. Sofia, pp 78–82

Twinn P, Harding P (1999) Provisional atlas of the longhorn beetles (Coleoptera, Cerambycidae) of Britain. Biological Records Centre, Huntingdon

Tzean SS, Tang JS (1985) The occurrence of the pine wood nematode, *Bursaphelenchus xylophilus*, in Taiwan. In: Proceedings of the 6th ROC symposium on electron microscopy, pp 38–39

Vetrova VP, Isaev AS, Pashenova NV et al (1998) Estimating the threat of a mass outbreak of *Monochamus urussovii* in the dark coniferous stands of the Lower Angara region after damage by *Dendrolimus sibiricus*. Lesovedenie 3:58–67

Victorsson J, Wikars LO (1996) Sound production and cannibalism in the larvae of the pine-sawyer beetle *Monochamus sutor* L. (Coleoptera: Cerambycidae). Entomol Tidskr 117:29–33

Villiers A (1946) Coleoptéres Cerambycidae de l'Afrique du Nord. Faune de l'Empire Français, Office Recherche Scientifique Coloniale

Vincent B (2007) Relations entre les nematodes du genre Bursaphelenchus le insecte vecteur Monochamus galloprovincialis et leurs arbres hôtes. Thèse Doctorat, Univ Orléans, Orléans

Vincent B, Altemayer V, Roux G et al (2008a) Competitive interaction between *Bursaphelenchus xylophilus* and the closely related species *Bursaphelenchus mucronatus*. Nematology 10:219–230

Vincent B, Koutroumpa F, Altemayer V et al (2008b) Occurrence of *Bursaphelenchus mucronatus* (Nematoda; Aphelenchoididae) in France and association with *Monochamus galloprovincialis* (Coleoptera: Cerambycidae). Ann For Sci 65:111

Vives E (2000) Insecta Coleoptera Cerambycidae. Consejo Superior de Investigaciones Científicas, CSIC. Museo Nacional de Ciencias Naturales

Wallin H, Schroeder M, Kvamme T (2013) A review of the European species of *Monochamus* Dejean, 1821 (Coleoptera, Cerambycidae) – with a description of the genitalia characters. Norw J Entomol 60:11–38

Walsh KD, Linit MJ (1985) Oviposition biology of the pine sawyer, *Monochamus carolinensis* (Coleoptera: Cerambycidae). Ann Entomol Soc Am 78:81–85

Warren JE, Linit MJ (1992) Within-wood spatial dispersion of the pinewood nematode, *Bursaphelenchus xylophilus*. J Nematol 24:489–494

Warren JE, Linit MJ (1993) Effect of *Monochamus carolinensis* on the life history of the pinewood nematode, *Bursaphelenchus xylophilus*. J Nematol 25:703–709

Warren JE, Edwards OR, Linit MJ (1995) Influence of bluestain fungi on laboratory rearing of pinewood nematode infested beetles. Fundam Appl Nematol 18:89–92

Webster JM (1999) Pine wilt disease: a worldwide survey. In: Futai K, Togashi K, Ikeda T (eds) Sustainability of pine forests in relation to pine wilt and decline: proceedings of International Symposium. Shokado Shote, Kyoto, pp 254–260

Webster J, Mota M (2008) Pine wilt disease: global issues, trade and economic impact. In: Mota M, Vieira P (eds) Pine wilt disease: a worldwide threat to forest ecosystems. Springer, London, pp 1–3

Wegensteiner R (2004) Pathogens in bark beetles. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Dordrecht, pp 291–313

Wilson LF (1962) White-spotted sawyer, USDA forest pest leaflet. USDA Forest Service, Washington, DC. ISBN 74

Wingfield MJ (1983) Transmission of pine wood nematode to cut timberand girdled trees. Plant Dis 67:35–37

Wingfield MJ, Blanchette RA (1983) The pine-wood nematode, *Bursaphelenchus xylophilus*, in Minnesota and Wisconsin: insects associates and transmission studies. Can J For Res 13:1068–1076

Wingfield MJ, Blanchette RA, Nicholls TH et al (1982) The pine wood nematode: a comparison of the situation in the United States and Japan. Can J For Res 12:71–75

Witrylak M (2008) Studies of the biology, ecology, phenology, and economic importance of *Ips amitinus* (Eichh.) (Col., Scolytidae) in experimental forests of Krynica. Acta Sci Pol Silv Colendar Rat Ind Lignar 7:75–92

Yang ZQ, Cao LM, Zhang YL et al (2014) A new egg parasitoid species (Hymenoptera: Pteromalidae) of *Monochamus alternatus* (Coleoptera: Cerambycidae), with notes on its biology. Ann Entomol Soc Am 107:407–412

Yüksel B (1998) The damaging insects at Oriental spruce (*Picea orientalis* (L.) Link) forests and their predators and parasites – 1 (Pest Insects). Eastern Black Sea For Res Inst, Tech Bull 4:1–143

Zamoroka AM, Panin RY, Kapelukh YI et al (2012) The catalogue of the longhorn beetles of western Podillya, Ukraine (Coleoptera: Cerambycidae). Munis Entomol Zool 7:1145–1177

Zhang Q, Liu Z, Sun Y et al (1990) Vertical distribution of larch bark beetle, *Ips subelongatus*, on the burned trees of larch. J Northeast For Univ 18:14–18

Zhao BG (2008) Pine wilt disease in China. In: Zhao BG, Futai K, Sutherland JR et al (eds) Pine wilt disease. Springer, Tokyo, pp 18–25

Zhao L, Zhang S, Wei W et al (2013) Chemical signals synchronize the life cycles of a plant-parasitic nematode and its vector beetle. Curr Biol 23:2038–2043

Zhao L, Mota M, Vieira P et al (2014) Interspecific communication between pinewood nematode, its insect vector, and associated microbes. Trends Parasitol 30:299–308

Chapter 13
Invasive Insects in the Mediterranean Forests of Chile

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Abstract The Mediterranean ecosystem of Chile comprises the most populated region of the country as well as the most important passageways for international trade. This has caused the rate of introductions of exotic insects to be the highest of the country. As a consequence, it has been observed an increasing number of exotic insects currently being established in three different situations: natural forests, commercial forest plantations and urban trees.

In natural forests, the most serious threat is the invasion of *Cinara cupressi*, causing severe damage on the endangered native Cupressaceae, *Austrocedrus chilensis.* Apart from this case, records of exotic insects attacking native trees are scarce. On the other hand, forest plantations of exotic species, mainly *Pinus radiata* and *Eucalyptus spp*., have been affected for several insect invasions in the last years. These new invasions represent a challenge for the Chilean forest industry, making necessary the adoption of new silvicultural techniques and sanitary protocols for exporting wood products. Besides commercial plantations, insect invasions are also taking place in urban areas: poplars, elms and other ornamental trees have undergone the introduction of several exotic insects. The effect of this pests has been perceived as a major threat for the environmental quality of cities, and public opinion is increasingly demanding actions from the government to minimize their effects.

Considering the increasing rate of detection of exotic insects in Chile, it becomes clear that invasive insects represent a current threat for Chilean forests and immediate actions are needed from the government, private companies and society to minimize their negative consequences.

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13.1 Introduction

13.1.1 Mediterranean Chile

The Mediterranean region of Chile represents one of the world's intensively exploited Mediterranean ecosystems. With a rapid economic growth, and a increased centralization of human activities, this ecosystem has suffered significant changes in structure and disturbance regimes over the past last decades (Fuentes et al. 1993; Rundel 1998; Armesto et al. 2007; Schulz et al. 2010). In Chile, Mediterranean forests are located between 30°S and 38°S Lat (Donoso 1993). This region comprises the three largest metropolitan areas of the country: Santiago city, and the conurbations Valparaiso-Viña del Mar and Concepción-Talcahuano, summing nearly 13.5 million people (INE 2014).

Topographically, this region contains two parallel mountain ranges oriented from north to south: the Coastal and the Andes mountain ranges. They are separated by a narrow basin, which is an 80–100 km wide tectonic depression named Central Depression. The climate is semiarid with hot and dry summers and cold and wet winters with most precipitation concentrated between April and September (Luebert and Pliscoff 2006). Considering Chile as a rather narrow country, in this article all geographic descriptions are given in latitude only.

A high floristic richness and diversity of plant communities is present in this region resulting from the high heterogeneity in topography, moisture, soil types and nutrient availability (Arroyo et al. 1993, 1995). Several and contrasting natural forest types are distributed following the North–South and Coast-Mountain gradients. In the northern-coastal part of the region we may found the Olivillo Forest. This is a relict forest dominated by Olivillo, *Aextoxicon punctatum*, a common species of the south of Chile, which is immersed in a matrix of xerophytic vegetation (Armesto et al. 2007).

The emblematic genus Nothofagus is also present in Mediterranean Chile. In the highest peaks of the Coastal mountain range, around the city of Santiago, there are fragments of the deciduous *N. macrocarpa*. Besides, it is also possible to find mixed stands of deciduous Nothofagus species in a formation locally known as the Maulino forest (San Martín and Donoso 1996). At both slopes of the Coastal and Andes mountain range, evergreen sclerophyllous vegetation dominates the landscape (Armesto et al. 2007). According to Armesto et al. (2007) this formation, dominated by evergreen trees and shrubs, is the most common plant formation in central Chile. Xerophytic open woodlands typically associated with grazing pastures, with the physiognomic aspect of savannas (Fuentes et al. 1990), are widespread (Armesto et al. 2007). Above 1500 masl, an upland sclerophyllous woodland called Andean Montane Woodlands is present. Finally, above treeline and about 2300 masl, the Montane Woodland is replaced by a low subalpine shrubland (Arroyo et al. 1981). Scattered patches of the conifer *Austrocedrus chilensis* (Cupressaceae) also occur near the treeline at various locations between 32°S and 36°S (Rundel 1981). Others forest types, like Palm and Swamp Forests, are also present in this region, although limitedly distributed. For further details the reader can consult to Armesto et al. (2007) and Luebert and Pliscoff (2006).

Immersed in this matrix of natural ecosystems and human settlements are the commercial forest plantations. The most important species of these plantations are the exotic *Pinus radiata* and two Eucalyptus species, *E. nitens* and *E. globulus*. From these, *Pinus radiata* is the most important one and the basis for the forestry industry of the region. Currently, Chile has 1.5 million ha of *P. radiata* plantations established across different site types and climate conditions ranging from 30°S to 43°S Lat. (INFOR 2014). Eucalyptus plantations sum 800,000 ha located between 29°S and 45°S Lat. (INFOR 2014).

Finally, it is important to highlight the presence of urban environments. Many exotic tree species can be found all over the country in parks and streets. These trees are highly appreciated by citizens and have a direct impact on the neighborhoods' appraisal within the city (Gutiérrez 2011).

13.1.2 Propagule Pressure

Currently, habitat fragmentation, changes in the land use and pollution are important processes in the Mediterranean Chile. Furthermore, this region constitutes the most important passageway for international trade in and out of the country. Therefore, the propagule pressure for the introduction of exotic species is likely to be high (Estay et al. 2012). As a matter of fact, several exotic insect species have already been reported in the region (Grooves and Di Castri 1991; Rundel et al. 1998; Ruz 2002; Grez et al. 2010). However, the way in which these human-related habitat modifications are affecting the diversity of native and exotic insect species, and whether their establishment can be unequivocally associated to human-related activities are still unknown (but see Estay et al. 2012).

Due to the high concentration of shipping ports, Mediterranean Chile undergoes a high pressure of exotic insect introductions. Ferrada et al. (2007) and Ide et al. (2014) estimated this pressure using the number of intercepted exotic insects in wood articles in Chilean ports. 1,440 interceptions of live insects were registered between 1996 and 2009. From these, 17.6 % were classified as quarantine forest pests and 80 % of the interceptions took place in the Mediterranean region (Ide et al. 2014).

This high propagule pressure is mostly represented by insects of the order Coleoptera, accounting for the 86.5 % of the interceptions (Ide et al. 2014). It is particularly important the high rate of insect interceptions from the Cerambycidae and Scolytidae families. Both comprise several species known to be harmful for coniferous trees like *Pinus spp*. Regarding the origin of the interceptions, Ferrada et al. (2007) and Ide et al. (2014) showed that most of the invasive insects came from Brazil, India, China, Spain and USA.

13.2 Invasive Insects in the Mediterranean Chile

13.2.1 Natural Forests

Despite the high propagule pressure described for the Mediterranean Chile, there are few records of exotic insects attacking native trees, and only in few cases the magnitude of the attack may be considered severe enough to represent a threat to natural forests. For example, Barriga et al. (1993), after almost 10 years of sampling natural and artificial landscapes along Chile (between 26°S and 38°S), did not detect any exotic xylophagus Coleoptera on native plants. A similar situation is described by Fuentes-Contreras et al. (1997) in their review of aphids in Chile. These authors listed the presence of just two exotic species associated to native trees, and in both cases the records are anecdotal. However, from this short list, two cases deserve special attention: *Cinara cupressi* and *Nematus oligospilus*.

13.2.1.1 *Cinara cupressi*

The cypress aphid, *Cinara cupressi* (Hemiptera: Aphididae), is a well known pest of Cupressaceae, damaging natural forests and plantations worldwide (FAO 2009). Currently, it is accepted that *C. cupressi* is a complex of several anatomically similar species (Watson et al. 1999). FAO (2009) indicates that the Cinara species presents in Chile is *C. cupressivora.* However, this classification is still controversial, and in this review the name *C. cupressi* will be used hereafter.

The origin of the species is unclear. Following Watson et al. (1999), the species becoming a pest in several countries corresponded to *C. cupressivora,* original from the region between eastern Greece and the Caspian Sea. Nevertheless, the origin of the remainder of the complex (*C. cupressi sensu lato*) is North America. Despite this unclear origin, the cypress aphid has caused serious damage to natural and planted forests in Africa, Europe, Latin America and the Caribbean, and the Near East (FAO 2009).

Adult cypress aphids are typically 2–5 mm length, dark brown and covered with a powdery wax (FAO 2009). Colonies typically have between 20 and 80 nymphs and winged and non-winged adults, located at the host's branches (FAO 2009). Adults and nymphs suck the plant sap retarding new growth and causing desiccation and progressive dieback until death on heavily infested trees (Ciesla 1991). A secondary problem caused by aphid feeding is the copious quantities of honeydew, which promotes the growth of sooty mold (Ciesla 1991). The cypress aphid have been described attacking several genera in the Cupressaceae family like Cupressus, Juniperus, Thuja, Chamaecyparis, among others, and some authors suggest that any Cupressaceae could be a suitable host (FAO 2009).

Several authors have pointed out the high economic and environmental impacts of the cypress aphid. In Africa, economic losses has been quantified in Kenya, where over 2 years 12 % of the trees were killed (Orondo and Day 1994). Also in the southern and eastern African region the cypress aphid caused losses for US$27.5 million in 1991 with a loss in annual growth increment of US$9.1 million per year (Murphy et al. 1996). In terms of environmental impacts, a major menace is the impact on the threatened Widdringtonia species in Africa. According to Chapman (1994), aphids attack are a key component of the pool of menaces acting over this trees.

In 2003 is detected for first time in Chile, in the district of Pica (20.5°S, 69.3°W, González et al. 2010; Montalva et al. 2010) and, by the end of 2008, its presence was confirmed across the whole country infesting native and exotic species of Cupresssacea (Peña and Altmann 2009; González et al. 2010; Montalva et al. 2010). Aphid's most important threath is its adaptation to *Austrocedrus chilensis*, a conifer species endemic to Chile and Argentina classified as "vulnerable" (Hechenleitner et al. 2005). In the year 2005, 52 % of the 48 survey stations on *A. chilensis* forests detected the presence of *C. cupressi*, and the prevalence increased to 74 % by 2007 (INFOR 2008; Peña and Altmann 2009). Field data collected in 2005 and 2008 for three administrative regions of Mediterranean Chile (between 34°S and 38°S Lat.) showed that 42 %, 5 %, and 10 %, respectively, of the surveyed *A. chilensis* trees exhibited >50 % loss of and necrotic foliage combined (Peña and Altmann 2009). Mortality, depending on the region, was 0.2–5 % of trees by the year 2005 in central Chile (34.5°S–38°S Lat., INFOR 2008; Peña and Altmann 2009). In 2007, *C. cupressi* was detected attacking isolated trees of another emblematic native conifer, *Fitzroya cupressoides* (González et al. 2010; Montalva et al. 2010).

To minimize the impact of *C. cupressi* on *A. chilensis*, several governmental agencies promote a pest management program with emphasis on biological control. During 2004, *Pauesia juniperorum* (Hymenoptera: Braconidade) was found parasitizing *C. cupressi*, suggesting this parasitoid enter the country together with *C. cupressi*. Unfortunately, the efficiency of this parasitoid seems to be low (González et al. 2010; Montalva et al. 2010). Subsequent introductions of *Pauesia sp*. from Spain and Italy have been reported unsuccessful (González et al. 2010).

13.2.1.2 *Nematus oligospilus*

The willow sawfly (Hymenoptera: Tenthredinidae) is a wasp native of the Holartic Region that feed on willows (Salix), and since 1980 has been introduced in many localities in the Southern Hemisphere (Koch and Smith 2000). It is a green wasp of 5–7 mm (female) or 4.7–5.3 mm (male) length (Koch and Smith 2000), and strictly parthenogenetic in the Southern Hemisphere (Gonzalez 1989; Caron et al. 2014).

This species was first detected in central Chile in 1984, feeding on the exotic weeping willow (*Salix babylonica*) and the native pencil willow (*S. humboldtiana*) (Gonzalez et al. 1986). Currently the willow sawfly is distributed from 28°S to 40°S in Chile, covering a large part of the distribution of *S. humboldtiana* (Gonzalez 1989; Klein–Koch and Waterhouse 2000; Estay 2004). Attacks on *S. humboldtiana are* specially severe in central Chile, causing complete defoliation of trees (Gonzalez 1989; Klein–Koch and Waterhouse 2000).

Control strategies are not clearly established, because chemical, cultural and biological control seems to be inefficient and in some cases showing strong collateral effects (Alderete et al. 2010). In particular, parasitoids observed in South America have shown a very low efficacy (Alderete et al. 2010).

13.2.1.3 Other Exotic Insects of Native Forests

There are few other reports of exotic insects attacking native trees in Mediterranean Chile and none in the magnitude of the two previous cases. The first one in this list is the olive scale, *Saissetia oleae* (Hemiptera: Coccidae), introduced to Chile in the nineteenth century and nowadays widespread in Mediterranean Chile. This scale has been reported feeding on several native trees such as *Maytenus boaria, Kageneckia oblonga, Luma apiculata,* or *Raphithamnus spinosus*, but in any case the damages can be considered a real threat for natural populations of these trees (Gonzalez 1989; González and Lamborot 1989; Artigas 1994). *Aspidiotus nerii* is another scale reported attacking native trees. According to Artigas (1994), this species has been found on several native species like *Prosopis chilensis, Beilschimiedia miersii, Peumus boldus* and *Cryptocaria alba*. Despite the economic importance of this scale in fruit cultivation, *A. nerii* is considered just locally important for some stands of *P. chilensis* (Klein–Koch and Waterhouse 2000). In the order Coleoptera, the Powder-post beetle, *Lyctus brunneus*, a cosmopolitan pest of dead-wood, has been occasionally reported feeding in the wood of some native species, but they could be easily misidentified with *L. chilensis* (Rojas and Gallardo 2004).

Some other anecdotal records can also be found in literature. Two Hemiptera have been reported on native trees: *Phylloxera similans* on *Nothofagus alpina* (Carrillo and Cerda 1987; Klein–Koch and Waterhouse 2000), and *Aphis nasturtii* on *Drymis winteri* (Eastop et al. 1997; Fuentes–Contreras et al. 1997). Both records correspond to particular observations and no information about damage is available. Klein–Koch and Waterhouse (2000) indicate the presence of the *Megachile rotundata* (Hymenoptera) cutting leaves of *Persea lingue*, but at a negligible rate. Lanfranco (2010a) describe the presence of *Orgya antiqua* (Lepidoptera: Lymantriidae) on native plants, but without reporting the host species.

A special note deserves the yellowjacket wasp, *Vespula germanica.* Although this is not an insect exclusively associated to forests, its impact on native insects, agriculture, apiculture, wildlife, and recreation activities in national parks is substantial (Beggs 2001; Curkovic et al. 2004; Kasper 2004). In Chile, this insect was introduced more than 30 years ago (Edwards 1976; Archer 1998; Estay and Lima 2010), showing at the present time high densities, especially in Central Chile, where it has become a real threat for recreational and touristic activities, causing also serious damage to fruit farms and vineyards (Curkovic et al. 2004; Estay and Lima 2010).

13.2.2 Forest Plantations

Chilean forestry industry is based on exotic species. Currently Chile has 2.4 million of ha of planted forest, 88 % immersed in the Mediterranean ecosystem (INFOR 2014). 61 %, 22 % and 10 % correspond to plantations of *Pinus radiata, Eucalyptus globulus* and *Eucalyptus nitens*, respectively. In this section we will review the major insect pests of these three species.

13.2.2.1 Invasive Insects of *Pinus radiata*

As the same time that *P. radiata* plantations turned into the main resource of the Chilean forestry industry, at the beginning of the twentieth century, concerns about its phytosanitary conditions started to arise. However, it is only at the end of that century that occurred the major and, still today, more mediatic introduction of an exotic forest insect. *Rhyacionia buoliana* (Lepidoptera: Tortricidae) was detected in Southern Chile in 1980, and today is distributed between 32°S and 42°S Lat (Lanfranco 2010). Native of Europe, this moth destroy pine shoots causing deformities such as forked or crooked stems, bushy growth, multiple tops and a lowered timber quality (Harris and Wood 1967; Miller et al. 1961). The severity of the damage seems to increase from north to south of Chile (Klein–Koch and Waterhouse 2000). Alzamora et al. (2002) quantified the economic losses in Southern Chile between 2 % and 30 % of the expected land value depending on the quality of the forest site. To minimize the impact of this pest, several actions were taken during the 1980s in an unprecedented effort of the government, companies and research centers. This effort capitalized into the development of new management schemes, monitoring programs and several control programs. Chilean government, through the Agricultural and Livestock Service (SAG) and the National Forest Service (CONAF), concentrated control efforts in the importation of natural enemies, starting a biological control program using *Orgilus obscurator* (Hymenoptera: Braconidae). On this regard, Lanfranco (2010) pointed out that followed a successful establishment an initial control, the efficiency of *O. obscurator* as biological control has decreased in the last decade, reaching in some localities, values not higher than 40 %.

Taking a jump in time to the present day, we found the introduction to Chile of *Sirex noctilio* (Hymenoptera: Siricidae). Probably this is the major threat to *P. radiata* plantations in the last 20 years. The Sirex woodwasp is native of Europe, Asia, and North Africa, where it is a minor pest (Ciesla 2003). However, this species turned into a serious pest of pines in New Zealand, Australia, South Africa, Argentina, Uruguay, Brazil and Chile, where it has become one of the most economically significant pests of softwood forestry (Villacide and Corley 2012). Damage occurs when females oviposit eggs into stressed or suppressed trees, along with a phytotoxic mucus and a wood decay fungus (*Amylostereum areolatum*) (Madden 1988; Carnegie et al. 2006). Trees are drilled by larvae and soon die due to the combination of the mucus and fungus (Ciesla 2003; Carnegie et al. 2006). In Chile, this insect was first detected in January 2001 in the Valparaiso Region (32.5°S Lat.), and almost simultaneously, a second detection occurred in Los Lagos Region (40.4°S Lat.), being both events different events of introduction (Rojas and Beèche 2010; Beèche et al. 2012). Today this pest is under official control by the Agricultural and Livestock Service, however, its current distribution cover most of the commercial plantations of *P. radiata* (SAG 2015). Suppression strategies currently applied in Chile consist in cultural and biological control, using the nematode *Deladenus siricidicola* and *Megarhyssa nortoni* (Hymenoptera: Ichneumonidae), combined with restriction to the movement of wood from infested areas (Rojas and Beèche 2010; Beèche et al. 2012).

Another important group of exotic pests in *Pinus* plantations in Chile are the bark beetles (Coleoptera: Scolytidae). Three species belong to this group: *Hylurgus ligniperda, Hylastes ater* and *Orthotomicus erosus*, all of them detected in Chile during the 1980s (Ciesla 1988; Lanfranco et al. 2002). The three species are native of Eurasia and Africa. *Hylastes ater* was first detected in Chile in 1983, *H. ligniperda* in 1985 and *O. erosus* in 1986. *Hylurgus ligniperda* and *H. ater* are now distributed from 33°S to 41°S Lat., and *Orthotomicus erosus* shows a more restricted distribution in Chile, between 35°S and 41°S Lat. (Lanfranco et al. 2002). The three species invade fresh stumps and use this material as breeding sites (Ciesla 1988; Lanfranco et al. 2002). Adults feed on the root collars and in roots of 1 and 2-year-old pines, and in case of heavy attacks, they can cause mortality of seedling (Ciesla 1988; Lanfranco et al. 2002).

Many other exotic insects have established in pine plantations in Chile, but with minor or no economic impact. Among Coleoptera species, *Buprestis novenmaculata* was detected in Chile in 1940, and nowadays is distributed between 32°S and 40°S Lat. This insect is native from Europe and Northern Africa, but its impact on commercial plantations is negligible because it is associated with deadwood (Lanfranco et al. 2002). On suppressed or dead trees it is also possible to find *Ernobius mollis* (Anobiidae) and *Xyleborinus saxeseni* (Scolytidae). Both species were introduced to Chile in the 1950–1960s, and currently they are distributed between 32°S and 37°S (Gonzalez 1989; Lanfranco et al. 2002). In the order Hemiptera, two species deserve mention: *Pineus borneri* (adelgidae) and *Eulachnus rileyi* (Aphididae). The North American *P. borneri* is a long resident in Chile. Some authors suggest that their introduction would have occurred at the beginning of the twentieth century (Olalquiaga 1952). At the present time, this species is widespread in Chile, although it seems to be more abundant above 40°S Lat. (Klein–Koch and Waterhouse 2000). The second Hemiptera species, the European *E. rileyi* was first reported in Chile in 1990 (Cerda and Beeche 1989), but probably its introduction occurred long before. No clear description of its current distribution is available, but putting several references and personal communications together, it can be inferred its current distribution range from 35°S to 42°S Lat. (Fuentes–Contreras et al. 1997; Klein–Koch and Waterhouse 2000). Finally, another Siricidae, *Urocerus gigas* from Eurasia, was discovered in Chile in the 1970s (FAO 2008). Currently, it is distributed between 32°S and 42°S Lat. without causing major damage (Lanfranco et al. 2002).

13.2.2.2 Invasive Insects of *Eucalyptus* Plantations

If we analyze the history of forest pest introductions in the last 20 years, we can notice that more introductions of Eucalypt pests than pine pests have occurred in the Mediterranean Chile. The major problems are caused for two species of the Australian genus *Phoracantha* (Coleoptera: Cerambycidae): *P. semipunctata* and *P. recurva*. The former was officially detected in Chile in 1973, however, there is an individual collected in Chile in 1931, which is deposited in the collection of the Museum of the University of Concepción (Artigas 1994). *Phoracantha recurva*, on the other hand, was first detected in Chile in 1997 (Lanfranco and Dungey 2001; Beéche et al. 2003). Both species are serious pests of Eucalyptus plantations located in arid environments or in poorly irrigated sites (Artigas 1994; Lanfranco and Dungey 2001). Klein–Koch and Waterhouse (2000) report that the current distribution of *P. semipunctata* is between 18°S and 40°S Lat while *P. recurva* is distributed from 32°S to 34.5°S Lat. Forest industry and the government has focused management efforts in two directions. First, towards an improvement of silvicultural techniques, specially linked to irrigation, in order to avoid stressed individuals susceptible to attacks (Lanfranco and Dungey 2001). Second, towards biological control using *Avetianella longoi* (Hymenoptera: Encyrtidae), which is now successfully established in Chile achieving variable levels of parasitism depending on location (Beéche et al. 2003).

Immediately after the detection of *P. recurva*, *Gonipterus scutellatus* was discovered on Eucalyptus trees in central Chile (Beéche et al. 1999; Estay et al. 2002). Since their introduction, this defoliator has been recognized as a major threat for *E. globulus* plantations, specially due to its great adaptation to the climatic conditions of the Mediterranean Chile, where is able to produce three to four generations per year (Estay et al. 2002). According to Klein-Koch and Waterhouse (2000), *G. scutellatus* is the most serious Eucalyptus pest in central Chile. Today the species is widespread from 32°S to 40°S Lat. (Elgueta 2010). Governmental agencies have introduced *Anaphes nitens* and *Anaphes tasmaniae* (Hymenoptera: Mymaridae) as biological control with significant success (Beéche et al. 1999). A recent study suggest that *G. scutellatus* is actually a complex and that the species already present in New Zealand, Spain, California and Chile is *G. platensis*, native of Tasmania (Mapondera et al. 2012). Nevertheless, more studies are necessaries to clarify the taxonomy of this group.

In the order Hymenoptera, two introduced insects deserve special mention. The first one is *Ophelimus eucalypti* (Eulophidae). Native of Australia, this gall-forming insect was introduced in 2003 and now is widespread in Mediterranean Chile (Carnieletto 2006; SAG 2006). However, its impact on Eucalyptus plantations does not seem to be of relevance. The second one is *Leptocybe invasa* (Eulophidae), recently introduced (2014) and restricted to central Chile (32–33°S Lat.). Native of Australia, it is considered a serious pest of young trees and saplings (SAG 2014). No information is available of its current situation in Chile. Finally, two other Hemiptera have been reported to Chile, but with very different implications. *Blastopsylla occidentalis* (Psyllidae) was reported in 2000 in central Chile (32°S, Burckahardt and Elgueta 2000), but it does not represent a sanitary problem for Eucalyptus plantations. On the other hand, another Psyllidae, *Ctenarytaina eucalipty* represents a serious pest of *E. globulus* sapling and young trees. It was introduced in Chile in 1999 (Olivares 2000; Goycoolea et al. 2002), and currently is widespread in Chile at least from 20°S to 40°S Lat (Rodrígues and Sáiz 2014). Due to the importance of this pest, governmental and private agencies developed a biological control program using *Psyllaephagus pillosus* (Hemiptera: Encyrtidae) reported as successful (Goycoolea et al. 2002).

13.2.3 Invasive Insects of Urban Trees

Urban environments in Chile concentrate the major diversity of exotic insects. Gardens, parks and other human-made plantations form a mosaic of refugees and alternative food sources for insects and other small sized organisms, enhancing the richness of exotic species. Using a extensive sampling for 2 years in the Metropolitan Region of Chile (33°S), Estay et al. (2012) reported 81 exotic insect species on trees, more than 30 % of the identified species.

The diversity of urban trees in Chilean Mediterranean cities has facilitated the establishment of many well-known insect pests in recent times. Considering the high number of reported exotic pests in urban environments, this review will focus on the most important and notable examples.

Glycaspis brimblecombei (Hemiptera: Psylidae) is an Australian insect pest of several Eucalyptus species such as *E. camaldulensis, E. tereticornis* and *E. rudis* (Valente and Hodkinson 2009). This insect was introduced to Chile in 2002, and at present is distributed from 30°S to 38°S Lat. (Ide et al. 2006). In Chile its main host has been *E. camaldulensis*, a species commonly used in urban parks. Its damage is impressive since trees get covered by the cone-shaped protection of nymphs (lerp). Successive attacks caused defoliation and weakening facilitating the attack of secondary pests like *Phoracantha spp*. (Estay 2004; Ide et al. 2006). Immediately after introduction, governmental agencies planned the introduction of natural enemies, which was finally carried out in 2003 with the importation of *Psyllaephagus luteus* (Hymenoptera: Encyrtidae). However, this effort had variable success depending on location (Ide et al. 2006).

Another defoliator causing serious damage in elms is *Xanthogalerucella luteola* (Coleoptera: Chrysomelidae). Although it was reported in Chile as early as 1982 (Askevold 1991), it was not until 1994 when this pest was formally reported as established in Chile (SAG 2005). This insect is easily observable in elms in all Chilean Mediterranean cities between 32°S and 38°S Lat. causing serious defoliations. Considering the level of damage, authorities have started the implementation of chemical control (Estay 2004; SAG 2010). This insect is able to develop four generations per year in central Chile, amplifying the severity of its damage (Huerta et al. 2011).

Poplars are widely used in urban streets and also as sherterbelts in rural and semirural landscapes. These trees have undergone the attack of several insects, but probably the more important ones are *Tremex fuscicornis* (Hymenoptera: Siricidae) and *Chaitophorus leucomelas* (Hemiptera: Aphididae). *Tremex fuscicornis* is a wood borer wasp native of Asia and Eastern Europe, where is not considered a pest (Parra 2010). In Chile was detected in 2000 on *Populus nigra*, but probably its introduction occurred at least 2 years earlier (Parra 2010). Nowadays, its impact on urban trees is high and its damage is observable on several hosts like poplars, willow, black locust, ashleaf maple or common walnut (Estay 2004; Parra 2010). Its current distribution span from 32°S to 37°S Lat. with one generation per year (Parra 2010). A natural enemy, *Megarhyssa praecellens* (Hymenoptera: Ichneumonidae), was introduced simultaneously with the pest, but its effectiveness has been reported only about 30 % mainly due to its low dispersal ability (Parra 2010). To compensate for this, continuous releases of this parasitoid are needed. Cultural control strategies are effective to prevent the attack of *T. fuscicornis* such as irrigation or destruction of infested trees by burning or chipping (Estay 2004; Parra 2010). The second important pest for poplars, *C. leucomelas,* was first described as present in Chile in 1995 (Muñoz and Beéche 1995). Aphid nymphs feed on leaves and buds of poplar causing in some cases earlier leaves fall (Estay 2004). However, the main problem associated to this species in Central Chile is the abundant production of honeydew that stains sidewalks, houses, cars, benches or any other object located below the tree (Estay 2004) causing annoyance on citizens. It is currently distributed from 18° to 36° (Klein–Koch and Waterhouse 2000). Although there was an intent of biological control in 2001 using *Adialytus salicaphis* (Hymenoptera: Braconidae), this was reported as failed (Stanković et al. 2015).

Native to Perú and Bolivia *Schinus molle* is a very common urban tree in Santiago, capital of Chile. It has been suggested that this tree was introduced to Chile at the time of the Inca Empire (Silva et al. 2005). At present almost all trees are infested with *Calophya schini* (Hemiptera: Calophyidae). This small insect causes small galls in the leaves, sometimes dozen per leaflet (Downer et al. 1988; Estay 2004; Zina et al. 2012). This massive presence of galls completely deform leaves and provoke a grayish appearance on infested trees, followed by extensive foliage drop (Downer et al. 1988; Zina et al. 2012). Despite the high visibility of the damage, there is no information of its ecology on Mediterranean Chile.

As previously mentioned, there are tens of other exotic insects on urban trees in Mediterranean Chile, but it is out of the scope of this review to check all of them. For some of them, simply there is no literature available. On spite of this, Table 13.1 offer to the reader information about some other species present in urban trees of Chile. For a more complete overview, readers may consult Estay (2004).

Table 13.1 Exotic insects present in the urban environments of Mediterranean Chile not discussed in the main text

Order	Family	Species	Hosts	References for Chile
Coleoptera	Buprestidae	*Melonophila picta*	*Populus sp.*	Estay (2004)
Coleoptera	Scolytidae	*Scolytus rugulosus*	*Ulmus sp., Crataegus sp. Betula sp.*	Elgueta and Marvaldi (2006)
Hemiptera	Aleyrodidae	*Siphoninus phillyreae*	*Catalpa bignonioides, Cercis siliquastrum, Magnolia grandiflora, Fraxinus excelsior, Ligustrum vulgare, Punica granatum,* among others	Muñoz and Beéche (1995)
Hemiptera	Aphididae	*Drepanoshipum oregonensis*	*Acer sp.*	SAG (2010)
Hemiptera	Aphididae	*Essigella californica*	*Pinus sp., Pseudotsuga menziesii*	SAG (2004)
Hemiptera	Aphididae	*Myzocallis boerneri*	*Quercus suber, Q. ilex*	SAG (2005)
Hemiptera	Aphididae	*Tinocallis saltans*	*Ulmus sp.*	
Hemiptera	Coccidae	*Parthenolecanium corni*	*Robinia pseudoacacia, Fraxinus excelsior, Ulmus sp., Acer sp., Crataegus sp., Platanus sp., Salix babylonica, Tilia sp.,* among others	Gonzalez (1989)
Hemiptera	Diaspididae	*Carulaspis minima*	Several *Cupressaceae*	Estay (2004)
Hemiptera	Diaspididae	*Hemiberlesia rapax*	*Ficus sp., Gleditsia triacanthos, Melia azedarach, Robinia pseudoacacia, Acer sp., Schinus molle, Pyttosporum sp.,* among others	Gonzalez (1989)

(continued)

Table 13.1 (continued)

Order	Family	Species	Hosts	References for Chile
Hemiptera	Diaspididae	*Lepidosaphes beckii*	*Magnolia grandiflora, Acer sp., Eleagnus sp.*	Gonzalez (1989)
Hemiptera	Diaspididae	*Parlatoria pittospori*	*Pittosporum sp., Pinus sp., Phoenix sp., Acacia sp., Chamaecyparis lawsoniana,* among others	Estay (2004)
Hemiptera	Pseudococcidae	*Pseudococcus calceolariae*	*Schinus molle, Pinus sp., Abutilon sp., Ficus sp., Salix sp,* among others	Gonzalez (1989)
Hemiptera	Psyllidae	*Psyllopsis fraxinicola*	*Fraxinus excelsior* and *F. monophylla*	Burckhard (1994)
Hemiptera	Thaumastocoridae	*Thaumastocoris peregrinus*	*Eucalyptus sp.*	Ide et al. (2011)
Hemiptera	Tingidae	*Corythuca ciliata*	*Platanus sp, Fraxinus sp., Tilia sp.*	Estay (2004)

13.3 Conclusions

Our review allows us to make some generalizations about the status of invasive insects in Chile. It seems that native forests have not yet experienced a high rate of introductions of exotic insects. However, the few successful introductions have been highly harmful. *Cinara cupressi* represents a major threat to native endangered conifers, and recognizing that eradication is probably not a realistic option, the conservation of these conifers will require a major effort that considers continuing monitoring and the development of a new biological control program using more effective natural enemies.

Forest plantations have been affected for the introduction of exotic insects. Assuming the increasing exchange of goods, the most likely future scenario shows new introductions of forest pests as harmful as the currently established in Chile. This scenario (will) require that the forest industry develop new policies such as a better coordination with governmental agencies, improvements in contingency plans and an increased investment in the necessary science and technology required to minimize the impact of these current and future pests.

Society's demands for a healthy environment incorporate more and more the sanitary condition of urban vegetation. Citizen's concern about the impact of forest pests on urban trees is a social phenomenon that arises in the last decade in Chile. These demands are an opportunity for joining efforts with citizens, local groups or municipalities into invasive species programs. "Citizen Science" has demonstrated to be very useful for conservation science, and could be a significant step forward for monitoring and early alert systems.

This review will be incomplete without mention the effects of global change. Several studies suggest an important reduction of precipitations in Mediterranean Chile, which will affect tree's health. This scenario will promote outbreaks and range expansion of current forest pests, but will also facilitate the establishment of opportunistic insects. The development of national policies to ameliorate these impacts is an urgent task.

References

Alderete M, Liljesthrom G, Fidalgo P, Alderete M, Liljesthrom G, Fidalgo P (2010) Bio–ecología y perspectivas para el manejo de la avispa sierra del sauce, *Nematus oligospilus*, Manejo Integrado de Plagas Forestales n° 10. INTA, Bariloche

Alzamora R, Apiolaza LA, Ide S (2002) Evaluación física y económica de pérdidas en volumen debido al daño de *Rhyacionia buoliana* (Schiff.) en plantaciones de Pinus radiata (D. Don) en la Novena y Décima Regiones de Chile. Bosque 23:29–42

Archer M (1998) The world distribution of the Euro–Asian species of Paravespula (Hym, Vespine). Entomol Mon Mag 134:279–284

Armesto JJ, Arroyo MTK, Hinojosa LF (2007) The Mediterranean environment of Central Chile. In: Veblen TT, Young KR, Orme AR (eds) The physical geography of South America. Oxford University Press, New York, pp 184–199

Arroyo MTK, Armesto JJ, Villagrán C (1981) Plant phenological patterns in the high Andean Cordillera of central Chile. J Ecol 69:205–223

Arroyo MTK, Armesto JJ, Squeo F et al (1993) Global change: the flora and vegetation of Chile. In: Mooney H, Fuentes E, Kronberg B (eds) Earth–system responses to global change: contrasts between North and South America. Academic Press, New York, pp 239–264

Arroyo MTK, Cavieres L, Marticorena C et al (1995) Convergence in the Mediterranean floras in central Chile and California: insights from comparative biogeography. In: Arroyo MTK, Zedler PH, Fox MD (eds) Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia. Springer, New York, pp 43–88

Artigas J (1994) Entomología Económica: Insectos de interés agrícola, forestal, médico y veterinario (nativos, introducidos y susceptibles de ser introducidos). Editorial Universidad de Concepción, Concepción

Askevold IS (1991) On some poorly known, misidentified and mislabelled Chilean Chrysomelidae Coleoptera. Rev Chilena Entomol 19:11–15

Barriga TJE, Curkovic T, Fichet T et al (1993) Nuevos antecedentes de coleópteros xilófagos y plantas hospederas en Chile, con una recopilación de citas previas. Rev Chilena Entomol 20:65–91

Beéche M, Sandoval A, Rothmann S et al (1999) Detección y control del gorgojo del eucalipto en Chile, *Gonipterus scutellatus* Gyllenhal (Coleoptera: Curculionidae). Servicio Agrícola y Ganadero, Santiago

Beéche M, Goycoolea C, Rothman S et al (2003) Detección y control biológico de los taladradores del eucalipto en Chile, *Phoracantha semipunctata* Fabricius y *Phoracantha recurva* Newman (Coleoptera: Cerambycidae). Servicio Agrícola y Ganadero, Chile

Beèche M, Lanfranco D, Zapata M et al (2012) Surveillance and control of the Sirex woodwasp: the Chilean experience. In: Slippers B, de Groot P, Wingfield MJ (eds) The Sirex woodwasp and its fungal symbiont. Springer, Dordrecht, pp 229–245

Beggs J (2001) The ecological consequences of social wasps (*Vespula spp.*) invading an ecosystem that has an abundant carbohydrate resource. Biol Conserv 99:17–28

Burckhard D (1994) Generic key to the Chilean jumping plant-lice (Hemiptera: Psylloidea) with inclusion of potential exotic pests. Rev Chilena Entomol 21:57–67

Burckhardt D, Elgueta M (2000) *Blastopsylla occidentalis* Taylor (Hemiptera: Psyllidae), a new introduced eucalypt pest in Chile. Rev Chilena Entomol 26:57–61

Carrillo R, Cerda L (1987) Zoofitófagos de Nothofagus Chilenos. Bosque 8:99–103

Carnegie AJ, Matsuki M, Haugen DA et al (2006) Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of Pinus plantations. Ann For Sci 63:119–128

Carnieletto C (2006) *Ophelimus eucalypti* Gahan (1922), (Hymenoptera: Eulophidae), la avispa formadora de agallas. Chile For 327:47–48

Caron V, Ede F, Sunnucks P et al (2014) Distribution and rapid range expansion of the introduced willow sawfly *Nematus oligospilus* Förster (Hymenoptera: Tenthredinidae) in Australasia. Aust Entomol 53:175–182

Cerda LA, Beéche MA (1989) Análisis general de las plagas insectiles asociadas a pino insigne y eucalipto en Chile. Proceedings of the national symposium on forestry plant protection problems in Chile. IICA, Santiago

Chapman JD (1994) Notes on Mulanje cedar–Malawi's national tree. Commonwealth For Rev 73:235–242, 272–273

Ciesla WM (1988) Pine bark beetles: a new pest management challenge for Chilean foresters. J For 86:27–31

Ciesla WM (1991) Cypress aphid, *Cinara cupressi*, a new pest of conifers in eastern and southern Africa. FAO Plant Protect B 39:82–93

Ciesla WM (2003) European woodwasp: a potential threat to North America's conifer forests. J For 101:18–23

Curkovic T, Araya J, Guerrero M (2004) Avances en el manejo de la avispa chaqueta amarilla en Chile. Aconex 84:19–24

Donoso C (1993) Bosques templados de Chile y Argentina. Variación, estructura y dinámica. Editorial Universitaria, Santiago

Downer JA, Svihra P, Molinar RH et al (1988) New psyllid pest of California USA pepper tree. Calif Agric 42:30–32

Eastop VF, Heie OE, Fuentes–Contreras E et al (1997) Notes on two new aphid species (Hemiptera: Aphididae) detected in Chile. Rev Chilena Entomol 24:81–84

Edwards R (1976) The world distribution pattern of the German wasp, *Paravespula germanica* (Hymenoptera: Vespidae). Entomol Ger 3:69–271

Elgueta M (2010) *Gonipterus scutellatus* el "gorgojo del eucalipto" (Coleoptera: Curculionidae) en Chile. In: Lanfranco D, Ruiz C (eds) Entomología Forestal en Chile. Ediciones Universidad Austral de Chile, Valdivia, pp 425–442

Elgueta M, Marvaldi AE (2006) Lista sistemática de las especies de Curculionoidea (Insecta: Coleoptera) presentes en Chile, con su sinonímia. Boletín del Museo Nacional de Historia Natural 55:113–153

Estay SA (2004) Insectos del arbolado urbano. Servicio Agrícola y Ganadero, Santiago

Estay SA, Lima M (2010) Combined effect of ENSO and SAM on the population dynamics of the invasive yellow jacket wasp in central Chile. Popul Ecol 52:289–294

Estay SA, Araya JE, Guerrero MA (2002) Biología de *Gonipterus scutellatus* Gyllenhal (Coleoptera: Curculionidae) en San Felipe, Chile. Boletín de Sanidad Vegetal Plagas 28:391–397

Estay SA, Navarrete SA, Rothmann SR (2012) Effects of human mediated disturbances on exotic forest insect diversity in a Chilean Mediterranean ecosystem. Biodivers Conserv 21:3699–3710

FAO (2008) Overview of forest pests, Chile. Forest Health & Biosecurity working papers (FBS/12E). Forest Resources & Development Service, Rome

FAO (2009) Global review of forest pests and diseases. FAO forestry paper 156, Rome

Ferrada R, Ide S, Valenzuela J et al (2007) Intercepciones de insectos vivos realizadas en embalajes de madera de internación en el período 1995–2005. Servicio Agrícola y Ganadero, Santiago

Fuentes ER, Avilés R, Segura A (1990) The natural vegetation of a heavily man–transformed landscape: the savanna of central Chile. Interciencia 15:293–295

Fuentes ER, Miethke S, Avilés R (1993) Contemporary patterns of landscape change in areas with a Mediterranean–type climate in central Chile. In: Turner BL, Gómez A (eds) Consequences of the Columbian encounter. CSIC, España, pp 90–99

Fuentes–Contreras E, Munoz R, Niemeyer H (1997) Diversidad de áfidos (Hemiptera: Aphidoidea) en Chile. Rev Chil Hist Nat 70:531–542

González RH, Lamborot L (1989) El género Saissetia Deplanche en Chile:(Homoptera: Coccidae). Acta Entomol Chil 15:237–241

González RH (1989) Insectos y ácaros de importancia agrícola y cuarentenaria en Chile. Edit. Ograma, Santiago

González RH, Barría G, Guerrero (1986) *Nematus desantisi* Smith, a new species of forest importance in Chile (Hymenoptera: Tenthredinidae). Rev Chil Entomol 14:13–15

González P, Ide S, Jaques L (2010) *Cinara cupressi* Buckton (Hem: Aphididae), el pulgón del ciprés. In: Lanfranco D, Ruiz C (eds) Entomología Forestal en Chile. Ediciones Universidad Austral de Chile, Valdivia, pp 473–486

Goycoolea C, Beéche M, González P et al (2002) Detección y control del psílido de los eucaliptos *Ctenarytaina eucalypti* (Hemiptera: Psyllidae). Servicio Agrícola y Ganadero, Santiago

Grez A, Zaviezo T, González G, Rothmann S (2010) *Harmonia axyridis* in Chile: a new threat. Ciencia e Investigación Agraria 37:145–149

Grooves RH, Di Castri F (1991) Biogeography of Mediterranean invasions. Cambridge University Press, Cambridge

Gutiérrez R (2011) Valor del arbolado urbano: la experiencia de la Municipalidad de Santiago. Mundo For 21:4–6

Harris JWE, Wood RO (1967) The European pine shoot moth, *Rhyacionia buoliana* (Lepidoptera: Olethreutidae), another introduced forest pest. J Entomol Soc BC 64:14–16

Hechenleitner V, Gardner MF, Thomas PI et al (2005) Plantas amenazadas del centro–sur de Chile. Distribución, conservación y propagación. Universidad Austral de Chile y Royal Botanical Garden of Edinburgh, Valdivia

Huerta A, Gómez IC, Puga K et al (2011) Life cycle of *Xanthogaleruca luteola* (Coleoptera: Chrysomelidae) in Santiago, Chile, and sex fenotypo differentiation of adults. Boletín de sanidad vegetal Plagas 37:57–64

Ide S, Muñoz C, Beéche M et al (2006) Detección y control biológico de *Glycaspis brimblecombei* Moore (Hemiptera: Psyllidae). Servicio Agrícola y Ganadero, Santiago

Ide S, Ruiz C, Sandoval A et al (2011) Detección de *Thaumastocoris peregrinus* (Hemiptera: Thaumastocoridae) asociado a *Eucalyptus spp*. en Chile. Bosque 32:309–313

Ide S, Valenzuela J, Estay SA et al (2014) Presión de ingreso de insectos forestales exóticos a Chile desde 1996. In: Jaksic F, Castro S (eds) Invasiones biológicas en Chile: causas globales e impactos locales. Ediciones UC, Santiago, pp 437–457

INE (2014) Estadísticas demográficas y vitales. http://www.ine.cl/. Accessed 23 Jan 2015

INFOR (2008) Manejo integrado: técnica para la recuperación del crecimiento de *Austrocedrus chilensis*. CORFO, Santiago

INFOR (2014) Estadísticas forestales chilenas 2014. http://www.infor.cl. Accessed 23 Jan 2015

Kasper M (2004) The population ecology of an invasive social insect, *Vespula Germanica* (Hymenoptera: Vespidae) in South Australia. Thesis, University of Adelaide, School of Earth and Environmental Sciences, Discipline of Environmental Biology, Adelaide

Klein–Koch C, Waterhouse DF (2000) The distribution and importance of arthropods associated with agriculture and forestry in Chile. Australian Centre for International Agricultural Research, Canberra

Koch F, Smith DR (2000) *Nematus oligospilus* Förster (Hymenoptera: Tenthredinidae), an introduced willow sawfly in the Southern Hemisphere. Proc Entomol Soc Wash 102:292–300

Lanfranco D (2010a) Insectos defoliadores y sus efectos sobre sobre los sistemas forestales presentes en Chile. In: Lanfranco D, Ruiz C (eds) Entomología Forestal en Chile. Ediciones Universidad Austral de Chile, Valdivia, pp 181–202

Lanfranco D (2010b) La polilla del brote del pino: como se enfrentó la primera y más importante plaga forestal en Chile y sus implicancias actuales. In: Lanfranco D, Ruiz C (eds) Entomología Forestal en Chile. Ediciones Universidad Austral de Chile, Valdivia, pp 409–424

Lanfranco D, Dungey HS (2001) Insect damage in Eucalyptus: a review of plantations in Chile. Austral Ecol 26:477–481

Lanfranco D, Ide S, Ruiz C et al (2002) Agentes Entomopatógenos asociados a Productos Forestales Primarios de Exportación. Editorial El Kultrún, Valdivia

Luebert F, Pliscoff P (2006) Synopsis of bioclimate and vegetation of Chile. Editorial Universitaria, Santiago

Madden JL (1988) Sirex in Australasia. In: Berryman AA (ed) Dynamics of forest insect populations: patterns, causes, implications. Plenum Press, New York, pp 407–429

Mapondera TS, Burgess T, Matsuki M et al (2012) Identification and molecular phylogenetics of the cryptic species of the *Gonipterus scutellatus* complex (Coleoptera: Curculionidae: Gonipterini). Aust J Entomol 5:175–188

Miller WE, Hastings AR, Wootten JF (1961) European pine shoot moth. Forest insect and disease leaflet 59. USDA Forest Service, Ohio

Montalva C, Rojas E, Ruiz C et al (2010) El pulgón del ciprés en Chile: una revisión de la situación actual y antecedentes del control biológico. Bosque 31:81–88

Muñoz R, Beéche M (1995) Antecedentes sobre dos especies de reciente identificación para Chile (Homoptera: Aleyrodidae, Aphididae). Rev Chilena Entomol 22:89–91

Murphy ST, Nair KSS, Sharma JK (1996) Status and impact of invasive conifer aphid pests in Africa. In: Varma RV (ed) Impact of diseases and insect pests in tropical forests. Proceedings of the IUFRO Symposium, Peechi, pp 289–297

Olalquiaga FG (1952) El pulgón de los pinos en Chile. Rev For 16:91–92

Olivares TS (2000) *Ctenarytaina eucalypti* (MASKELL 1890): el psílido del eucalipto en Chile (Hemiptera: Sternorryncha: Psylloidea: Spondyliaspininae). Gayana 64:239–241

Orondo SB, Day RK (1994) Cypress aphid (*Cinara cupressi*) damage to a cypress (*Cupressus lusitanica*) stand in Kenya. Int J Pest Manag 40:141–144

Parra P (2010) La avispa taladradora de la madera de latifoliadas *Tremex fuscicornis* Fabricius (Hymenoptera: Siricidae) en Chile. In: Lanfranco D, Ruiz C (eds) Entomología Forestal en Chile. Ediciones Universidad Austral de Chile, Valdivia, pp 323–336

Peña MA, Altmann SH (2009) Use of satellite–derived hyperspectral indices to identify stress symptoms in an *Austrocedrus chilensis* forest infested by the aphid *Cinara cupressi*. Int J Pest Manag 55:197–206

Rodríguez F, Sáiz F (2014) Parasitoidism of *Psyllaephagus pilosus* Noyes (Hym.: Encyrtidae) on the blue gum psyllid, *Ctenarytaina eucalypti* (Maskell) (Hem.: Psyllidae) in V Region eucalypts plantations. Agric Técn 66(4):342–351

Rojas E, Beèche M (2010) Detección y control de *Sirex noctilio* F. en Chile (Hymenoptera: Siricidae). In: Lanfranco D, Ruiz C (eds) Entomología Forestal en Chile. Ediciones Universidad Austral de Chile, Valdivia, pp 303–322

Rojas E, Gallardo R (2004) Manual de insectos asociados a maderas en la zona sur de Chile. Servicio Agrícola y Ganadero, Santiago

Rundel PW (1981) The matorral zone of central Chile. In: di Castri F, Goodall DW, Specht RL (eds) Mediterranean–type Shrublands. Elsevier, Amsterdam, pp 175–201

Rundel PW (1998) Landscape disturbance in Mediterranean–type ecosystems: an overview. In: Rundel PW, Montenegro G, Jaksic F (eds) Landscape disturbance and biodiversity in Mediterranean–type ecosystems. Springer, Berlin, pp 3–22

Rundel PW, Montenegro G, Jaksic F (1998) Landscape disturbance and biodiversity in Mediterranean–type ecosystems. Springer, Berlin

Ruz L (2002) Bee pollinators introduced to Chile: a review. In: Kevan P, Imperatriz Fonseca VL (eds) Pollinating bees- the conservation link between agriculture and nature. Ministry if Environment, Brazil, pp 155–167

SAG (2004) Informe anual 2004 subdepartamento de vigilancia y control de plagas forestales y exóticas invasoras. Servicio Agrícola y Ganadero, Santiago

SAG (2005) Informativo fitosanitario forestal N°2. Servicio Agrícola y Ganadero, Santiago

SAG (2006) Informativo fitosanitario forestal N°3. Servicio Agrícola y Ganadero, Santiago

SAG (2010) Informativo fitosanitario forestal N°4. Servicio Agrícola y Ganadero, Santiago

SAG (2014) *Leptocybe invasa* Fischer & Lasalle (Hymenoptera: Eulophidae) Microavispa formadora de agallas en Eucalipto. Plagas y enfermedades. http://www.sag.cl/ambitos–de–accion/leptocybe–invasa–fischer–lasalle–hymenoptera–eulophidae–microavispa–formadora–de. Accessed 23 Jan 2015

SAG (2015) Sirex noctilio o avispa de la madera del pino. Plagas y enfermedades. http://www.sag.cl/ambitos–de–accion/sirex-noctilio-o-avispa-de-la-madera-del-pino. Accessed 23 Jan 2015

San Martín J, Donoso C (1996) Estructura florística e impacto antrópico en el bosque Maulino de Chile. In: Armesto JJ, Villagrán C, Arroyo MTK (eds) Ecología de los Bosques Nativos de Chile. Editorial Universitaria, Santiago, pp 153–168

Schulz JJ, Cayuela L, Echeverria C et al (2010) Monitoring land cover change of the dryland forest landscape of Central Chile (1975–2008). Appl Geogr 30:436–447

Silva SI, Bozinovic F, Jaksic FM (2005) Frugivory and seed dispersal by foxes in relation to mammalian prey abundance in a semiarid thornscrub. Austral Ecol 30:739–746

Stanković SS, Petrović A, Ilić Milošević M et al (2015) Morphological and molecular characterization of common European species Adialytus (Hymenoptera: Braconidae: Aphidiinae) based on the mtCOI barcoding gene and geometric morphometrics of the forewings. Eur J Entomol 112:165–174

Valente C, Hodkinson I (2009) First record of the Red Gum Lerp Psyllid, *Glycaspis brimblecombei* Moore (Hem.: Psyllidae), in Europe. J Appl Entomol 133:315–317

Villacide JM, Corley JC (2012) Ecology of the woodwasp *Sirex noctilio*: tackling the challenge of successful pest management. Int J Pest Manag 58:249–256

Watson GW, Voegtlin DJ, Murphy ST et al (1999) Biogeography of the *Cinara cupressi* complex (Hemiptera: Aphididae) on Cupressaceae, with description of a pest species introduced into Africa. B Entomol Res 89:271–283

Zina V, Lima A, Caetano F et al (2012) First record of the pepper tree psyllid, *Calophya schini* Tuthill (Hemiptera, Calophyidae), in the Palaearctic region. Phytoparasitica 40:127–130

Chapter 14
Insects and Diseases of Mediterranean Forests: A South African Perspective

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Abstract The Mediterranean climate zone (MCZ) covers approximately 94,000 km^2 along the southern and western tip of South Africa. Roughly coinciding with the Cape Floristic Province encompassing Fynbos, Renosterveld and Succulent Karoo biomes, the area has very few native forests. Most occur in sparse patches on south-facing slopes and in a few areas of contiguous Afromontane forest. Plantations in this region, as well as the pests and diseases that damage them, comprise primarily exotic species in the genera *Pinus, Eucalyptus* and Australian *Acacia* (wattle), both as planted crops and as wilding escapes. At least 22 of 43 insect pests are present on plantation trees in South Africa and 16 of 33 pathogens are present in the MCZ, some causing serious damage. A small number have also been intentionally introduced for biological control of invasive wattles. This chapter summarizes current knowledge on the insects and pathogens of *Pinus, Eucalyptus* and Australian *Acacia* in the MCZ South Africa. Special attention is given to examples where the biology, life history or expression of damage or disease differs from the summer rainfall areas of the country.

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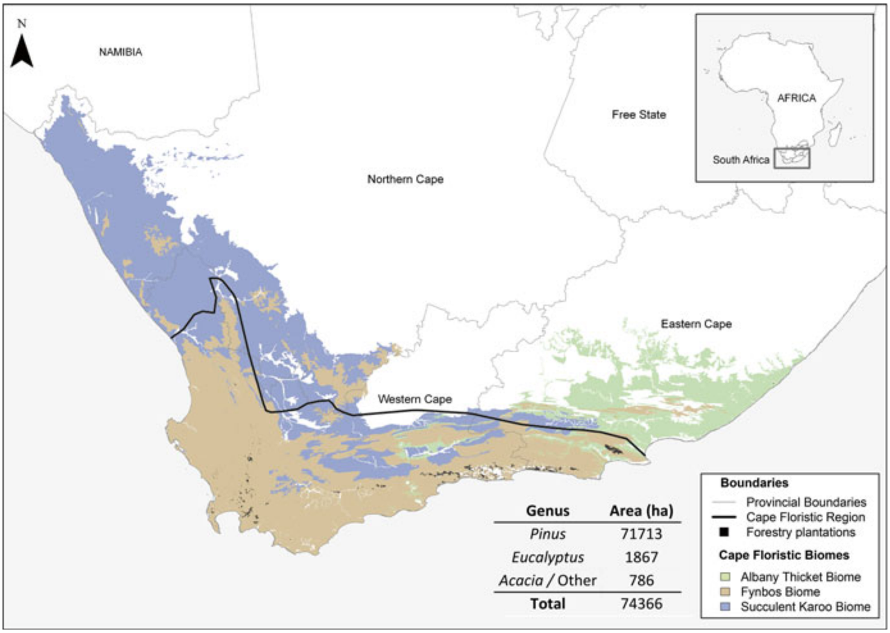
14.1 Introduction: The Mediterranean Climate Zone in Southern Africa

As in other parts of the world, precise definitions or delineation of the Mediterranean climate zone (MCZ) are elusive in southern Africa (Blumler 2005; Kruger 2014). Characteristic Mediterranean climate conditions – hot, dry summers and cool, wet winters – occur principally in the Western Cape province of South Africa in the southwest corner of the country (Rundel 1998; Schulze 2007, Fig. 14.1). Many authors extend the boundaries of MCZ to the east as far as Port Elizabeth (Eastern Cape) where rain can fall year round, and midway to the Namibian border along the Atlantic coast, where conditions are highly seasonal, but exceedingly arid (20–290 mm per annum with most areas receiving <10 mm, though additional moisture enters the system as coastal fog; Mucina and Rutherford 2006). The core of the MCZ is centered on the areas of the southwestern Cape Province where annual rainfall ranges from 366 to 1607 mm, with more than 75 % falling in winter (April-September in the Southern Hemisphere: Cowling et al. 2005, Fig. 14.2).

The historical climate, geological history and natural ecology of the MCZ in South Africa are most similar to that of the southwest coast of Australia (Rundel 1998). Both have remained relatively stable geologically and climatically for millions of years, and are characterized by ancient, highly leached, nutrient-poor soils



Genus	Area (ha)
Pinus	71713
Eucalyptus	1867
Acacia / Other	786
Total	74366

Fig. 14.1 Map of southern Africa showing the three major biomes that broadly occur within the Mediterranean climate zone (MCZ). The *bold line* corresponds to the Cape Floristic Province and roughly delineates the MCZ

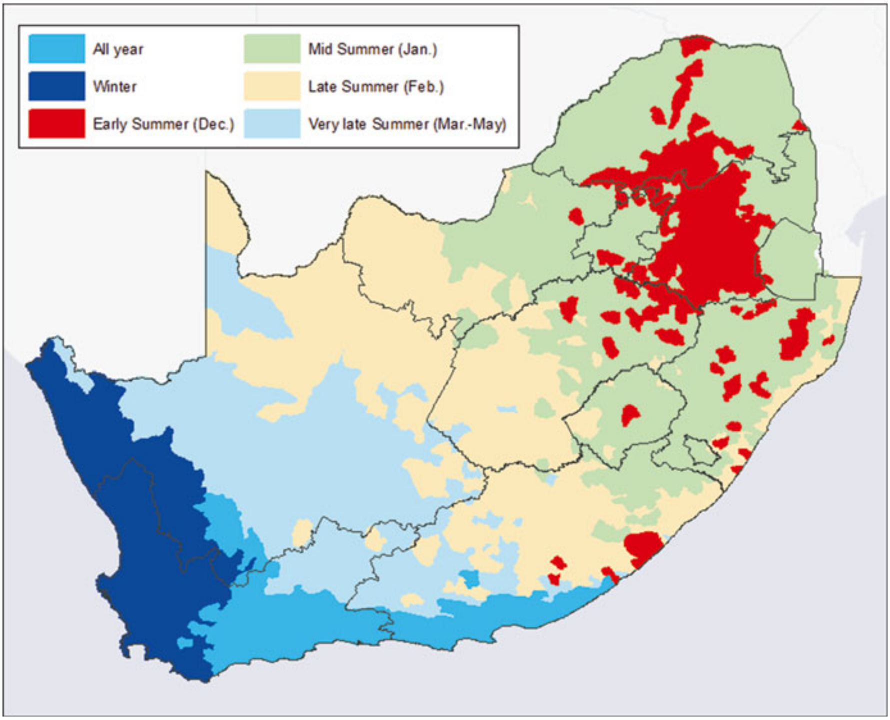


Fig. 14.2 Rainfall seasonality in South Africa [Data from Schulze (2007)]

and by frequent fires (every 10–15 years in the case of South Africa, considerably more frequent than Chile, California or the Mediterranean basin; Rundel 1998). The MCZ roughly corresponds to the Cape Floristic Region (CFR), which harbors astonishing plant diversity: over 9000 species in nearly 1000 genera and an endemism rate approaching 70 %, but with very few trees (Rouget et al. 2003). The dominant vegetation types of the CFR are shrubs and perennial herbs that fall broadly into the Fynbos or Renosterveld types. Fynbos, or “fine leaved” in Afrikaans, comprises diverse sclerophyllous, fire-adapted and mostly-evergreen plants in the Proteceae, Ericaceae and Restionaceae. The Renonsterveld derives its name from the “renosterbos”, Afrikaans for rhinoceros bush (*Elytropappus rhinocerotis*), but in fact is dominated by perennial grasses and numerous species in the Asteraceae, of which the rhinoceros bush is one (Rouget et al. 2003; Mucina and Rutherford 2006; Kruger 2014). At the northern reaches of the CFR is the Succulent Karoo, characterized by dwarf vegetation in the families Mesembryanthemaceae, Crassulaceae and Aloaceae, as well as diverse and abundant geophytes, which spend at least part of their annual life cycle underground as dormant corms, tubers or bulbs (Born et al. 2006; Mucina and Rutherford 2006).

One stark difference between the MCZ in South Africa compared with the rest of the world is the almost complete lack of forests. Small patches of Afromontane forest occur scattered around the CFR, primarily on south-facing ridges and along steep ravines. One larger contiguous swath that occurs within the region – the Knysna/Tsitsikamma *forest* along the southern Cape coast – occupies 568 km^2 in an area with patchy, but continuous year-round rain that falls predominately in the summer months (Midgley et al. 1997). Such forests, while they occur broadly within the MCZ, clearly experience conditions uncharacteristic of Mediterranean climates and represent a distinct ecozone.

14.2 Mediterranean Afforested Landscapes: Past and Present

When Europeans first established permanent settlements in 1652 in what was to become the Western Cape of South Africa, they encountered a landscape with limited timber resources that were depleted quickly (Olivier 2009; Bennett and Kruger 2013). Perhaps as a result, afforestation linked to the planting of exotic species commenced almost immediately. Land proprietors were prompted by decree to plant 100 young oaks on all holdings as early as 1689, though it was not until around 1820 that the first commercial plantation is known to have been established (Olivier 2009). By the early twentieth century, numerous species of *Pinus*, *Eucalyptus* and Australian *Acacia* were actively being cultivated for timber, tannins, and fuelwood, as well as for shade and as windbreaks. Several of these species, notably *Pinus pinaster* (maritime pine), *Acacia melanoxylon* (Tasmanian Blackwood), as well as *A. mearnsii, A. longifolia and A. cyclops* (black, long-leaf and red-eyed wattle) and several eucalypts, have become aggressive invaders in the region (Richardson 2000; Richardson et al. 2011; Richardson and Rejmánek 2011). Many form dense stands that outcompete fynbos and grassland vegetation and can inhibit indigenous tree regeneration on harvested or burned sites (Bennett and Kruger 2013). Tree invasions represent a major threat to biodiversity in the region, a fact which has caused considerable conflict and controversy around exotic plantation forestry since the early twentieth century (Bennett and Kruger 2013). Forest growers, in adherence with government regulations and requirements set by sustainable forest certification authorities, have modified planting and management practices considerably. In many cases this has meant utilizing species that are less prone to escape, enforced buffer zones around riparian areas to limit effects on streamflow, and limited the extent of exotic plantations (Bredenkamp et al. 2012). Nevertheless, current trends appear to favour reductions in planted area, at least partly due to conservation concerns (Anonymous 2012).

Conflicts aside, nearly all forests within the core of the winter rainfall zone in the MCZ are exotic plantations and areas of natural recruitment of *Pinus*, *Eucalyptus* and Australian *Acacia*. A handful of other tree species are particularly invasive in the region, including *Hakea sericea, Sesbania punicea* as well as *Prosopis* species to the north in the Succulent Karoo (Moran et al. 1999; Van den Berg et al. 2013).

In 2014, the reported forest plantation cover in the region was 74,366 ha and was mostly pine (71,713 ha; principally *Pinus radiata*). There was only a modest *Eucalyptus* (1,867 ha) component, and *Acacia mearnsii* and other species of minor importance (e.g., poplar) contributed only 786 ha (DAFF 2014). Taken together, this area represents just less than 1 % of the land area of the MCZ. The contribution of exotic escapes to total forested land area is difficult to calculate as little of the invaded landscape is characterized by closed canopy or contiguous forest, but rather as distributed patches of trees with some dense thickets occurring along riparian zones (Rouget et al. 2002; Le Maitre et al. 2000).

14.3 Pests and Diseases of Forests in the South African MCZ

Very little is known about the insects and diseases of the southern Afromontane forest in the MCZ of South Africa. In light of limited knowledge and scant occurrence of major biotic threats to these forests, the proportionally small land area contributed and the fact that climate conditions associated with the biome are uncharacteristic of other Mediterranean forests, we focus this review exclusively on cultivated plantation forestry trees and forestry trees imported for cultivation that later escaped and spread, all of which are non-native to the region. Forest plantations and areas of natural recruitment by exotic species in the genera *Pinus*, *Eucalyptus* and *Acacia* support a number of insects and pathogens of both native and exotic origin, many of which are shared with and/or have relevance to the other MCZ's in the rest of the world.

Detailed knowledge of patterns of distribution and abundance specific to the MCZ within South Africa is lacking. Tables 14.1 and 14.2 summarize the insect and pathogen threats of current and historical importance in southern Africa. We divide these taxa into those that are unique or endemic to the MCZ, those that are known to be widespread with clear impacts in the MCZ, and those that are known from South Africa but not specifically documented in the MCZ (or where only anecdotal reports exist). Perhaps surprisingly in light of the climatic distinctiveness of the MCZ relative to the rest of South Africa, the majority of insect threats appear to be shared across the whole country, particularly those of exotic origin. More subtle differences (e.g., in behaviour, abundance and/or phenology) do exist, however, and are treated in greater detail below.

14.3.1 Forest Insects in the MCZ

Of the 43 insect pests of *Pinus*, *Eucalyptus* and Australian *Acacia* found in South Africa (Table 14.1), 26 (60 %) have been reported or are assumed present on hosts within the MCZ. Distributional data are difficult to interpret, however, as sporadic attacks by native insects often go unreported. All of the most serious pests of *Pinus*

Table 14.1 Insect pests of plantation trees in South Africa, with focus on the Mediterranean Climate Zone (MCZ)

Scientific name(s)	Common name	Trees affected[b]	Feeding guild	Native/introduced	Presence in MCZ
Achaea lienardi	Wattle semi-looper	*Acacia*	Defoliator	N	No report
Agrotis spp.	Cutworms	*Acacia, Eucalyptus Pinus*	Establishment pest	N	Assumed present
Blastopsylla occidentalis	Eucalyptus shoot psyllid	*Eucalyptus*	Sap-sucker	I	No report
Catamonus sp.	Catamonus weevil	*Acacia*	Defoliator	N	No report
Cinara cronartii	Black pine aphid	*Pinus*	Sap-sucker	I	Confirmed present (Prinsloo and Uys 2014)
Cleora herbuloti	Pine looper	*Eucalyptus Pinus*	Defoliator	N	Assumed absent (Hepburn and Leodolff 1964)
Colasposoma spp.	Green bronze beetle	*Eucalyptus Pinus*	Establishment pest Defoliator	N	Assumed absent (van Webb 1974)
Coryphodema tristis	Cossid moth	*Eucalyptus nitens*	Wood borer	N	Not present (Gebeyehu and Hurley 2005)
Ctenarytaina eucalypti	Blue gum psyllid	*Eucalyptus*	Sap-sucker	I	No report
Dasineura rubiformis	Black wattle gall midge	*Acacia*	Gall former	I[a]	Confirmed present (Impson et al. 2013)
Drosophila favohirta	Eucalypt nectar fly	*Eucalyptus*	Pollen feeder	I	Confirmed present (Tribe 1991a)
Ellimenistes laesicollis	Grey weevil	*Eucalyptus Acacia*	Establishment pest Defoliator	N	No report
Eulachnus rileyi	Pine needle aphid	*Pinus*	Sap-sucker	I	Confirmed present (Prinsloo and Uys 2014)
Euproctis terminalis	Pine brown tail moth	*Pinus*	Defoliator	N	Assumed absent (Tooke 1938; Prinsloo and Uys 2014)

Eutricha capensis	Brown lappet moth	*Acacia Eucalyptus Pinus*	Defoliator	N	Confirmed present (van Webb 1974)
Glycaspis brimblecombei	Red gum lerp psyllid	*Eucalyptus*	Sap-sucker	I	Confirmed present (authors, pers. obs)
Gonipterus n. sp. 2	Eucalyptus weevil	*Eucalyptus*	Defoliator	I	Confirmed present (Tooke 1953; Mapondera et al. 2012)
Gynanisa maia	Wattle emperor moth	*Acacia*	Defoliator	N	No report
Hylastes angustatus	Pine bark beetle	*Pinus*	Establishment pest Bark borer	I	Confirmed present (Tribe 1990b)
Hylurgus ligniperda	Red-haired pine bark beetle	*Pinus*	Bark borer	I	Confirmed present (Tribe 1991c)
Imbrasia cytherea	Pine emperor moth	*Acacia, Pinus*	Defoliator	N	Confirmed present (van Webb 1974)
Imbrasia tyrrhea	Willow tree emperor moth	*Eucalyptus, Pinus*	Defoliator	N	Confirmed present (Prinsloo and Uys 2014)
Kotochalia junodi	Wattle bagworm	*Acacia*	Defoliator	N	No report
Leptocybe invasa	Blue gum chalcid	*Eucalyptus*	Gall former	I	Confirmed present (authors, pers. obs.)
Lygidolon laevigatum	Wattle mirid	*Acacia*	Sap-sucker	N	No report
Monochelus calcaratus	Lesser wattle chafer	*Acacia*	Defoliator	N	No report
Odontionopa sericea	Fruit nibbler	*Eucalyptus, Pinus*	Defoliator	N	Mainly in MCZ (Tribe 1991b)
Oosomus various	Diamond-back pine snout beetle	*Eucalyptus, Pinus*	Defoliator	N	Exclusively in MCZ (Tribe 1991b)
Ophelimus maskelli	Eucalyptus gall wasp	*Eucalyptus*	Gall former	I	No report
Orthotomicus erosus	Mediterranean pine engraver beetle	*Pinus*	Bark borer	I	Confirmed present (Tribe 1990a)

(continued)

Table 14.1 (continued)

Scientific name(s)	Common name	Trees affected[b]	Feeding guild	Native/introduced	Presence in MCZ
Pegylis sommerii	Wattle chafer	*Acacia, Pinus*	Defoliator	N	Confirmed present (du G. Harrison 2014)
Phorocantha recurva and *P. semipunctata*	Eucalyptus longhorn beetle	*Eucalyptus*	Wood borer	I	Confirmed present (van Webb 1974)
Pineus boerneri	Pine woolly aphid	*Pinus*	Sap-sucker	I	Confirmed present (Bruzas 1983)
Pissodes nemorensis	Deodar weevil	*Pinus*	Bark borer	I	Confirmed present (van Webb 1974)
Pseudobunea irius	Poplar emperor moth	*Acacia, Eucalyptus Pinus*	Defoliator	N	Assumed absent (Hepburn 1966)
Sirex noctilio	Sirex woodwasp	*Pinus*	Wood borer	I	Confirmed present (Tribe 1995)
Spondyliaspis plicatuloides	Shell lerp psyllid	*Eucalyptus*	Sap-sucker	I	No report
Thaumastocoris peregrinus	Bronze bug	*Eucalyptus*	Sap-sucker	I	Confirmed present
Trachymela tincticollis	Eucalyptus tortoise beetle	*Eucalyptus*	Defoliator	I	Exclusively in MCZ (Tribe 2000)
Various species	Grasshoppers and crickets	*Acacia, Eucalyptus Pinus*	Establishment pest	N	Assumed present
Various species	Termites	*Acacia, Eucalyptus*	Establishment pest	N	Confirmed present (van Webb 1974)
Various species of Scarab beetle larvae	Whitegrubs	*Acacia, Eucalyptus Pinus*	Establishment pest	N	Assumed present
Xyleborus spp. *Xyleborinus* spp.	Ambrosia beetles	*Pinus*	Wood borer	I	Confirmed present (Mandelshtam and Danielsson 2004)

[a] Intentionally introduced for the biological control of invasive weeds

[b] "Trees affected" column reflects examples of moderate to several and/or recurring damage occur and do not include native or occasional hosts

Table 14.2 Pathogens[a] of plantation trees in South Africa, with a focus on the Mediterranean Climate Zone (MCZ)

Scientific name(s)	Disease name/type	Plantation species affected	Other host records	Native/introduced	Presence in MCZ
Armillaria fuscipes *Armillaria species*	Armillaria root rot	*Eucalyptus, Pinus*	Several native South African tree species; non-native fruit tree species, oak	N I	No report of *A. fuscipes*, but several reports of *A. mellea* on non-plantation hosts (Doidge et al. 1953)
Aulographina eucalypti	Aulographina leaf spot	*Eucalyptus*	–	I	Assumed
Camptomerris albizziae	Camptomerris leaf spot	*Acacia mearnsii*	–	I	Yes
Ceratocystis albifundus	Wattle/Ceratocystis wilt	*Acacia mearnsii, A. decurrens*	Native African tree species in more than ten plant families	N	Yes
Cercoseptoria pini-densiflorae	Needle blight	*Pinus*	–	I	No report
Chrysoporthe austroafricana	Cryphonectria canker	*Eucalyptus*	Non-native ornamental *Tibouchina*	N	No report
Cyclaneusma minus	Cyclaneusma needle spot	*Pinus*	–	I	Yes (Crous et al. 1991)
Diplodia sapinea	Diplodia canker	*Pinus*	–	I	Yes (Burgess et al. 2004)
Dothistroma septosporum	Dothistroma needle blight	*Pinus*	None	I	No report
Erythricium salmonicolor	Pink disease	*Acacia mearnsii* *Eucalyptus*	*Ekebergia capensis* *Dais cotonifolia,* *Podocarpus henkelii*	U	No report
Fusarium circinatum	Pine pitch canker	*Pinus*	Grass species	I	Yes (Coutinho et al. 2007)
Grosmannia alacris	Blue stain and root disease associated with root infecting bark beetles	*Pinus*	–	I	Yes (Wingfield and Knox-Davies 1980a, b)

(continued)

Table 14.2 (continued)

Scientific name(s)	Disease name/type	Plantation species affected	Other host records	Native/introduced	Presence in MCZ
Holocryphia eucalypti	Holocryphia (Endothia) canker	*Eucalyptus*	*Metrosideros angustifolia*	I	Yes on *M. angustifolia* (Chen et al. 2013)
Lasiodiplodia theobromae	Blue stain Canker	*Acacia, Eucalyptus, Pinus*	Several native South African tree species; non-native fruit tree species	I	Assumed absent; typically restricted to tropical and sub-tropical areas. (Slippers and Wingfield 2007)
Lophodermium sp.	Needle spotting	*Pinus*	–	I	Yes (Crous et al. 1991)
Neofusiccocum spp.[b]	Botryosphaeria canker	*Eucalyptus*	Several native South African tree species; non-native fruit tree species	U	*N. australe*, *N. parvum*; others assumed present (Crous et al. 2000; Slippers et al. 2007, 2009; Van Niekerk et al. 2004)
Ophiostomatoid fungi[b]	Blue stain of pine (roots and bole)	*Pinus*	Many	I	*O. abietinum, P. piliferum, O. stenoceras;* No report for others but assumed present.
Pantoea ananatis	Bacterial blight	*Eucalyptus*	–	I	No report
Phytophthora boehmeriae	Phytophthora root rot of *Acacia*	*Acacia mearnsii*	–	U	No report

Phytophthora cinnamomi	Phytophthora root rot	*Eucalyptus, Pinus radiata*	Native and non-native plant species (e.g., *Quercus*, Proteaceae etc.)	I	Yes (Olivier 1951; Van der Merwe and Van Wyk 1973; von Broembsen and Kruger 1985; Oh et al. 2011)
Phytophthora parasitica	Black butt disease (root rot)	*Acacia mearnsii*	–	U	No report
Pseudophaeolus baudonii	Pseudophaeolus root rot	*Eucalyptus* *Pinus* species	–	N	No report
Puccinia psidii	Myrtle rust	Not detected on *Eucalyptus* yet, but present in country	*Myrtus communis*	I	No report
Quambalaria eucalypti	Quambalaria leaf and shoot blight	*Corymbia* *Eucalyptus*	None	I	No report
Ralstonia solanacearum	Bacterial wilt	*Eucalyptus*	Various vegetable crops	U	No report
Rhizina undulata	Rhizina root rot	*Pinus*	None	I	Yes (authors, pers. obs.)
Sphaerotheca pannosa	Mildew	*Acacia, Eucalyptus, Pinus*	Numerous	U	Yes
Teratosphaeria suttonii	Leaf spot	*Eucalyptus*	None	I	Yes (authors, pers. obs)
Teratosphaeria nubilosa	Mycosphaerella leaf blotch	*Eucalyptus*	None	I	Yes (Crous et al. 1991)
Teratosphaeria zuluensis	Coniothyrium stem canker	*Eucalyptus*	None	I	No report
Uromycladium alpinum	Uromycladium rust	*Acacia mearnsii*	None	I*	Yes (authors, pers. obs)
Xanthomonas vasicola	Bacterial blight	*Eucalyptus*	Sugarcane	U	No report

*Intentionally introduced for the biological control of invasive weeds

[a] "Pathogens" listed are only examples of moderate to severe pathogens causing plant death and economic losses and do not include those resulting in only sporadic or negligible damage

[b] Multiple species, many previously recorded as *Botryosphaeria dothidea* and *B. ribis*

and *Eucalytpus* are present in the MCZ (with the exception of *Ophelimus maskelli*, which was only recently detected in 2014 near Johannesburg; Bush et al., *in prep.*). The wattle insects in Table 14.1 are largely known from black wattle (*Acacia mearnsii*) plantations from the interior, which together with green wattle (*Acacia decurrens*), comprise the majority of cultivated plantation wattles in South Africa. Many of these insects have not actually been reported in the MCZ, and while they may be present, none is of importance either as a pest species of plantation-grown or escaped wattles, and do not appear to limit the spread of these trees into native areas (Impson, pers. comm.).

Native insects damaging exotic trees appear to be characterized by an over-representation of broad generalists. Fourteen of the twenty-two native insects listed in Table 14.1 are known as pests for at least two genera of exotic trees, though several of these insects are actually groups of related species (e.g., grasshoppers and crickets, cutworms, termites, and white grubs) and are primarily pests of establishment. Of those known to be present in the MCZ, only the Pine and Willow Tree Emperor Moths (*Imbrasia cytherea* and *Imbrasia tyrrhea* respectively) and the brown lappet moth (*Pachypasa capensis*) are pests of mature trees, and in some years cause severe defoliation, particularly on *Pinus* species (van Webb 1974).

The dominance of generalist insects stands in stark contrast to the introduced pests, all of which are restricted to a single host genus. Many are further restricted or show strong preference for a subset of species or clades within those genera (Tooke 1953; Santana and Burckhardt 2007; Dittrich-Schröder et al. 2012). Not surprisingly, there is also a marked discrepancy between the levels of damage caused by exotic and native species, with a small number of the most damaging introduced pests causing the bulk of economic losses. The effects of major *Eucalyptus* pests (i.e., *Leptocybe invasa, Gonipterus* spp., *Thaumastocoris peregrinus* and *Glycaspis brimblecombei*), as well as *Sirex noctilio* on *Pinus* are severe. For example, the blue gum chalcid, *Leptocybe invasa*, is the most devastating and widespread pest on *Eucalyptus* in South Africa, and perhaps worldwide (Mendel et al. 2004; Nugnes et al. 2015; Nyeko et al. 2010).

In the MCZ, however, *Eucalyptus* is of relatively minor importance as a forestry crop, and the effects of these insects may be more pronounced for beekeepers who value the pollen and nectar of at least 13 species of *Eucalyptus* as a source of honey. The combination of the success of biocontrol (species swapping) and the diminished importance of *Eucalyptus* has resulted in reduced attention to some pests (e.g., *Phoracantha recurva* and *P. semipunctata*) in the MCZ. This is despite the fact that some were formerly of major consequence and even changed the face of forestry in the region (e.g., the *Gonipterus* leaf weevil, discussed in detail below).

Together with pathogens and fire, these insects represent serious threats to forest plantations countrywide. All are the subject of active research on management and biological control. Research and management to control the spread of the trees themselves (particularly Australian *Acacia*) are also ongoing, and numerous insects and one rust pathogen have been imported and have become established (see Sect. 14.3.3). Impacts also vary widely when considering the MCZ versus the summer rainfall areas, a reflection of a complex interplay among climate, management regime (i.e., mainly pulp in the summer rainfall versus mainly timber in the MCZ) and regional variation in the planting and importance of certain host tree species. Climate, however, appears to be a weak driver of the distribution of introduced pests.

Considerable work has been published on the biology and life history of many of the pests from Table 14.1 (Wingfield et al. 2013; Slippers et al. 2014; Nadel et al. 2015). Many have been studied principally in the primary growing areas of the Mpumalanga and KwaZulu-Natal Provinces. Forestry in the MCZ contributes only about 8 % to the total plantation area of the country and is largely dominated by pine (96 % in the region; Fig. 14.1). As such, pests of *Eucalyptus* of major importance elsewhere in South Africa (e.g., *L. invasa*, *T. peregrinus*, *G. brimblecombei*), together with some of the insects specific to wattle, are of only passing interest in the MCZ. However, three pests of pine (*S. noctilio*, *I. cytherea* and *P. nemorensis*) and two of *Eucalyptus* (*Gonipterus* beetles and *T. tinticollis*) have in part shaped forestry in the region and/or exhibit behaviours, ecologies or have distributions that are specific to the MCZ. We focus on these five insects in greater detail in the following section and also include a brief discussion of the native wood-boring moth (*Coryphodema tristis*) present in the region but acting as a forest pest only to the north of its distribution in the summer rainfall zone.

14.3.2 Case Studies: Insects of Relevance to Plantation Forests of the MCZ

14.3.2.1 Sirex Woodwasp: *Sirex noctilio*

The Sirex woodwasp (*Sirex noctilio*; Siricidae; Fig. 14.3a) is Eurasian in origin and was first recorded from South Africa in a *P. radiata* plantation in Tokai, Cape Town in 1994 (Tribe 1995). The presence and apparent age of emergence holes indicated that it was present at least 2 years earlier. The *S. noctilio* life cycle has been written about at length elsewhere (Slippers et al. 2012a). Briefly, *S. noctilio* adults attack primarily stressed trees (though healthy trees are also vulnerable when wasps are at high densities in the invasive range). Female wasps probe trees, placing arthrospores of a symbiotic fungus, *Amylostereum aereolatum* (typically, but see Hajek et al. 2013; Wooding et al. 2013), a phytotoxin, and sometimes one or a few eggs (Madden 1974). Larvae develop within the sapwood for 1–3 years depending on temperature, though no life cycles greater than 1 year have been recorded in South Africa. Within the first few months post-oviposition, trees decline and die (Fig. 14.3b).

The arrival of *S. noctilio* to South Africa was not unexpected given that the wasp had been introduced and was widely distributed across the Southern Hemisphere, infesting plantations of *Pinus* in Mediterranean climates in New Zealand, Australia and South America (Slippers et al. 2014). The wasp's rapid spread and aggressive establishment in the continental and subtropical climates in the east of the country

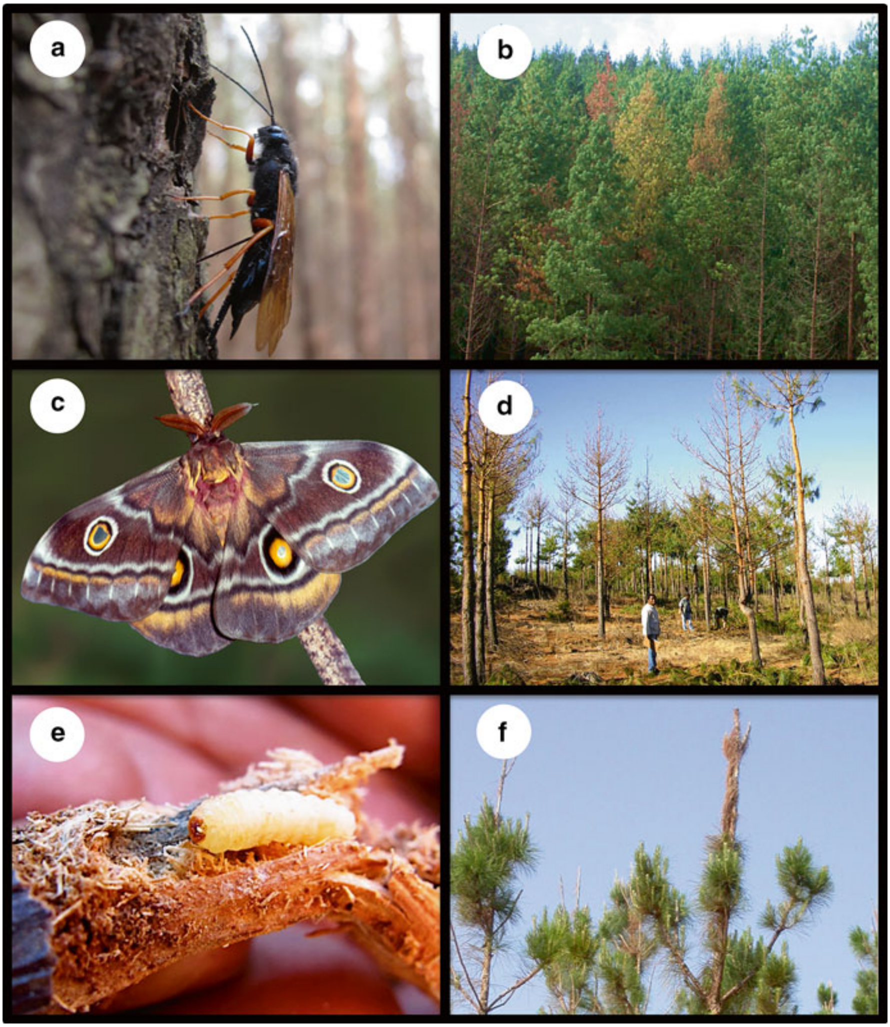


Fig. 14.3 Insects and damage relevant to exotic forestry in the Mediterranean climate zone (MCZ), South Africa. Subfigures are as follows: female *Sirex noctilio* ovipositing on *Pinus patula* (**a**); dead and dying pines after attack by *S. noctilio* (**b**); *Imbrasia cytherea cytherea* adult (**c**) and defoliation (**d**) *Pissodes nemorensis* larvae if the terminal leader of *Pinus radiata* (**e**) and associated tip dieback in the Western Cape of South Africa Photos by Jeff Garnas (**a**), Brett Hurley (**b, e** and **f**), Rolf Oberprieler (**c**), and Stuart Charlton (**d**)

(dominated by *P. patula*, and to a lesser degree *P. elliottii* and *P. taeda* plantations) and its rapid switch to the altered phenology in the summer rainfall zone, was considerably more surprising (Hurley et al. 2011). *Sirex noctilio* has since established throughout plantations in South Africa, including all plantations in the MCZ and stretching to plantations in northern Limpopo (Lantschner et al. 2014).

Major differences in population dynamics and impact of *S. noctilio* populations exist in the eastern summer rainfall regions of South Africa in comparison to the MCZ (Hurley et al. 2011). For example, climatic differences strongly influence flight phenology, which occurs from late October to December in the east of the country (peaking in November), and from December to April in the Cape (peaking in March/April). In the Cape region, the populations of *S. noctilio* have only rarely reached outbreak levels. Only one relatively mild outbreak (10 % mortality in localized patches) has been recorded to date in the MCZ, recorded near the town of George in 2002. In contrast, outbreaks resulting in up to 35 % tree mortality have been recorded in some *P. patula* plantations in the east of the country (Hurley and Slippers 2007). These differences in population densities and impacts are almost certainly driven largely by vastly different management regimes. In general, commercial pine production is characterized by timber in the MCZ (mainly using *P. radiata* in the MCZ, with regular pruning and thinning that reduces stand stress) and by pulp production in much of the summer rainfall area (dominated by *P. patula* at high planting densities – up to 1600 stems ha.$^{-1}$ – where no density reductions are performed; Hurley et al. 2011). Nevertheless, the influence of climate and pine host species on wasp population dynamics is difficult to discount.

An intensive biological control program has been implemented for *S. noctilio* in South Africa. *Ibalia leucospoides*, a parasitoid of egg and first instar *S. noctilio* larvae, was introduced from Uruguay in 1998 into the Cape (Hurley et al. 2008). This parasitoid has established well throughout the MCZ, parasitizing between 0 % and 50 % of *S. noctilio* larvae in plantations across the region (Hardus Hatting and Brett Hurley, *unpublished data*). Natural spread of *Ibalia leucospoides* into the summer rainfall areas has been slow, and wasps are still collected in the MCZ to be released in plantations in the east of South Africa. While impacts of *Ibalia* on *Sirex* in Cape plantations appear to be considerable, parasitoid effectiveness as a biocontrol agent outside the MCZ is unclear.

Deladenus siricidicola, a parasitic nematode that sterilizes the females of *S. noctilio*, was first introduced in the MCZ in plantations around the Cape peninsula in 1995–1996 (Tribe and Cillié 2004). Nematode-infested logs have since been moved to other plantations in the MCZ along the south coast. The nematode has established in the MCZ, although at rates of background parasitism (i.e., percent occurrence in wasps emerging from un-inoculated trees) ranges from 0 % to 64 % depending on site and year (Slippers et al. 2012b).

The Tree Protection Cooperative Programme (TPCP) at the Forestry and Agricultural Biotechnology Institute (FABI: www.fabinet.up.ac.za) manages a massive programme of inundative control using these nematodes, where close to 1 billion nematodes are reared, transported and inoculated into thousands of *S. noctilio*-infested trees annually, both inside and outside the MCZ (Hurley et al. 2008, 2011). Inoculation success and early establishment of *D. siricidicola* was higher in the MCZ than in the summer rainfall regions of the country (Tribe and Cillié 2004; Hurley et al. 2008). This difference is hypothesized to relate to differences in wood moisture content at time of inoculation between these two regions. Low moisture content at time of inoculation in the summer rainfall regions is thought to result in poor establishment of the fungus *Amylostereum areolatum*, which serves as a food source for the nematodes in the mycetophagous (fungus-feeding) stage (Hurley et al. 2012).

14.3.2.2 Pine Emperor Moth: *Imbrasia cytherea*

The Pine Emperor Moth (*Imbrasia [Nudaurelia] cytherea*) is a large and striking insect in the emperor moth family (Saturniidae; Fig. 14.3c). Larvae can reach 120–130 mm in length and are intricately and colorfully patterned; adult moths have wingspans of approximately 150 mm with colorfully ringed eyespots on the hindwings (Fig. 14.3d). In addition to their size and appearance, *I. cytherea* is impressive for both its wide host range and its capacity for rapid population growth. Larvae feed on a minimum of 40 native and exotic species across families and orders and are capable of completely defoliating large areas, including plantations of pine, wattle and *Eucalyptus*.

Capable of sustained outbreaks causing severe damage over hundreds of hectares on both wattle and pine (particularly *P. radiata*), this insect represents a serious threat to tree growers in the region. The list of recorded host plants includes the native sugarbush (*Protea repens*), as well as apple, quince, oak and several of the introduced wattles (*A. mearnsii, A. cyclops, A. longifolia* and *A. saligna*), among numerous other species (Tooke and Hubbard 1941). The species occurs from the southern tip of Africa north into Zimbabwe and is usually treated as comprising two sub-species. These are the dark brown nominate sub-species (*Imbrasia cytherea cytherea*) in the Western Cape and the yellow sub-species (*I. cytherea clarki*) in the Eastern Cape and Highveld area to the north (Geertsema 1971). Pupae are found in the soil, and massive hand collection efforts were made during the 1920's as a means of control in *P. radiata* plantations. In 1924, 230,000 of the insects were manually removed from a single 121-ha infestation of *P. radiata* (together with "100 lbs. of eggs and 163 bags of egg-infested twigs"), but the effort was still insufficient to stop the outbreak (Tooke and Hubbard 1941). Two years later, 50 pigs were enclosed in the same plantation to substitute for hand collection. Pig foraging reduced population density from 150 to 175 pupae per tree to 12. Larval mortality is also incurred due to infection by a suite of small RNA viruses present in populations (Tripconey 1969; Walter et al. 2008), as well as numerous parasitoids of all life stages and several vertebrate predators (Tooke and Hubbard 1941).

In addition to *I. cytherea cytherea* (and *I. cytherea clarki* to the north), the related Willow Tree Emperor moth (*Imbrasia [Gonimbrasia] tyrrhea)* is occasionally problematic in the MCZ on forestry crops (Hepburn 1966; van Webb 1974). Both *I. tyrrhea* and its close relative *Imbrasia [Gonimbrasia] belina* (the so-called Mopane worm) are consumed by humans. The former is consumed locally, largely in Namaqualand (Northern Cape Province) while the latter is harvested in huge numbers from xeric woodlands in the Limpopo Province of South Africa to as far north as the Democratic Republic of the Congo and extensively traded as an important source of protein (Hrabar et al. 2009). *Imbrasia belina* has also been reported to feed on *P. radiata* (Oberprieler 1986) though only well outside of the MCZ.

14.3.2.3 Deodar Weevil: *Pissodes nemorensis*

Pissodes nemorensis (the deodar weevil) was first discovered in South Africa in 1942 infesting logs of *P. radiata* in Port Elizabeth (Eastern Cape Province) and has now spread throughout the country (van Webb 1974). Throughout most of its range, the beetle attacks dead or dying trees, where larvae typically develop in the phloem and pupate in shallowly excavated chambers on the surface of the xylem (Fig 14.3e). As a result of this behavior, *P. nemorensis* is generally of little economic consequence for growers of *Pinus* for pulp or timber. However, as in its native range of North America, oviposition and larval development within the terminal leader of vigorously growing trees can also occur (Fig. 14.3f). The corresponding tip death causes fork formation or crooked growth resulting in a reduction in timber values. Interestingly, tip colonization by *P. nemorensis* appears to be considerably more common in the MCZ (Gebeyehu and Wingfield 2003; Prinsloo 2005). Whether this is a result of different insect-host dynamics on *P. radiata* or an indirect effect of climate (i.e., via shifted oviposition phenology) is currently unknown. Efforts to quantify and to improve mechanistic understanding of the drivers of this pattern are currently underway (Mesfin Gossa, unpublished).

Immature stages of the weevil are parasitized by an endemic pteromalid wasp, *Pycnetron pix*, a native parasitoid of the cycad seed weevil (*Antliarhinus peglerae*) (Prinsloo 2005). This parasitoid is regularly recovered at low frequency and has been reported as absent from the MCZ (Prinsloo 2005). However, recent sampling has recovered *P. pix* from *P. radiata* plantations of the Western Cape (Mesfin Gossa, *unpublished data*). A species of fly in the genus *Gobertina* (Diptera:Stratiomyidae) apparently parasitizing larvae and/or pupae has also been recovered, though its effect on populations is unknown (Gebeyehu and Wingfield 2003).

14.3.2.4 Eucalyptus Tortoise Beetle: *Trachymela tinticollis*

The Eucalyptus Tortoise Beetle (*Trachymela tinticollis)* is a chrysomelid beetle in the Tribe Paropsini discovered in the Cape Peninsula of South Africa in 1982 (Tribe and Cillié 1997). In its native range of southwestern Australia, *T. tinticollis* appears to be a complex of species that can be distinguished on the basis of host preference and subtle aspects of behaviour (Tribe 2000). Initial outbreaks in South Africa were *on Eucalyptus gomphocephala* though the beetles feed on at least 13 species of *Eucalyptus* in the MCZ, including the commercially important *E. grandis* (Tribe and Cillié 1997; Tribe 2000). As with most paropsine beetles, both larvae and adults feed and together are capable of serious defoliation. Feeding takes place in the predawn and dusk hours; adults often hide in bark crevices during the day. Larvae are present between September and February (peaking in November) and adult dispersal occurs in February and March in the MCZ of South Africa (Tribe and Cillié 1997).

A suite of parasitoids is known from the native range in Australia, including at least five hymenopteran egg parasitoids (plus four hyper-parasitoids), six tachinid fly larval parasitoids and one egg-feeding predatory mite. Four of the wasp egg parasitoids were ultimately imported and released in 1986, including three pteromalids (*Enoggera reticulata*, *E. nassaui and Neopolycystus insectifurax)* and the encyrtid *Procheiloneurus* sp. nr. *triguttatipennis*. Only *E. reticulata* successfully established, and within 2 years had spread naturally throughout the range of its host (>1300 km to the east in Port Elizabeth) and achieved up to 96 % parasitism during the oviposition period of *T. tinticollis* (Tribe 2000; Tribe and Cillié 2000). Regarded as a success story in biological control, *T. tinticollis* can still be found in the MCZ, but populations appear to be under strong top-down control. Interestingly, this species has never moved into the summer rainfall zone of South Africa, despite the widespread occurrence of suitable hosts. Rapid colonization throughout the range of *Eucalyptus* in the MCZ would appear to preclude dispersal as a limiting factor in the beetle's distribution, and natural enemies were apparently absent during initial spread. This leads to the hypothesis that the species is limited by climate, though no detailed studies on climate niche or range limitation have been performed to date.

14.3.2.5 Eucalyptus Snout Beetle: *Gonipterus "scutellatus"*

The first major insect pest to arrive and establish in South African forestry plantations was the Eucalyptus snout beetle, originally identified and long referred to as *Gonipterus scutellatus*. Recent morphological work (using internal sclerites of the male aedeagus) as well as a region of the cytochrome oxidase (COI) mitochondrial gene has demonstrated that *Gonipterus scutellatus* in fact comprises a complex of at least eight cryptic species (as well as two additional species outside the complex; Mapondera et al. 2012). The species introduced into South Africa, as well as into Italy and France, currently carries the provisional name "*Gonipterus* n. sp. 2" and is currently being described (R. Oberpreiler, *pers. comm.*). Spain and Portugal, parts of South America (Argentina, Chile, Brazil and Uruguay) and North America (California, Hawaii), as well as Western Australia (outside the native range of the beetles) support large populations of *G. platensis*. A third related species, *G. pulverulentus* (once referred to as *G. gibberus*) has been introduced into southeastern South America and is now found in Argentina, Uruguay and Brazil (Rosado-Neto and Marques 1996; Mapondera et al. 2012).

In 1916, "green, slug-like larvae" of what is now known as *Gonipterus* n. sp. 2 were first discovered feeding on *Eucalyptus* just outside of Cape Town. The weevils multiplied rapidly and quickly became a serious pest of *E. viminalis, E. globulus, E. maideni* and other highly preferred species in the region (Tooke 1953). At the time, these *E. globulus* and *E. viminalis* together comprised 70 % of the *Eucalyptus* plantations in the Cape and were an important source of poles for the mining industry. This led to the search for natural enemies suitable for biological control, and in 1926 the egg parasitoid myrmarid wasp (*Anaphes nitens*) was released. Nearly 50,000 wasps were liberated at 24 sites, including at least 3200 individuals in the Western Cape, all reared from individuals collected from a single source population in Penola, South Australia (Tooke 1953).

By 1930, the establishment success of *A. nitens* was considerable, with parasitism rates reaching upwards of 90–95 % or even higher across the country. Still, *Gonipterus* beetles had profound and lasting effects on forestry both in and out of the MCZ. After what was referred to as a “countrywide defoliation” of *Eucalyptus* (Tribe 2005), several of the most susceptible (and profitable) species, particularly *E. viminalis* and *E. globulus* (the latter also as a result of high susceptibility to *Mycosphaerella* leaf disease – see Pathogens section, this chapter), could no longer be planted in high numbers. In recent years, defoliation rates have increased in several regions of South Africa, which at least in the Highveld, may be due to differences between *Gonipterus* and *Anaphes* in overwintering survival and facultative diapause phenology (Tribe 2005).

14.3.3 Insects Introduced as Biocontrol Agents Against Exotic Woody Escapes

The juxtaposition of forestry and exotic invasion linked to many of the same species of woody plants creates considerable conflict and highly divergent perspectives regarding land management and conservation. These issues are particularly acute in the MCZ of South Africa owing to both the diversity and density of woody invaders and the ideal of conservation of the unique and biodiverse ecosystems present there (McConnachie et al. 2015). Considerable effort has been devoted to managing the spread of *Pinus*, *Eucalyptus* and wattle, in some cases using introduced insects (and pathogens) as agents of biocontrol agents. Insects that feed on flowers and seeds are ideal for this purpose, as long as their effects are limited to plant reproduction. To date, only biocontrol agents for control of invasive wattle have been successfully introduced. Nine insects in total have been introduced, as well as a rust fungus (*Uromycladium tepperianum*, see Table 14.2) (Impson et al. 2011). South Africa is the only country to date to have introduced biological controls against Australian wattles, despite the fact that many species are invasive in numerous countries (Impson et al. 2011; Richardson et al. 2011).

All nine insects released for the biological control of invasive acacias between 1982 and 2008 have established. All five species of weevil are in the genus *Melanterius* (*M. acaciae, M. ventralis, M. servulus, M. compactus* and *M. maculatus*) and attack developing seedpods, with larvae feeding on seeds. In several cases these weevils have been estimated to cause either “considerable” or “extensive” damage to hosts, where little or no seed production is observed (Impson et al. 2011). Two species of gall wasp in the genus *Trichilogaster* (*T. acaciaefoliae* and *T. signiventris*) have been similarly successful, eliminating seed production and inducing galls that act as carbon sinks with the potential to reduce tree growth rate. Finally, two species of cecidomyiid fly in the genus *Dasineura* (*D. dielsi* and *D. rubiformis*) attack single florets forming galls that both preclude pod development due to deformation of the floral ovary and prevent flower abscission (Adair 2004). These midges are multivoltine with up to five generations per year and exhibit an incredible capacity for population growth and spread (Adair 2004, 2005). In all cases, indications of successful control are present at least locally and on some species of wattle. However, given that trees and associated seed banks are long-lived and abundant, the battle against Australian wattle is likely to endure for decades to come.

There has been considerable debate concerning the possible introduction of the cone-infesting *Pissodes validorostris* to control seed production in pine, particularly as a method to curtail invasive spread of the weedy maritime pine (*P. pinaster*). Extensive collections of cones across various species in Europe (including most but not all of the species grown in South Africa) revealed reasonable specificity and clear preference for *P. pinaster* and other Mediterranean pines (Roques et al. 2004). There is, however, evidence that host range expansion and preference changes can occur in this species (Roques et al. 2006), and maturation feeding by adults is more general with respect to pine species (though preference is correlated with larval host; Roques et al. 2004). The specter of a potential association of *P. validorostris* with the Pitch Canker fungus (*Fusarium circinatum*) has led to opposition to the introduction of this insect by the commercial forestry companies (Gebeyehu and Wingfield 2003). Studies under quarantine conditions showed that *P. validorostris* could transmit *F. circinatum* to healthy *Pinus* spp. (Lennox et al. 2009) and the insect has consequently not been released.

14.3.4 Forest Pathogens in the MCZ

In comparison to the rest of South Africa, studies on the diseases of commercial plantation forestry species in the MCZ are limited. This is a reflection of the relative size of the industry in the region (<5 % of landholdings; DAFF 2014) and uncertainty with respect to the future of commercial forestry there (Anonymous 2012). As for insects, the most devastating pathogens of commercial forest trees are introduced. Introduced pathogens represent at least 21 of the 32 (64 %) disease agents or groups of agents listed in Table 14.2. The origin of seven of the remaining microbial pathogens is unknown. Of the four species thought to be native, two (*Armillaria fuscipes and Pseudophaeolus baudonii*) are pathogens of *Eucalyptus*, one (*Camptomerris albizziae*) causes a leaf spot of minor to no importance on *Acacia mearnsii*, and one (*Ceratocystis albifundis*) causes a serious canker disease of *A. mearnsii* (Lückhoff 1955; Gibson 1975; Roux et al. 2012).

The pathogens listed in Table 14.2 include only those considered to have had some economic impact on plantation trees in South Africa – few cause widespread damage in the MCZ. Some (i.e., members of the Botryosphaeriaceae) occur commonly as endophytes and represent latent pathogens, causing disease opportunistically where other stressors are present (Slippers and Wingfield 2007). Still others are obligate associates of insects and usually only weakly or moderately pathogenic (i.e., Ophiostomatoid fungi). Some, however, represent serious threats to plantation forestry in the MCZ. Two important pathogens of pine – *Diplodia sapinea* and *Fusarium circinatum* – dramatically affect plantations of these trees in the region. Additionally, the wattle wilt pathogen, *Ceratocystis albifundus,* occurs on *A. mearnsii* and *A. decurrens*, as well as on commercially cultivated species of the Proteaceae in the region. These three species together with the generalist root pathogen *Phytopthora cinnamomi* are discussed in greater detail below (Fig. 14.4).

The majority of pathology research of plantation species in the MCZ dates back more than 20 years (Laughton 1937; Lückhof 1964; Wingfield and Knox-Davies 1980a, b; Crous et al. 1989, 1991; Zwolinski et al. 1990; Swart and Wingfield 1991). The oldest known diseases from the region are Diplodia die-back and canker (Laughton 1937; Lückhoff 1964), Mycosphaerella leaf blotch (Crous and Wingfield 1996) and *Rhizina undulata* (Lundquist 1986). In addition there were studies on patches of tree mortality in *P. radiata* and *P. pinaster* plantation areas where bark beetles and associated Ophiostomatoid fungi were implicated (Wingfield et al. 1988). In more recent years, the focus of plantation disease studies in the region has been on the pitch canker fungus, *F. circinatum*, with the first outbreak of pitch canker on established trees in South Africa occurring on *P. radiata* near Cape Town (Coutinho et al. 2007, see below).

Of the most important pathogens of plantation-grown *Acacia mearnsii*, *Eucalyptus* and *Pinus* species in South Africa (Roux et al. 2012), few have been reported as economically damaging in the MCZ (Table 14.2). At least twelve pathogens have been reported from plantation trees in the region, including species of Botryosphaeriaceae on *Eucalyptus* and *Pinus* species, *Harknessia*, *Lophodermium*, several Ophiostomatoid fungi and many others (Table 14.2). However, of these only *D. sapinea* and *F. circinatum* cause economically significant damage in the region. This can partly be explained by the commercial tree species planted in the region and partly by environmental conditions. The important eucalypt canker pathogens in the genera *Chrysoporthe* and *Lasiodoplodia*, for example, are known to be most problematic in tropical and sub-tropical regions (Wingfield 2003; Slippers and Wingfield 2007).

Information regarding the origin of pathogens of plantation species in the MCZ and the rest of South Africa is limited. The wilt pathogen, *C. albifundus*, is hypothesized to be native to Africa, while *D. sapinea*, *F. circinatum* and *P. cinnamomi* are introduced pathogens (see below). In the past few years a number of fungal species related to important plantation forestry pathogens have been recorded from native trees in the MCZ. This is of concern due to the increasing number of examples of the broadening of host range by microbial plant pathogens also in South Africa. In the MCZ, a recent study investigating the potential for pathogen sharing between a native, endemic tree in the Myrtaceae, *Metrosideros angustifolia* and non-native *Eucalyptus* species identified three new species in a previously unknown genus in the Cryphonectriaceae on *M. angustifolia* (Chen et al. 2013). The study shows that at least one of these species, *Holocryphia capensis*, is likely to have been introduced

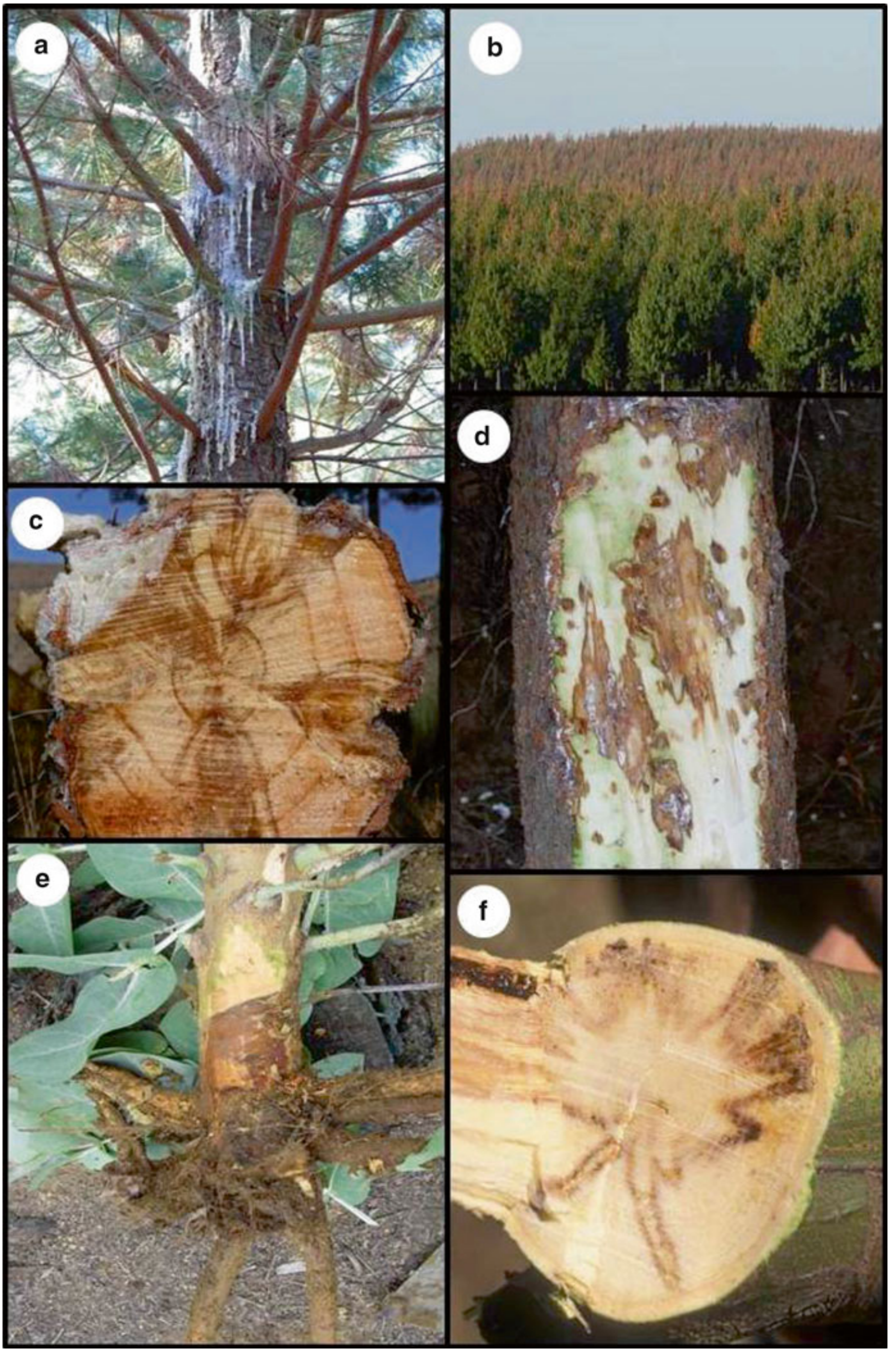


Fig. 14.4 Pathogens and disease symptoms/damage relevant to exotic forestry in the Mediterranean climate zone (MCZ), South Africa. Subfigures are as follows: resin exudation from a *Pinus* sp. infected by the pine pitch canker pathogen, *Fusarium circinatum* (**a**); hail and *Diplodia sapinea* associated death of *P. patula* (**b**); pitch/resin soaked wood of a tree infected by *F. circinatum* (**c**); *Diplodia sapinea* infection of *Pinus* sp. stem associated with hail wounds (**d**); root and collar rot of a *Eucalyptus nitens* tree caused by *Phytopthora cinnamomi* (**e**); wood staining (streaking) of an *A. mearnsii* tree infected by the wilt pathogen, *Ceratocystis albifundus* (**f**)

into the region (Chen et al. 2015 submitted). Similarly, a newly described species in the Cryphonectriaceae, *Knoxdavesia immersiporthe*, has been identified as the cause of a canker disease of native *Rapanea melanophloeos* in the MCZ (Chen et al. 2012).

14.3.5 Case Studies: Pathogens of Relevance to Plantation Forests of the MCZ

14.3.5.1 Wattle Wilt: *Ceratocystis albifundus*

Ceratocystis albifundus has been reported in the MCZ from invasive stands of Australian *Acacia* species, as well as from native Proteaceae where these shrubs are in intensive production systems for the cut-flower industry (Crous et al. 2013). It is, however, considered the most important constraint to the production of *A. mearnsii* in the KwaZulu-Natal Province where it was first described as a pathogen of these trees (Roux and Wingfield 1997).

The wattle wilt pathogen, *Ceratocystis albifundus*, was first described in the 1990s after it was reported as the cause of a wilt and canker disease of jungle and plantation *A. mearnsii* trees in the KwaZulu-Natal Midlands of South Africa (Wingfield et al. 1996). Typical symptoms include a rapid wilt and death of affected trees and staining of the vascular tissue. In some cases, gum-filled blisters can be found in the bark of trees, accompanied by yellowing and cracking of the bark around these blisters (Morris et al. 1993; Roux et al. 1997). Tree death can result within 6 weeks of infection (Roux et al. 1999).

Ceratocystis albifundus has been reported in several countries of Africa, occurring on both native trees (Roux et al. 2007) and exotic Australian wattles (Roux and Wingfield 2013). Natural occurrence of this pathogen on native African hosts in more than eight families (often in the absence of disease), together with high population genetic diversity and structure (Roux et al. 2001a; Barnes et al. 2005), suggests that *C. albifundus* is native to Africa. It has also been reported in association with several insect species in both native and non-native stands of trees (Heath et al. 2009). For example, nitidulid beetles are attracted to sap flow and sometimes breed within mechanical wounds and/or cankers where the adults and larvae encounter a number of pathogens, including *C. albifundus* (Heath et al. 2009). Nitidulid beetles have been shown to carry this fungus on their bodies, though whether or not they are primary vectors between trees is unclear (Heath et al. 2009).

The extensive geographic range of *C. albifundus*, its wide host range (Roux et al. 2007) and its association with generalist insects (Heath et al. 2009) makes *C. albifundus* a potential risk for other continents. It has been recorded from Mediterranean, temperate and subtropical climate zones (Roux et al. 2001b, 2005, 2007; Roux and Wingfield 2009) and has a known host range including more than 10 plant families (Roux et al. 2007). Australia, however, is considered especially vulnerable because of the many Proteaceae and *Acacia* species native to that country.

14.3.5.2 Diplodia or Sphaeropsis Dieback: *Diplodia sapinea*

Diplodia sapinea is one of the best-known pathogens of plantation forestry trees in South Africa (Lundquist 1987), having first been reported from *Pinus* species in the country in the first two decades of the previous century (Laughton 1937; Swart and Wingfield 1991). It is also particularly well known in the MCZ because of the susceptibility of *P. radiata* to infection and the long history of the pathogen in the region (Swart and Wingfield 1991). Infection by this pathogen can result in branch and shoot death, stem cankers and blue stain of the sapwood. Disease symptoms commonly occur in association with hail and pruning wounds (Zwolinski et al. 1990), insect attack (including by the deodar weevil, *P. nemorensis;* Swart and Wingfield 1991; Zwolinksi et al. 1995). At least 30 species of *Pinus* at all ages are affected (Swart et al. 1985; Rees and Webber 1988). The high level of susceptibility of *P. radiata* is the primary reason why this species is not planted in summer rainfall areas where hail damage is common (Laughton 1937; Zwolinski et al. 1990; Swart and Wingfield 1991).

Diplodia sapinea was introduced into South Africa (Burgess et al. 2004), most likely with the importation of seeds and planting stock (Wingfield et al. 2001; Burgess and Wingfield 2002; Bihon et al. 2010). It can be isolated from healthy seed (albeit at very low levels) and can be an endophyte in the absence of symptoms on small plants that have been grown in the presence of inoculum, which facilitates cryptic introduction (Bihon et al. 2012). Given the clear association with tree stress and its wide distribution, *D. sapinea* has the potential to increase in importance where drought stress is predicted as a consequence of climate change (Van Staden et al. 2003).

14.3.5.3 Pine Pitch Canker: *Fusarium circinatum*

The pine pitch canker pathogen, *Fusarium circinatum,* was first detected in a single nursery in the Mpumalanga Province of South Africa in the late 1980s (Viljoen et al. 1994). Since then this pathogen has spread to all pine growing nurseries in the country (Steenkamp et al. 2014). It is also a major constraint to plantation establishment, particularly of *P. patula*, killing young seedlings within the first few months after field planting (Morris 2010; Mitchell et al. 2012). More recently *F. circinatum* has become increasingly important as a pathogen of established *Pinus* species in various regions of the country, causing typical pitch canker disease. It is considered the single most important constraint to plantation forestry using *Pinus* species, particularly *P. patula* and *P. radiata*, in the country (Mitchell et al. 2011).

In its nursery manifestation, *F. circinatum* mostly affects the roots of young seedlings, causing root rot and death of plants. In some cases mortality levels of more than 50 % have been reported from nurseries (Morris 2010; Mitchell et al. 2012). A major problem with *F. circinatum* is that it often occurs asymptomatically in nursery plants, but when transplanted into the field and subjected to stress, it results in plant death. A reduction in *P. patula* survival after planting from ~88 % to 64 % has been reported by some companies (Crous 2005; Morris 2010; Mitchell et al. 2012).

During the mid-2000s typical symptoms of pitch canker disease of established *P. radiata* trees were observed in a plantation in the MCZ, near Cape Town, South Africa (Coutinho et al. 2007). The cause of the disease was identified as *F. circinatum* – this represented the first report of pitch canker disease in the country. Since then, pitch canker disease has been recorded from *P. radiata* and *P. greggii* in the Eastern and Southern Cape Provinces of the country. Field symptoms include the death of single branches (flagging), tree tops and entire trees. Affected plants exude copious amounts of resin, and their xylem is soaked with pitch.

Fusarium circinatum is believed to be native to Central America and the southern USA (Gordon 2012), from where it spread to other regions in the USA and several countries worldwide (Wikler and Gordon 2000; Wingfield et al. 2008; Steenkamp et al. 2014). It has been shown to occur in pine seed, and also in association with cone and twig beetles in the United States (Gordon 2012), as well as with *P. nemorensis* (Coutinho et al. 2007). In South Africa, populations of this pathogen have established from multiple introductions (Steenkamp et al. 2014) and the pathogen has spread widely through the movement of infected plant material. Studies of populations of *F. circinatum* on *P. radiata* trees in the MCZ of South Africa suggest that there are no barriers to the movement of the pathogen in the region (Steenkamp et al. 2014). Most recently, *F. circinatum* was found to occur on grass species in the USA and South Africa, providing possible alternative reservoirs of inoculum that could influence disease outbreaks (Swett et al. 2014).

To date, field outbreaks of the disease are most common in coastal and montane areas of the country, characterized by higher frequencies of mist and thus higher humidity. This is similar to the situation reported from the USA (Wingfield et al. 2008). In contrast to the situation elsewhere, only a single mating type (*mat-1*) of *F. circinatum* has been found in the MCZ in South Africa (Steenkamp et al. 2014). Efforts to restrict the movement of the pathogen should therefore continue in order to reduce the chances of sexual recombination and the generation of novel and perhaps more virulent genotypes.

14.3.5.4 Phytophthora Root Rot: *Phytophthora cinnamomi*

The oomycete root rot pathogen, *Phytopthora cinnamomi*, has been present in South Africa for many years (Olivier 1951; Van der Merwe and Van Wyk 1973). It has been reported to affect numerous tree hosts, including species of plantation *Eucalyptus* and *Corymbia* trees (Linde et al. 1994, 1999). Some isolates have also been obtained from *Pinus radiata, P. pinaster* and *P. patula* in the country, but not associated with serious disease outbreaks on these hosts (Linde et al. 1999). The species has been found to occur in near-pristine, high-altitude mountain streams and on plants in more than five families in native communities in the MCZ (Olivier 1951; Van der Merwe and Van Wyk 1973; Von Broembsen and Kruger 1985). Native plants in the MCZ affected by *P. cinnamomi* include species of Cupressaceae

(*Widdringtonia cedarbergensis*), Ericaceae, Fabaceae, Proteaceae (*Leucadendron* species) and Rosaceae (Olivier 1951; Van der Merwe and Van Wyk 1973; Von Broembsen and Kruger 1985; Linde et al. 1999). It is also a pathogen of ornamental, non-native tree species such as *Quercus cerris* (Oh et al. 2011) and has been reported from Pine nurseries and mature *P. radiata* in the MCZ (Wingfield and Knox-Davies 1980).

Phytophthora cinnamomi is most likely native to Southeast Asia (Zentmeyer 1988) and was introduced to South Africa via trade in living plants (Linde et al. 1999). Population genetic studies ranging from isozyme studies to RFLP and microsatellite studies all suggest Papua New Guinea or surrounding areas as the centre of origin for this pathogen (Hardham 2005). Studies by Dobrowolski et al. (2003) showed high population diversities for isolates from Papua New Guinea and the existence of only three clonal lineages throughout the rest of the world. Populations in South Africa are very similar to those in Australia, where both mating types (A1, A2) of the pathogen have been described (Linde et al. 1997, 1999). The A1 mating type is, however, dominant in the MCZ, while the A2 mating type is broadly distributed (Linde et al. 1997).

Phytophthora cinnamomi causes root rot and basal cankers on affected trees, resulting in stunting and tree death. It is of significant concern to the *Eucalyptus* industry in South Africa, particularly for companies planting cold-tolerant species such as *E. smithii, E. nitens, E. macarthurii* and *E. fraxinoides* (Linde et al. 1999; Nagel et al. 2013). Temperate and sub-tropical species of eucalypts such as *E. grandis* and others seem to have a higher resistance to infection by *P. cinnamomi*; reports of disease on these trees in the MCZ of South Africa is limited. The majority of problems associated with *P. cinnamomi* in the MCZ occur on native Proteaceae and other fynbos vegetation, as well as on non-native ornamental tree species (Oh et al. 2011) and in some cases grapevine (Van der Merwe and Van Wyk 1973; Linde et al. 1999; Nagel et al. 2013). On plantation species in the MCZ, *P. cinnamomi* has been reported only from *P. radiata*, killing mature trees (age 40–50 years) as well as seedlings from forest nurseries in the region (Wingfield and Knox-Davies 1980a). Although the MCZ in South Africa has not yet experienced the same devastation as seen with native vegetation in Australia, the possibility of increased virulence and damage to native and other vegetation in the region should not be ignored. This is especially important in light of the occurrence of both mating types (A1 and A2) of the pathogen in the MCZ, providing opportunity for sexual recombination and thus the generation of new genotypes.

14.4 Conclusions

Ecologists and evolutionary biologists have long been fascinated by the apparent convergence of plant traits together with ecosystem structure and function across Mediterranean climate zones worldwide. A new age of convergence is now upon us, driven by the introduction and cultivation of non-native trees which are largely shared (at least at the generic level) across these zones and constitute similar ecologies. Not surprisingly, one result of this homogenization with respect to woody ecosystems (together with facile movement as a consequence of global trade) is that insects and pathogens are broadly shared across continents and geographically distinct but climatically similar biomes (see discussion of drivers in Garnas et al. 2012).

Despite the apparent similarities between MCZ's around the world, important differences in the composition and behaviour of biotic communities do exist. A considerable proportion of sporadic pests and diseases in the region are native species, typically broad generalist that can feed or infect across orders of plants. Some of these are endemic to the MCZ. The distinct climate of the region has generally not been a determining factor for the establishment and spread of exotic pests and diseases, with some exceptions (i.e., *Trachymela tinticollis*, and the possible influence of climate on nematode biocontrol success of *S. noctilio*). The preponderance of threats and by far the most consistently damaging are exotic plantation pests and pathogens, many of which are common around the world. *Gonipterus* weevils, *Mycosphaerella* spp., and *D. sapinea* have had major effects that have altered the face of plantation forestry in the MCZ. Pests and pathogens such as *S. noctilio* and *F. circinatum* continue to seriously threaten what remains of pine plantation forestry in the region.

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References

Adair RJ (2004) Seed-reducing Cecidomyiidae as potential biological control agents for invasive Australian wattles in South Africa, particularly *Acacia mearnsii* and *Acacia cyclops*. University of Cape Town, Cape Town

Adair RJ (2005) The biology of *Dasineura dielsi* Rübsaamen (Diptera: Cecidomyiidae) in relation to the biological control of *Acacia cyclops* (Mimosaceae) in South Africa. Aust J Entomol 44:446–456

Anonymous (2012) Cape forestry land in limbo. SA Forestry Magazine. http://www.saforestry-mag.co.za/articles/detail/cape_forestry_land_in_limbo/. Accessed 17 Dec 2015

Anonymous (2014) Abstract of South African forestry facts for the year 2011/2012. Published by Forestry South Africa, Sept 2014. www.forestry.co.za

Barnes I, Nakabonge G, Roux J et al (2005) Comparison of populations of the wilt pathogen *Ceratocystis albifundus* in South Africa and Uganda. Mol Plant Pathol 54:189–195

Bennett BM, Kruger FJ (2013) Ecology, forestry and the debate over exotic trees in South Africa. J Hist Geogr 42:100–109

Bihon W, Slippers B, Burgess T et al (2010) Sources of Diplodia pinea endophytic infections in *Pinus patula and P. radiata* seedlings in South Africa. For Pathol. doi:10.1111/j.1439-0329.2010.00691.x

Bihon W, Burgess T, Slippers B et al (2012) High levels of genetic diversity and cryptic recombination is widespread in introduced *Diplodia pinea* populations. Australas Plant Pathol 41:41–46

Blumler MA (2005) Three conflated definitions of Mediterranean climates. Middle States Geogr 38:52–60

Born J, Linder HP, Desmet P (2006) The greater cape floristic region. J Biogeogr 34:147–162

Bredenkamp BV, Upfold S, Ackerman PA et al (2012) South African forestry handbook, 5th edn. Menlo Park, South Africa

Bruzas A (1983) The pine woolly aphid, *Pineus pini* (Macquart) Adelgidae. Pests and diseases of South African forests and timber, vol 273

Burgess TI, Wingfield MJ (2002) Quarantine is important in restricting the spread of exotic seed-borne tree pathogens in the Southern Hemisphere. Int For Rev 4:56–65

Burgess TI, Wingfield MJ, Wingfield BD (2004) Global distribution of *Diplodia pinea* genotypes revealed using simple sequence repeat (SSR) markers. Australas Plant Pathol 33:513–519

Chen SF, Wingfield MJ, Roets F et al (2012) A serious canker disease caused by *Immersiporthe knoxdavesiana* gen. et sp. nov. (Cryphonectriaceae) on native *Rapanea melanophloeos* in South Africa. Plant Pathol 62:667–678. doi:10.1111/j.1365-3059.2012.02671.x

Chen SF, Wingfield MJ, Roux J (2013) *Diversimorbus metrosiderotis* gen. et sp. nov. and three news species of *Holocryphia* (*Cryphonectriaceae*) associated with cankers on native *Metrosideros angustifolia* trees in South Africa. Fungal Biol 117:289–310. doi:10.1016/j.funbio.2013.02.005

Chen SF, Van der Merwe NA, Wingfield MJ et al (2015) Diversity of *Holocryphia capensis* from native *Metrosideros angustifolia* and its pathogenicity on *Eucalyptus* in South Africa. S Afr J Bot (Submitted)

Coutinho TA, Steenkamp TA, Mongwaketsi K et al (2007) First reports of pitch canker in a South African plantation. Australas Plant Pathol 36:256–261

Cowling RM, Ojeda F, Lamont BB et al (2005) Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire prone Mediterranean-climate ecosystems. Glob Ecol Biogeogr 14:509–519

Crous PW, Wingfield MJ (1996) Species of Mycosphaerella and their anamorphs associated with leaf blotch disease of *Eucalyptus* in South Africa. Mycologia 88(3):441–458

Crous JW (2005) Post establishment survival of *Pinus patula* in Mpumalanga, one year after planting. S Afr For J 205:3–8

Crous PW, Knox-Davies PS, Wingfield MJ (1989) A summary of fungal leaf pathogens of *Eucalyptus* and the diseases they cause in South Africa. S Afr For J 149:9–16

Crous PW, Wingfield MJ, Park RF (1991) *Mycosphaerella nubilosa*, a synonym of *M. molleriana*. Mycol Res 95:628–632

Crous PW, Phillips AJL, Baxter AP (2000) Phytopathogenic fungi from South Africa. University of Stellenbosch, Department of Plant Pathology Press/University of Stellenbosch Printers, Stellenbosch

Crous, PW, Denman S, Tayler JE, et al (2013) Cultivation and diseases of Proteaceae: *Leucadendron*, *Leucospermum* and *Protea*. APS, 36pp

DAFF (2014) Report on commercial timber resources and primary roundwood processing in South Africa. Department of Agriculture, Forestry and Fisheries, Republic of South Africa

Dittrich-Schröder G, Wingfield MJ, Hurley BP et al (2012) Diversity in *Eucalyptus* susceptibility to the gall-forming wasp *Leptocybe invasa*. Agric For Entomol 14:419–427

Dobrowolski MP, Tommerup IC, Shearer BL et al (2003) Three clonal lineages of *Phytophthora cinnamomi* in Australia revealed by microsatellites. Phytopathology 93:695–704

Doidge EM, Bottomley AM, Van der Plank JE et al (1953) A revised list of plant diseases in South Africa. Union of South Africa, Department of Agriculture, Science Bulletin No 346, pp 1–122

du Harrison GJ (2014) Review of the South African species of *Pegylis* Erichson, 1847 (Coleoptera: Scarabaeidae: Melolonthinae) commonly known as large wattle chafers. Afr Entomol 22:685–713

Garnas JR, Hurley BP, Slippers B, Wingfield MJ (2012) Biological control of forest plantation pests in an interconnected world requires greater international focus. Int J Pest Manag 58:211–223

Gebeyehu S, Hurley B (2005) A new lepidopteran insect pest discovered on commercially grown *Eucalyptus nitens* in South Africa. S Afr J Sci 101:26–28

Gebeyehu S, Wingfield M (2003) Pine weevil *Pissodes nemorensis*: threat to South African pine plantations and options for control. S Afr J Sci 99:535–536

Geertsema H (1971) Descriptions of the stages of two subspecies of the pine tree emperor moth, *Nudaurelia cytherea* (Fabr.) (Lepidoptera:Saturniidae). Annale Universiteit van Stellenbosch, v. 46 Serie A no. 1, vol Accessed from http://nla.gov.au/nla.cat-vn1972679. Universiteit van Stellenbosch, Stellenbosch

Gibson IAS (1975) Diseases of forest tress widely planted as exotics in the tropics and Southern Hemisphere. Part I. Important members of the Myrtaceae, Leguminosae, Verbenaceae and Meliaceae. Commonwealth Forestry Institute. University of Oxford

Gordon T (2012) Biology and management of *Gibberella circinata,* the cause of pitch canker of pines. In: Alves-Santos FM, Diez J (eds) Control of Fusarium diseases. Research Signpost, Trivandrum, pp 195–208

Hajek AE, Nielsen C, Kepler RM et al (2013) Fidelity among sirex woodwasps and their fungal symbionts. Microb Ecol 65:753–762

Hardham AR (2005) Pathogen profile. *Phytophthora cinnamomi*. Mol Plant Pathol 6:589–604

Heath RN, Wingfield MJ, van Wyk M et al (2009) Insect associates of *Ceratocystis albifundus* and patterns of association in a native savanna ecosystem in South Africa. Environ Entomol 38:356–364

Hepburn GA (1966) *Lobobunaea epithyrena* M. & W. (Order Lepidoptera, Family Saturniidae): a potential pest of plantations. For S Afr 6:1–17

Hepburn GA, Leodolff J (1964) A new forest pest in South Africa (*Neocleora herbuloti* Fletcher, Order Lepididoptera family Geometridae. For S Afr 4:1–18

Hrabar H, Hattas D, du Toit JT (2009) Intraspecific host preferences of mopane moths (*Imbrasia belina*) in mopane (*Colophospermum mopane*) woodland. Afr Zool 44:131–140

Hurley BP, Slippers B (2007) A comparison of control results for the alien invasive woodwasp, Sirex noctilio, in the southern hemisphere. Agric For Entomol 9:159–171

Hurley BP, Slippers B, Croft PK et al (2008) Factors influencing parasitism of *Sirex noctilio* (Hymenoptera: Siricidae) by the nematode *Deladenus siricidicola* (Nematoda: Neotylenchidae) in summer rainfall areas of South Africa. Biol Contr 45:450–459

Hurley BP, Croft P, Verleur M et al (2011) The control of the Sirex woodwasp in diverse environments: the South African experience. In: Slippers B, de Groot P, Wingfield MJ (eds) The sirex woodwasp and its fungal symbiont: research and management of a worldwide invasive pest. Springer, Dordrecht, pp 247–264

Hurley BP, Hatting HJ, Wingfield MJ, Klepzig KD, Slippers B (2012) The influence of Amylostereum areolatum diversity and competitive interactions on the fitness of the Sirex parasitic nematode Deladenus siricidicola. Biol Control 61:207–214

Impson FAC, Kleinjan C, Hoffmann J et al (2011) Biological control of Australian *Acacia* species and *Paraserianthes lophantha* (Willd) Nielsen (Mimosaceae) in South Africa. Afr Entomol 19:186–207

Impson FAC, Post JA, Hoffmann JH (2013) Impact of the flower-galling midge, *Dasineura rubiformis* Kolesik, on the growth of its host plant, *Acacia mearnsii* De Wild, in South Africa. S Afr J Bot 87:118–121

Kruger FJ (2014) Patterns of vegetation and climate in the Mediterranean zone of South Africa. Bull Soc Bot Fr, Actualités Botaniques 131:213–224

Lantschner MV, Villacide JM, Garnas JR et al (2014) Temperature explains variable spread rates of the invasive woodwasp *Sirex noctilio* in the Southern Hemisphere. Biol Invasions 16:329–339

Laughton EM (1937) The incidence of fungal disease on timber trees in South Africa. S Afr J Sci 33:377–382

Le Maitre D, Versfeld D, Chapman R (2000) The impact of invading alien plants on surface water resources in South Africa: a preliminary assessment. Water SA 26:397–408

Lennox CL, Hoffmann JH, Coutinho TA et al (2009) A threat of exacerbating the spread of pitch canker precludes further consideration of a cone weevil, *Pissodes validirostris*, for biological control of invasive pines in South Africa. Biol Contr 50:179–184

Linde C, Kemp GHJ, Wingfield MJ (1994) *Pythium* and *Phytophthora* species associated with eucalypts and pines in South Africa. Eur J For Pathol 24:345–356

Linde C, Drenth A, Kemp GHJ (1997) Population structure of Phyphthora cinnamomi in South Africa. Phytopathology 87:822–827

Linde C, Drenth A, Wingfield MJ (1999) Gene and genotypic diversity of *Phytophthora cinnamomi* in South Africa and Australia revealed through DNA polymorphisms. Eur J Plant Pathol 105:667–680

Lückhoff HA (1955) Two hitherto unrecorded fungal diseases attacking pines and eucalypts in South Africa. J S Afr For Assoc 26:147–161

Lückhoff H (1964) Diseases of exotic plantation trees in the Republic of South Africa. FAO/IUFRO Symposium on Internationally Dangerous Forest Diseases and Insects, Oxford

Lundquist JE (1986) Fungi associated with *Pinus* in South Africa. Part I. The Transvaal. S Afr For J 138:1–14

Lundquist JE (1987) A history of five forest diseases in South Africa. S Afr For J 140:51–59

Madden JL (1974) Oviposition behaviour of the woodwasp, *Sirex noctilio* F. Aust J Zool 22:341–351

Mandelshtam M, Danielsson R (2004) Some African Scolytidae (Coleoptera) collected by Swedish Entomological Expeditions. Ann Transvaal Mus:1–3

Mapondera TS, Burgess T, Matsuki M et al (2012) Identification and molecular phylogenetics of the cryptic species of the *Gonipterus scutellatus* complex (Coleoptera: Curculionidae: Gonipterini). Aust J Entomol 51:175–188

McConnachie MM, van Wilgen BW, Richardson DM et al (2015) Estimating the effect of plantations on pine invasions in protected areas: a case study from South Africa. J Appl Ecol 52:110–118

Mendel Z, Protasov A, Fisher N et al (2004) Taxonomy and biology of *Leptocybe invasa* gen. & sp n (Hymenoptera: Eulophidae), an invasive gall inducer on *Eucalyptus*. Aust J Entomol 43:101–113

Midgley JJ, Cowling RM, Seydack AHW et al (1997) Forest. In: Cowling M, Richardson DM, Pierce SM (eds) Vegetation of Southern Africa. Cambridge University Press, Cambridge, pp 278–299

Mitchell RG, Steenkamp ET, Coutinho TA et al (2011) The pitch canker fungus, *Fusarium circinatum:* implications for South African forestry. South For 73:1–13

Mitchell RG, Coutinho TA, Steenkamp E et al (2012) Future outlook for *Pinus patula* in South Africa in the presence of the pitch canker fungus (*Fusarium circinatum*). South For 74:203–210

Moran V, Hoffmann J, Donnelly D et al (1999) Biological control of alien, invasive pine trees (*Pinus* species) in South Africa. In: Proceedings of the X international symposium on biological control of weeds, pp 4–10

Morris A (2010) A review of pitch canker fungus (*Fusarium circinatum*) as it relates to plantation forestry in South Africa. Sappi Shaw Research Centre, Howick

Morris MJ, Wingfield MJ, De Beer C (1993) Gummosis and wilt of *Acacia mearnsii* in South Africa caused by *Ceratocystis fimbriata*. Plant Pathol 42:814–817

Mucina L, Rutherford MC (2006) The vegetation of South Africa, Lesotho and Swaziland, Strelitzia, vol 19. South African National Biodiversity Institute (SANBI), Pretoria

Nadel RL, Wingfield M, Scholes MC et al (2015) Population dynamics of *Thaumastocoris peregrinus* in *Eucalyptus* plantations of South Africa. J Pest Sci 88:97–106

Nagel JH, Gryzenhout M, Slippers B et al (2013) The occurrence and impact of *Phytophthora* on the African continent. In: Lamour K (ed) *Phytophthora*: a global perspective. CAB International, Boston, pp 204–214

Nugnes F, Gebiola M, Monti MM, Gualtieri L, Giorgini M, Wang J, Bernardo U (2015) Genetic diversity of the invasive gall wasp Leptocybe invasa (Hymenoptera: Eulophidae) and of its Rickettsia endosymbiont, and associated sex-ratio differences. PLoS ONE 10:e0124660

Nyeko P, Mutitu KE, Otieno BO et al (2010) Variations in *Leptocybe invasa* (Hymenoptera: Eulophidae) population intensity and infestation on eucalyptus germplasms in Uganda and Kenya. Int J Pest Manag 56:137–144

Oberprieler R (1986) *Pinus radiata* D. Don: a new foodplant for *Imbrasia (Gonimbrasia) belina* (Westwood) (Lepidoptera: Saturniidae). J Entomol Soc South Afr 49:168–170

Oh E, Wingfield BD, Wingfield MJ et al (2011) First report of *Phytophthora cinnamomi* associated with stem cankers of *Quercus cerris* in South Africa. New Dis Rep 24:11–10

Olivier D (1951) Progress in the study of the silvertree disease. J Bot Soc S Afr 37:18–19

Olivier W (2009) There is honey in the forest: the history of South African forestry, 1st edn. South African Institute of Mining Forestry, Pretoria

Prinsloo GL (2005) Description of *Pycnetron pix* sp. n. (Hymenoptera: Pteromalidae), an indigenous parasitoid of the exotic pine weevil *Pissodes nemorensis* (Curculionidae) in South Africa, and comments on the identity of *Pycnetron longicauda* (Risbec). Afr Entomol 13:341–346

Prinsloo G, Uys V (2014) Insects of cultivated plants and natural pastures in southern Africa. Entomol Soc South Afr, Pretoria

Rees AA, Webber JF (1988) Pathogenicity of *Sphaeropsis sapinea* to seed, seedlings and saplings of some Central American pines. Trans Br Mycol Soc 91:273–277

Richardson DM (ed) (2000) Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge

Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species – a global review. Divers Distrib 17:788–809

Richardson DM, Carruthers J, Hui C et al (2011) Human-mediated introductions of Australian acacias – a global experiment in biogeography. Divers Distrib 17:771–787

Roques A, Roux-Morabito G, Hoffmann JH et al (2004) Determining the suitability of a European cone weevil, *Pissodes validirostris*, for biological control of invasive pines in South Africa. In: XI international symposium on biological control of weeds, p 315

Roques A, Auger-Rozenberg M-A, Boivin S (2006) A lack of native congeners may limit colonization of introduced conifers by indigenous insects in Europe. Can J For Res 36:299–313

Rosado-Neto G, Marques L (1996) Characteristics of adult, genitalia and immature forms of *Gonipterus gibberus* Boisduval and *G. scutellatus* Gyllenhal (Coleoptera, Curcuilionidae). Revista Bras Zool 13:77–90

Rouget M, Richardson D, Nel J (2002) Commercially important trees as invasive aliens–towards spatially explicit risk assessment at a national scale. Biol Invasions 4:397–412

Rouget M, Richardson DM, Cowling RM et al (2003) Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. Biol Conserv 112:63–85

Roux J, Wingfield MJ (1997) Survey and virulence of fungi occurring on diseased *Acacia mearnsii* in South Africa. For Ecol Manage 99:327–336

Roux J, Wingfield MJ (2009) *Ceratocystis* species: emerging pathogens of non-native plantation *Eucalyptus* and *Acacia* species. South For 71:115–120

Roux J, Wingfield M (2013) *Ceratocystis* species in Africa. In: Seifert K, Wingfield M (eds) The ophiostomatoid fungi: expanding frontiers, vol 12, CBS biodiversity series. CBS, Utrecht

Roux J, Dunlop R, Wingfield MJ (1999) Susceptibility of elite *Acacia mearnsii* families to Ceratocystis wilt in South Africa. J For Res 4:187–190

Roux J, Harrington TA, Steimel JP et al (2001a) Genetic variation in the wattle wilt pathogen *Ceratocystis albofundus*. Mycoscience 42:327–332

Roux J, Wingfield MJ, Byabashaija DM (2001b) First report of Ceratocystis wilt of *Acacia mearnsii* in Uganda. Plant Dis 85:1029 (D-2001-0622-01 N)

Roux J, Meke G, Kanyi B et al (2005) Diseases of plantation forestry trees species in Eastern and Southern Africa. S Afr J Sci 101:409–413

Roux J, Heath RN, Labuschagne L et al (2007) Occurrence of the wattle wilt pathogen, *Ceratocystis albifundus* on native South African trees. For Pathol 37:292–302

Roux J, Hurley BP, Wingfield MJ (2012) Diseases and pests of eucalypts, pines and wattle. In: Forestry handbook, 5th edn. Southern African Institute of Forestry (SAIF), Pretoria, pp 303–336, ISBN978-0-620-52932-7

Rundel PW (1998) Landscape disturbance in mediterranean-type ecosystems: an overview. In: Rundel P, Montenegro G, Jaksic F (eds) Landscape disturbance and biodiversity in mediterranean-type ecosystems, vol 136, Ecological studies. Springer, Berlin, pp 3–22

Santana DLDQ, Burckhardt D (2007) Introduced Eucalyptus psyllids in Brazil. J For Res 12:337–344

Schulze RE (2007) The South African atlas of agrohydrology and climatology. Water Research Commission, Pretoria

Slippers B, Wingfield MJ (2007) Botryosphaeriaceae as endophytes and latent pathogens of woody plants: diversity, ecology and impact. Fungal Biol Rev 21:90–106

Slippers B, Smit WA, Crous PW et al (2007) Taxonomy, phylogeny and identification of Botryosphaeriaceae associated with pome and stone fruit trees in South Africa and other regions of the world. Plant Pathol 56:128–139

Slippers B, Burgess T, Pavlic D et al (2009) A diverse assemblage of Botryosphaeriaceae infect *Eucalyptus* in native and non-native environments. South For 71:101–110

Slippers B, de Groot P, Wingfield MJ (2012a) The sirex woodwasp and its fungal symbiont: research and management of a worldwide invasive pest. Springer, Dordrecht

Slippers B, Hurley BP, Mlonyeni XO et al (2012b) Factors affecting the efficacy of *Deladenus siricidicola* in biological control systems. In: Slippers B, de Groot P, Wingfield MJ (eds) Sirex woodwasp and its fungal symbiont: research and management of a worldwide invasive pest. Springer, Dordrecht, pp 119–133

Slippers B, Hurley BP, Wingfield MJ (2014) Sirex woodwasp: a model for evolving management paradigms of invasive forest pests. Annu Rev Entomol 60:601–619

Steenkamp ET, Makhari OM, Coutinho TA et al (2014) Evidence for a new introduction of the pitch canker fungus *Fusarium circinatum* in South Africa. Plant Pathol 63:530–538

Swart WJ, Wingfield MJ (1991) Biology and control of *Sphaeropsis sapinea* on *Pinus* species in South Africa. Plant Dis 75:761–766

Swart WJ, Knox-Davies PS, Wingfield MJ (1985) *Sphaeropsis sapinea*, with special reference to its occurrence in *Pinus* spp. in South Africa. South Afr For J 35:1–8

Swett CL, Porter B, Fourie G et al (2014) Association of the pitch canker pathogen *Fusarium circinatum* with grass hosts in commercial pine production areas of South Africa. South For 76:161–166. doi:10.2989/20702620.2014.916087

Tooke F (1938) Investigations on the biology of *Euproctis terminalis* walk, the pine brown tail moth, and its control by aeroplane and ground dusting. Union S Afr, Dep Agric For Sci Bull 179:1–46

Tooke FGC (1953) The eucalyptus snout beetle *Gonipterus scutellatus* Gyll: a study of its ecology and control by biological means. Entomological Memoirs of the Department of Agriculture, Union South Africa, vol. 3. Government Printer, Pretoria, South Africa

Tooke FGC, Hubbard CS (1941) The pine tree emperor moth *Nudaurelia cytherea capensis* Stoll. A survey and examination of the measures employed in its control. Dept Agr S Afr (Pretoria) Sc Bull 210:1-571-59

Tribe GD (1990a) Phenology of *Pinus radiata* log colonization and reproduction by the European bark beetle *Orthotomicus erosus* (Wollaston) (Coleoptera: Scolytidae) in the southwestern cape province. J Entomol Soc South Afr 53:117–126

Tribe GD (1990b) Phenology of *Pinus radiata* log colonization by the pine bark beetle *Hylastes angustatus* (Herbst) (Coleoptera: Scolytidae) in the southwestern cape province. J Entomol Soc South Afr 53:93–100

Tribe GD (1991a) *Drosophila flavohirta* Malloch (Diptera: Drosophilidae) in *Eucalyptus* flowers: occurrence and parasites in eastern Australia and potential for biological control on *Eucalyptus grandis* in South Africa. Aust J Entomol 30:257–262

Tribe GD (1991b) Phenology of *Oosomus varius* (Curculionidae) and *Prasoidea sericea* (Chrysomelidae) on *Pinus radiata* in the southwestern Cape Province. South Afr For J 157:47–51

Tribe GD (1991c) Phenology of *Pinus radiata* log colonization by the red-haired pine bark beetle *Hylurgus ligniperda* (Fabricius) (Coleoptera: Scolytidae) in the southwestern Cape Province. J Entomol Soc South Afr 54:1–7

Tribe GD (1995) The woodwasp *Sirex noctilio* Fabricius (Hymenoptera: Siricidae), a pest of *Pinus* species, now established in South Africa. Afr Entomol 3:215–217

Tribe GD (2000) Ecology, distribution and natural enemies of the *Eucalyptus*-defoliating tortoise beetle *Trachymela tincticollis* (Blackburn) (Chrysomelidae : Chrysomelini : Paropsina) in southwestern Australia, with reference to its biological control in South Africa. Afr Entomol 8:23–45

Tribe GD (2005) The present status of *Anaphes nitens* (Hymenoptera: Mymaridae), an egg parasitoid of the Eucalyptus snout beetle *Gonipterus scutellatus*, in the Western Cape Province of South Africa. South Afr For J 203:49–54

Tribe GD, Cillié JJ (1997) Biology of the Australian tortoise beetle *Trachymela tincticollis* (Blackburn) (Chrysomelidae: Chrysomelini: Paropsina), a defoliator of *Eucalyptus* (Myrtaceae), in South Africa. Afr Entomol 5:109–123

Tribe GD, Cillié JJ (2000) Biological control of the Eucalyptus-defoliating Australian tortoise beetle *Trachymela tincticollis* (Blackburn)(Chrysomelidae: Chrysomelini: Paropsina) in South Africa by the egg parasitoid *Enoggera reticulata* Naumann (Hymenoptera: Pteromalidae: Asaphinae). Afr Entomol 8:15–22

Tribe GD, Cillié JJ (2004) The spread of Sirex noctilio Fabricius (Hymenoptera: Siricidae) in South African pine plantations and the introduction and establishment of its biological control agents. Afr Entomol 12:9–17

Tripconey D (1969) Studies on a nonoccluded virus of the pine tree emperor moth. J Invertbr Pathol 15:268–275

Van den Berg EC, Kotze I, Beukes H (2013) Detection, quantification and monitoring of *Prosopis* in the Northern cape orovince of South Africa using remote sensing and GIS. S Afr J Geomatics 2:68–81

Van der Merwe JJH, Van Wyk PS (1973) Host of *Phytophthora cinnamomi* in the Western cape province of South Africa. Plant Dis Rep 57:1005–1006

Van Niekerk JM, Crous PW, Groenewald JZE et al (2004) DNA phylogeny, morphology and pathogenicity of *Botryosphaeria* species on grapevines. Mycologia 96:781–798

Van Staden V, Erasmus BFN, Roux J et al (2003) Modelling the spatial distribution of two important South African plantation forestry pathogens. For Ecol Manage 187:61–73

van Webb DV (1974) Forest and timber entomology in the Republic of South Africa, vol 34, Department of agricultural technical services – Entomology memoirs. The Government Printer, Pretoria

Viljoen A, Wingfield MJ, Marasas WFO (1994) First report of *Fusarium subglutinans f.sp. pini* on pine seedlings in South Africa. Plant Dis 78:309–312

von Broembsen SL, Kruger FJ (1985) *Phytophthora cinnamomi* associated mortality of native vegetation in South Africa. Plant Dis 69:715–717

Walter CT, Tomasicchio M, Hodgson V et al (2008) Characterization of a succession of small insect viruses in a wild South African population of *Nudaurelia cytherea capensis* (Lepidoptera: Saturniidae). S Afr J Sci 104:147–152

Wikler K, Gordon TR (2000) An initial assessment of genetic relationships among populations of *Fusarium circinatum* in different parts of the world. Can J Bot 78:709–717

Wingfield MJ (2003) Increasing threat of diseases to exotic plantation forest in the Southern Hemisphere: lessons from Cryphonectria canker. Australas Plant Pathol 32:133–139

Wingfield MJ, Knox-Davies PS (1980a) Observations on diseases in pine and Eucalyptus plantations in South Afr. Phytophylactica 12:57–73

Wingfield MJ, Knox-Davies PS (1980b) Root disease, associated with *Verticicladiella alacris*, of pines in South Africa. Plant Dis 64:569–571

Wingfield MJ, van Wyk PS, Marasas WFO (1988) *Ceratocystiopsis proteae* sp.nov., with a new anamorph genus. Mycologia 80:23–30

Wingfield MJ, De Beer C, Visser C et al (1996) A new *Ceratocystis* species defined using morphological and ribosomal DNA sequence comparisons. Syst Appl Microbiol 19:191–202

Wingfield MJ, Slippers B, Roux J et al (2001) Worldwide movement of exotic forest fungi, especially in the tropics and the southern Hemisphere. Bioscience 15:134–140

Wingfield MJ, Hammerbacher A, Gangley RJ et al (2008) Pitch canker caused by *Fusarium circinatum* – a growing threat to pine plantations and forests worldwide. Australas Plant Pathol 37:319–334

Wingfield MJ, Roux J, Slippers B et al (2013) Established and new technologies reduce increasing pest and pathogen threats to Eucalypt plantations. For Ecol Manage 301:35–42

Wooding AL, Wingfield MJ, Hurley BP et al (2013) Lack of fidelity revealed in an insect-fungal mutualism after invasion. Biol Lett 9:1–4

Zentmeyer GA (1988) Origin and distribution of four species of *Phytophthora*. Trans Br Mycol Soc 91:367–378

Zwolinski JB, Swart WJ, Wingfield MJ (1990) Economic impact of post-hail outbreak of dieback induced by *Sphaeropsis sapinea*. Eur J For Pathol 20:405–411

Zwolinski JB, Swart WJ, Wingfield MJ (1995) Association of *Sphaeropsis sapinea* with insect infestation following hail damage of *Pinus radiata*. For Ecol Manage 72:293–298

Chapter 15
Native Defoliators of Australian Mediterranean Forest Trees

Martin J. Steinbauer and Helen F. Nahrung

Abstract Eucalypts (*Eucalyptus*, *Corymbia* and *Angophora*), as native stands and as plantations, dominate the two Mediterranean forest regions of Australia. These two geographically separated regions – south-western Australia, and areas of South Australia, including the Green Triangle region around the southern South Australian/Victorian border – have likewise largely separate native insect species, in spite of a common, albeit non-endemic, resource (*E. globulus* plantations). Almost half a million hectares of *E. globulus* and around 300,000 ha of softwoods is planted in Mediterranean Australia. Native defoliators have been largely unproblematic in pine plantations, but many have achieved significant pest status in hardwood plantations. Defoliators in native forest are less well-known, but there are several examples of species that have been studied in detail. Eucalypts typically receive (and tolerate) relatively high levels of defoliation, and have a diverse array of phytophagous insect fauna from several Orders (Lepidoptera, Coleoptera, Hemiptera, Hymenoptera and Orthoptera) feeding on their foliage, despite it being sclerophyllous and high in plant secondary compounds. Here, we provide an overview of the endemic folivores of Mediterranean forests in Australia.

15.1 Introduction

In the south-eastern parts of South Australia and in south-western Victoria, regions defined earlier in this volume as having Mediterranean-like climate, no economically important timber species of *Eucalyptus* or *Corymbia* (Myrtaceae) occur naturally, largely as a consequence of the shallow, nutrient-poor soils, low rainfall and frequent bushfires. The vegetation in this region is called mallee as a consequence of the growth-form of the species of eucalypt that dominate it. Mallee covers

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250,420 km^2 or approximately 3.3 % of the landmass between 25° and 36° (Parsons 1994; Steinbauer et al. 2015a). Mallee eucalypts are defined as multi-stemmed trees generally attaining heights of <5–10 m and arising from an underground lignotuber (Specht 1981). The aerial portions of mallee eucalypts arise from subterranean lignotubers and are as old as the last canopy-destroying bushfire (Clarke et al. 2010). The lignotubers themselves are likely to be significantly older than the canopies of individual trees since they persist between bushfires. Previously, mallee eucalypts have been economically important as firewood and for oil production but more recently some species have become important for carbon sequestration (Harris and Young 1989; Markham and Noble 1989; Boland et al. 1991; Goodger and Woodrow 2012). Species of *Callitris* (Cupressaceae) span the Mediterranean-climatic regions in eastern and western parts of the country and the genus supports a boutique timber industry (Ogden 1978). However, cypress-pines are only listed as hosts of some potential insect defoliators, e.g. a species of sawfly and a species of bagworm (Moore 1962; Common 1990). Otherwise, only a number of species of galling midge have been reported utilising *Callitris* (Kolesik 2000).

There is a marked contrast between the mallee vegetation and woodland forests found in the eastern Mediterranean-like climate region and the tall-open forests of the south-western corner of Western Australia. These forests are characterized as having a foliage projective cover of 30–70 % and comprise trees at least 30 m tall (Wardell-Johnson et al. 1997). The change in the composition of monocalypt eucalypts between these areas is evidence of east-west continental vicariance (Ladiges et al. 2010; Heads 2014). Three species of eucalypt which occur naturally in this region are economically important timber species; the species are *Eucalyptus marginata* (jarrah), *E. diversicolor* (karri), *Eucalyptus* (*Corymbia*) *calophylla* (marri) and, to a lesser extent, *E. wandoo* (wandoo). *Eucalyptus gomphocephala* (tuart), once harvested for timber, has declined dramatically, with altered fire regimes, soil microbes and pathogens implicated in its decline (Archibald et al. 2005; Taylor et al. 2009; Cai et al. 2010). The extent of the economically important jarrah/karri forest is 1.65 M ha which has been commercially exploited for 100–120 years (Abbott 1990). Jarrah/marri forest transitions to wandoo woodland with decreasing rainfall. In the mallee, the few studies of native insects that have been conducted document biodiversity rather than provide detailed biological or ecological information about individual species (Yen 1989; Gullan et al. 1997). Similar biodiversity studies of the insects found on the eucalypts in the south-western corner of Western Australia have also been conducted (Abbott et al. 1992, 2000; Majer et al. 2000).

Since most of the eucalypts that occur in the region which is the focus of this chapter have not been economically important species, there are only a few native insect defoliators about which much is known. We present syntheses of the published research concerning these species, as well as those that are associated with *E. globulus* plantations. Almost half a million hectares of *E. globulus* and around 300,000 ha of softwoods is planted in Mediterranean Australia (Gavran 2014). Native defoliators have been largely unproblematic in pine plantations, but many have achieved significant pest status in hardwood plantations. Eucalypts typically receive (and tolerate) relatively high levels of defoliation, and have a diverse array of phytophagous insect fauna from several Orders (Lepidoptera, Coleoptera, Hemiptera, Hymenoptera and Orthoptera) feeding on their foliage, despite it being sclerophyllous and high in plant secondary compounds. Here, we provide a systematic overview of the major endemic folivores in Mediterranean forests of Australia.

15.2 Lepidoptera

Although many species of Lepidoptera feed on eucalypts, most are associated with dead, rather than live leaves, and eucalypts are considered somewhat depauperate in diversity of lepidopteran defoliators, with several moth families and almost all butterflies absent from eucalypts (Common 1981). Despite the Mediterranean region of south-western Australia being recognised as a global floristic hotspot (Myers et al. 2000), it is not correspondingly enriched with Lepidoptera (Austin et al. 2004), although Cunningham et al. (2005) collected 295 species from 26 families in remnant and plantation habitat. However, only two Lepidoptera were listed in Mediterranean regions in Strauss (2001) and only 13 species are associated with *E. globulus* plantations in Western Australia and the Green Triangle, compared with >100 Coleoptera (Matsuki and Tovar 2012). Of these, only three are "moderate" pests, with the remainder not considered important in plantations; two of these are also important defoliators in native forest habitat in Mediterranean regions.

15.2.1 Jarrah Leafminer **Perthida glyphopa** *Common (Lepidoptera: Incurvariidae)*

One of the better studied of the lepidopteran defoliators of eucalypts of the tall-open forests of the south-western corner of Western Australia is the univoltine jarrah leafminer. An as yet undescribed species of *Perthida* defoliates flooded gum (*Eucalyptus rudis*) in the same region and *P. glyphopa* may also, in addition to *E. marginata*, mine leaves of *E. todtiana* (Mahon et al. 1982). The larvae of these small moths (wingspan: 6 mm) leave a characteristic hole surrounded by necrotic tissues in host leaves when they release the cell they create from binding together opposing sections of epidermis; the larvae take this cell into the soil with them and aestivate in it (Wallace 1970; Mazanec 1983). Based on a frequency distribution of head capsules, Wallace (1970) suggested there were four larval instars. Female *P. glyphopa* are solitary whereas males form aggregations on branches and twigs; males encounter females searching for oviposition sites in the axils of leaves (Mazanec and Justin 1986). Oviposition, most often on the abaxial surface, is influenced by leaf age with females laying significantly more eggs into leaves less than 6 months old than into older leaves; females were suggested to assess leaf age by tarsal contact (Wallace 1970; Mazanec and Justin 1986). Leaves in the lower portion of canopies are more likely to receive eggs as a consequence of the behaviour of females to retreat to the forest floor at night and when daytime conditions are unsuitable for oviposition; these leaves are more likely to be encountered by females returning to hosts to oviposit [Mazanec and Justin 1986 (contrast with findings of Abbott et al. (1994) who reported similar oviposition rates among crown and coppice leaves)]. Females achieve higher realised fecundities when hosts supported greater densities of young leaves, which was dependent upon rainfall the previous winter (Mazanec and Justin 1994).

Leaves damaged by larvae are abscised according to the extent of damage they experience. Heavily mined leaves are abscised within 1–2 months of larval cells dropping from leaves and less damaged leaves abscised at the start of summer when rainfall is lowest (Mazanec and Justin 1994). Defoliation by *P. glyphopa* rarely kills trees but can significantly reduce stem diameter and consequently wood production, especially of susceptible trees (Mazanec 1989, 1999). Natural resistance of *E. marginata* is a factor determining the severity of defoliation jarrah trees exhibit. Trees may either be resistant to larval feeding, egg development or both (Mazanec 1985). Resistance to eggs and larvae involve foliar hypersensitive responses whereby eggs are pushed from their point of insertion or tissues surrounding feeding larvae become necrotic causing larvae to starve (Mazanec 1985). Larval survival and performance, as determined by foliar nutritional quality, has yet to be quantified but was suggested to be an important agent of mortality explaining lower survival of larvae in coppice leaves compared to in crown leaves (Abbott et al. 1994). Interestingly, crown leaves were higher in N but lower in phenolics than coppice leaves. Abbott et al. (1994) implicated low N content of young leaves with resistance to larvae, not higher concentrations of phenolics.

Defoliation of jarrah by *P. glyphopa* was first reported from coastal south-west Western Australia in the early 1900s (Newman and Clark 1925, 1926). Subsequently, defoliation was reported at locations inland from the coast from 1917 onwards; the first outbreak occurred around 1957 (Abbott et al. 1999a). By 1978, approximately 1.45 million hectares of jarrah forest exhibited moderate to heavy damage (Beckman 1986). Outbreak densities were reached in 1980 and were estimated to affect >500,000 ha; the area of the outbreak decreased to 196,000 ha by 1992 (Abbott et al. 1995). Outbreak densities still occur in the region but appear in long term decline, possibly due to declining rainfall (Allan Wills, December 2014, personal communication). Mazanec and Justin (1994) suggested that forest management practices that increase the availability of young foliage for ovipositing females (e.g. fuel reduction prescribed burning and thinning/clearing) could initiate outbreaks. This hypothesis has been rejected by the work of Abbott et al. (1995, 1999b). The most important agents of mortality of larvae while they are still developing in host leaves are hymenopteran parasitoids and birds (Mazanec 1987). Later, after leaving the host, pre-aestivating and aestivating larvae are preyed upon by a range of epigaeic insects (ants, earwigs and carabid beetles) and there may be some (10 %) mortality of only partially buried larvae by radiant heat (Mazanec 1987). Inconsistent patterns of egg and larval mortality (from density dependent to inverse density dependent) suggest that more research is needed to understand the biology and ecology of the various natural enemies (Mazanec 1996). Another south-western leaf-mining lepidopteran, the tuart miner, *Nepticula* sp. (Nepticulidae) feeds on the leaves of *E. gomphocephala* in its native range (Ruthrof et al. 2002).

15.2.2 Gumleaf Skeletoniser **Uraba lugens** *Walker (Lepidoptera: Nolidae)*

The other important defoliator of jarrah forests, and one of the most studied right across Australia, is the gumleaf skeletonizer. The larvae of this species are readily recognised by their hairy bodies (with the longer setae arising from yellowish swellings) and the retention of multiple moulted headcapsules on the top of the head (the latter characteristic is exhibited after about the fifth larval instar). The other characteristic feature, acknowledged in the species' common name, is the skeletonisation of leaves by the gregarious larvae which is caused when earlier instars (i.e. up to about the fifth instar) eat the tissues of the lamina leaving veins and oil glands; later instars eat leaves from the margins and ingest all tissues. This ontogenetically-linked change in feeding habit is exhibited by a number of lepidopteran herbivores (including specialists of young and old leaves) of eucalypts (see Steinbauer and Matsuki 2004). Two forms of the species were recognised initially by Campbell (1962, 1969): the 'highland/montane form' the eggs of which are laid in unordered clutches of up to 200 eggs and which has 13 larval instars and the 'coastal/inland river valley form' the eggs of which are laid in parallel rows of up to 100 eggs, with rows separated by the diameter of a single egg, and which has 11 larval instars. While both forms occur on mainland Australia, only the highland/montane form occurs in the island state of Tasmania. A recent comprehensive review of the biology and ecology of the species was published by Berndt and Allen (2010).

Strelein (1988) reported that the form of the species which outbreaks in the jarrah forests of the south-western corner of Western Australia had some characteristics of the two forms recognised by Campbell (1962). Differences in voltinism of the species within Western Australia, a characteristic purportedly unique to each form, were attributed to variation in thermal accumulation and developmental rates from southern (univoltine) to northern (bivoltine) regions of its range in Western Australia, especially in years with warm winters (Farr 2002). Farr's modelling confirmed Morgan and Cobbinah's (1977) suggestion that differences in the characteristics of the two forms were likely to be temperature-induced. While differences in voltinism can now be explained, the causes of the differences in oviposition behaviour of the forms have not been addressed. Interestingly, the sex pheromone of the coastal/inland river valley form (from Queensland) attracted males of the highland/montane form when used in lures in New Zealand (Gibb et al. 2008). The same lure was found to be effective for monitoring abundances in Western Australia (Farr and Wills 2012).

Outbreaks of *U. lugens* have been reported in all Australian States and forest types throughout the species' region of endemism. The last severe outbreak on jarrah and marri in Western Australia between 1982 and 1988 defoliated 300,000 ha of native forest before the outbreak ended (Farr et al. 2004). This outbreak was found to have begun in localised pockets of jarrah forest which experience summer drought and winter waterlogging (Farr et al. 2004). This finding caused Farr et al. (2004) to implicate tree stress and associated changes in foliar quality in the development of incipient populations of the insect.

15.2.3 Lepidopteran Defoliators of Mallee Eucalypts

The species of lepidopteran defoliators of mallee eucalypts are likely to be numerous but little is known about many of them. McFarland (1988) gives the most comprehensive of the published information available concerning the Geometridae found throughout the Mediterranean-climate regions of Australia – albeit including species reliant on a range of plant species not just eucalypts. Two genera of geometrid likely to be among the species causing the most chewing damage to mallee eucalypts are *Mnesampela* and *Paralaea*. Both genera include species whose distributions encompass mallee vegetation, e.g. *Mnesampela arida* McQuillan, *Paralaea atralba* McQuillan et al. and *P. ochrosoma* (R. Felder & Rogenhofer) (McQuillan 1985; McQuillan et al. 2001). Larvae of a species of *Paralaea*, possibly *P. atralba*, have been observed by MJS eating expanded leaves of *E. dumosa* (dumosa or white mallee) in Bronzewing Flora and Fauna Reserve, south-western Victoria (Fig. 15.1a). Surprisingly, an outbreak of the autumn gum moth [*Mnesampela privata* (Guenée)], which is widely considered to be a pest of plantation *E. globulus* and *E. nitens* in temperate, mesic regions of Australia, occurred in Mildura, Victoria, on plantation *E. grandis* (Steinbauer et al. 2001). The range expansion of *M. privata* into a somewhat Mediterranean-climatic region (see Fig. 60 in McQuillan 1985) was presumably facilitated by the artificial irrigation of a species of eucalypt exotic to the region and which produces less sclerophyllous foliage than the endemic mallee eucalypts [Mildura lies within Hutchinson et al.'s (2005) agro-climatic region E6, i.e. 'semi-arid climate that is too dry to support field crops. Soil moisture tends to be greatest in winter']. Larvae, probably of *Clania ignobilis* (Walker) (Lepidoptera: Psychidae), have also been observed in small numbers feeding on *E. dumosa* in Bronzewing Flora and Fauna Reserve (Fig. 15.1b). This species has a wide distribution in Australia and is thought to feed exclusively on *Eucalyptus* (Common 1990). Larvae of the polyphagous [16 host plant families (Rhainds et al. 2009)] and most specialized of the Australian Psychidae [*Hylarcta huebneri* (Westwood)] have caused severe defoliation of plantation *Pinus radiata* in Queensland (Heather 1975, 1976). Interestingly, although most collection records for *H. huebneri* derive from subcoastal and coastal areas, it has also been collected from one location in Western Australia and a few in South Australia which have Mediterranean-climates (Heather 1975). The life-history traits of *H. huebneri* are associated with outbreak population

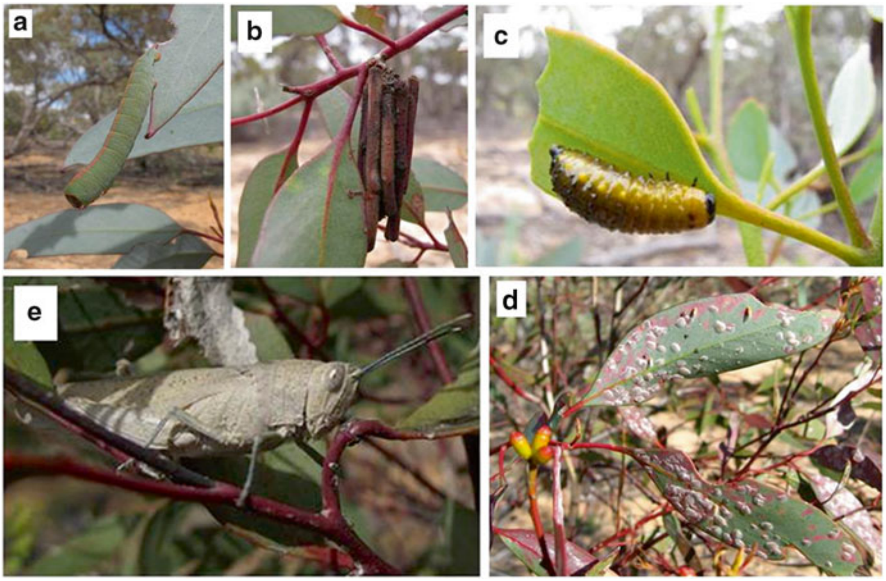

Fig. 15.1 Insect herbivores of *Eucalyptus dumosa* (dumosa or white mallee). (**a**) *Paralaea* sp. larva (Lepidoptera: Geometridae), (**b**) *Clania ignobilis* larva (Lepidoptera: Psychidae), (**c**) *Paropsis* sp. larva (Coleoptera: Chrysomelidae), (**d**) *Cardiaspina* sp. (possibly *squamula*) nymphs and newly eclosed adults (Hemiptera: Aphalaridae) and (**e**) *Goniaea vocans* adult (Orthoptera: Acrididae) (Images: MJ Steinbauer)

dynamics but too little is known about *C. ignobilis* to permit comparison of the two species (Rhainds et al. 2009).

15.3 Coleoptera

The Coleoptera (beetles) represent about one-third of all animal species on the planet, and with estimates exceeding 30,000 species in Australia (Lawrence and Britton 1991), it is not surprising that this group contains some of the most important and fascinating forest-associated species (see also Chap. 16). Cunningham et al. (2005) demonstrated significant differences in species composition, abundance and feeding guilds of beetles between remnant vegetation and plantations in Mediterranean forests in Western Australia, collecting >250 species of Coleoptera associated with foliage (Hobbs et al. 2003). Defoliators accounted for almost 70 % of specimens of the 20-most abundant coleopteran species collected by canopy knockdown across remnant and plantation habitat (Hobbs et al. 2003; Cunningham et al. 2005). The great dominance of leaf-eating beetles on eucalypts is in stark contrast to herbivory patterns in northern hemisphere forests (Ohmart and Edwards 1991). In Australia, the three largest beetle families, the Curculionidae (weevils), Chrysomelidae (leaf beetles) and Scarabaeidae (scarab beetles) all contain significant forest defoliators capable of causing significant mortality and growth and form loss of economically important Mediterranean forest trees. Unlike many other holometabolous groups, several of these species have adults and larvae which feed on the same hosts, potentially safeguarding host selection (Cooper 2001), but also compounding their impacts as defoliators. Significant growth loss resulting from defoliation by weevils and leaf beetles were recorded in exclusion trials in Mediterranean-climate *E. globulus* plantations in Australia (Loch and Matsuki 2010).

15.3.1 Chrysomelidae

The paropsine leaf beetles are among the most important in Mediterranean eucalypt forests in Australia, and worldwide where they have been accidentally introduced from Australia (Paine et al. 2011). Paropsine beetles from the genera *Trachymela, Faex, Dicranosterna, Peltoschema, Paropsis,* and *Paropsisterna* (some species formerly in *Chrysophtharta* and *Sterromela* – (see Reid 2006)) are found in Mediterranean Australian forests, associated with eucalypts, melaleucas and acacias. Eggs are laid singly, or in batches frequently in species-specific formations (Simmul and de Little 1999), and larvae consume the egg chorion before initiating feeding from the leaf margin of young leaves; the larvae of some species (e.g. *Paropsisterna agricola* (Chapuis)) are strongly gregarious, diurnal feeders, while some (e.g. *Trachymela tincticollis* (Blackburn)) are solitary and nocturnal. Larval gregariousness can facilitate feeding on tough eucalypt foliage (Nahrung et al. 2001). There are four larval instars (Fig. 15.1c), feeding preferentially on flush foliage (Simmul and de Little 1999), and defended with a pair of eversible dorsal abdominal glands (Moore 1967). Adults feed by scalloping the leaf edge towards the midrib, and their pre-overwintering feeding can be particularly severe (Simmul and de Little 1999).

Seventeen paropsine species are recorded from *E. globulus* plantations in Western Australia, and twelve from the Green Triangle region (Matsuki and Tovar 2012) with only two in common, and of these, only *Paropsisterna crocata* (Boisducal) appears endemic to both; the other, *P. m-fuscum* (Boheman), is invasive in Western Australia (and also North America – see Chap. 17). In both regions, *E. globulus* is a non-endemic host, but more paropsine species (and more individuals) were found associated with *E. globulus* plantations than with native remnant vegetation in Hobbs et al. (2003) study. Paropsine beetles are broadly oligophagous and have readily colonised extra-limital/novel hosts in other areas (Nahrung 2004; Nahrung et al. 2009), with limonene, α-pinene and 1,8-cineole implicated in host acceptance of *Paropsis atomaria* Olivier (Nahrung et al. 2009, 2011). Such plant secondary compounds, including tannins and other phenolics in host foliage do not appear to affect their growth and development rates, with larvae absorbing or metabolising terpenoids including 1,8-cineole (Fox and Macauley 1977; Macauley and Fox 1980; Ohmart and Larsson 1989). Physical plant characteristics, including glaucousness of eucalypt foliage, may also influence host use by paropsines (e.g. Edwards 1982). *Trachymela tincticollis* is endemic to Western Australia, where its distribution is contiguous with that of its major host *E. gomphocepala*; it also feeds on *E. lehmennii* and *E. cornuta* (Tribe 2000). This species oviposits into bark crevices in batches of about eight eggs coated with a sticky substance. Larvae hide in bark crevices during the day and emerge to feed on flush foliage at night (Tribe 2000).

The pest status of paropsine beetles in *E. globulus* plantations in Western Australia has changed over time: in the early 1990s none were mentioned (Abbott 1993); by 2001 they were described as "rarely encountered" (Loch and Floyd 2001), and a decade later two were considered moderate to severe (but occasional) pests (Matsuki and Tovar 2012). Elliott et al. (1998) reported *Paropsis elytrura* Blackburn and *P. geographica* Baly as noteworthy pests in Western Australia, and *P. aegrota* Boisduval in South Australia (Elliott et al. 1998), but these are no longer considered pests in these regions (Matsuki and Tovar 2012). The main pest paropsine species recorded in Mediterranean plantation forests are now *P. agricola* in the Green Triangle region, *P. obovata* (Chapuis) in Western Australia (= *P. variicollis* in Loch 2006), and *P. m-fuscum* in both areas (Matsuki and Tovar 2012). *Paropsisterna agricola*'s host range exceeds 20 eucalypt species (Nahrung 2004), and is attributed to leaf surface wax components (Li 1993). Voltinism in *P. agricola* is seasonally plastic, depending upon conditions (primarily temperature) experienced by immature stages influencing when new generation adults emerge relative to photoperiod (Nahrung et al. 2004; Nahrung and Allen 2004).

Peltoschema (formerly *Acacicola*, *Pyrgo* or *Pyrgoides* – Reid and Slipinski 2001) *orphana* (Erichson), the fireblight beetle, occurs in South Australia and causes a brown scorched appearance to *Acacia mearnsii* and *A. dealbata* – most damage occurs in regeneration stands, although trees in agricultural and urban areas can also be defoliated (Elliott et al. 1998).

The second significant group within the Chrysomelidae is the Cryptocephalinae, which can cause minor to severe damage to plantations, particularly beetles in the genera *Cadmus* and *Aporocera.* Unlike paropsines, only the adults feed on living foliage; larvae live concealed in faecal cases on the ground and feed on fallen leaves and litter (dos Anjos et al. 2002; Matsuki and Tovar 2012). Six species of *Cadmus* are associated with *E. globulus* plantations in Western Australia, and four in the Green Triangle region (Matsuki and Tovar 2012). *Cadmus excrementarius* Suffrian is one of the major pests of *E. globulus* in Mediterranean Western Australia (Loch and Floyd 2001; Matsuki and Tovar 2012). Adult beetles feed on expanded leaves, apical shoots and tender bark, causing defoliation and disbudding of the crown and deformed growth, and aggregate at both the plantation and individual tree scale (dos Anjos et al. 2002). *Cadmus litigiosus* Boheman is the most important of this group in the Green Triangle, feeding on new growth and coppice between January and April (Matsuki and Tovar 2012).

Aporocera melanocephala Saunders is a moderate to severely recurring pest of *E. globulus* plantations in the Green Triangle; it consumes new adult-phase growth of young plantation trees (Matsuki and Tovar 2012). It is one of seven species in the genus associated with Mediterranean-region plantations in Australia (Hobbs et al. 2003; Loch 2006; Matsuki and Tovar 2012).

Edusella sp. was most abundant native leaf-feeding beetle collected by canopy knockdown in *E. globulus* plantations by Cunningham et al. (2005). Two species in this genus were recorded by Loch (2006), and it feeds on adult and juveline phase foliage but is not considered a pest (Matsuki and Tovar 2012). The most abundant leaf beetle collected in remnant native habitat in Cunningham et al. (2005) was an unidentified species of *Livolia*.

15.3.2 Scarabaeidae

Fifty-four species of nocturnal scarab beetles have been reported from eucalypt plantations in Western Australia, and 46 from the Green Triangle region, where adults can cause severe and extensive damage; larvae feed on fine roots predominantly in pastures (Grimbacher et al. 2011). Swarms of nocturnal scarab beetles can cause severe damage to new growth on seedlings and the tops of older trees (Matsuki and Tovar 2012). *Heteronyx* spp. feed on new leaves of eucalypts in spring (Elliott et al. 1998) and can also damage pine seedlings (Philips 1993b). At least 17 *Heteronyx* species are associated with *E. globulus* plantations in Mediterranean Australia by adults feeding on foliage of seedlings and older trees (Matsuki and Tovar 2012). *Heteronyx elongatus* Blanchard larvae feed on the roots of eucalypt seedlings, especially where plantations are established on ex-pasture sites, and adults can defoliate young seedlings (Phillips 1993b). *Heteronyx dimidiata* (Erichson) is a diurnal species, for which most variation in activity is accounted for by levels of solar radiation and wind (Walker and Allen 2013), of moderate pest status in the Green Triangle region (Matsuki and Tovar 2012).

Liparetrus spp. are important in both Australian Mediterranean regions (Strauss 2001; Grimbacher et al. 2011), with *L. jenkensi* Britton and *L. discipennis* Guèrin-Mèneville the most important in Western Australia and the Green Triangle region, respectively (Grimbacher et al. 2011); eight other species occur in *E. globulus* plantations in the former region, and three in the latter (Matsuki and Tovar 2012).

Anoplognathus spp., and *Sericesthis nigrolineata* Boisduval (both defoliators as adults) can be moderate pests in the Green Triangle region (Matsuki and Tovar 2012); foliage consumption by *Anoplognathus* is negatively related to concentrations of the monoterpene 1,8-cineole (Matsuki et al. 2011), and similarities in terpene profiles to eucalypts explains their use of novel hosts (Steinbauer and Wanjura 2002). A further eight scarab genera were collected from eucalypt foliage in Western Australia (Hobbs et al. 2003; Loch 2006), including *Colpochila* which was listed as moderately injurious to young eucalypt plantations by Strauss (2001), and *Diphucephala*, a very common pest in Western Australia (Elliott et al. 1998).

15.3.3 Curculionidae

Sixty-four weevil species were associated with foliage in native and plantation trees in Western Australia (Hobbs et al. 2003). Loch (2006) recorded 24 native and 6 non-native weevil species collected from *E. globulus* canopy fogging, while Matsuki and Tovar (2012) listed 14 native and 5 non-native foliage-feeding weevil species of various pest status from Western Australia. Seven of these species overlap with those recorded in the Mediterranean Green Triangle Region, while a further four species are listed for the Green Triangle region alone (Matsuki and Tovar 2012). The only weevil mentioned in Strauss (2001) was *Gonipterus scutellatus* Gyllenhal as a minor pest in South Australia. *Gonipterus scutellatus* was considered the most important pest of eucalypt plantations in Mediterranean Western Australia (Loch and Floyd 2001) but was subsequently re-identified as *G. platensis* Marelli, native to Tasmania (Mapondera et al. 2012). More recently, a second, non-endemic, undescribed species was also found in Western Australia (Mapondera et al. 2012, and Chap. 17), along with *G. citriophagus* which is endemic to Western Australia and predominantly feeds on *E. rudis* (Grimbacher et al. 2011; Matsuki and Tovar 2012). Likewise, in South Australia, the species initially referred to as *G. scutellatus* (Phillips 1996; Strauss 2001) is now recognised endemically as the same undescribed species as that in Western Australia, with yet another undescribed species occurring on *E. globulus* in the Green Triangle region (Mapondera et al. 2012).

Despite their taxonomic complexity, the biology of *Gonipterus* spp. is similar, with eggs laid in excrement–covered batches of 1–14 eggs glued on new growth, and legless, slug-like, slime-covered, yellow larvae which undergo 4 instars trailing a characteristic frass filament (Elliott et al. 1998; Matsuki and Tovar 2012). *Gonipterus scutellatus* (=*platensis*) was the most abundant beetle collected by canopy knockdown both in remnant and plantation habitat in Western Australia, and the only species in common to both habitats (Cunningham et al. 2005). Defoliation of *E. globulus* in Western Australia, principally attributed to *G. scutellatus* (= *platensis*), reached levels of 40–80 % on tips and upper crowns between spring and autumn (Loch 2006). Larval feeding is most damaging – larvae mine the leaf surface in early instars and consume the lamina from the leaf edge in later instars – and growing tips can be completely defoliated and die, causing loss of height and poor tree form. Adult *Gonipterus* scallop the leaf edge and larval and adult feeding stages both prefer adult to juvenile foliage (Matsuki and Tovar 2012). The species of overlap between South Australia and Western Australia is also introduced to South Africa (*G*. sp. n. 2) (Mapondera et al. 2012) where it has been shown to discriminate between potential hosts using antenally-detected host volatiles, particularly of previously damaged plants (Bouwer et al. 2014).

Oxyops is another large and important genus in Mediterranean regions of Australia: 20 species are recorded from Western Australia, and two from South Australia (Plant Health Australia 2001). *Oxyops cf pictipennis* was associated with foliage in remnant and plantation forests in Western Australia, although more common in plantations (Hobbs et al. 2003; Cunningham et al. 2005) and collected year-round, with larvae feeding between March and October (Loch 2006), and occurring both on seedlings and older trees (Matsuki and Tovar 2012). Adults and larvae feed on surface leaf tissue, causing leaf browning and fall (Elliott et al. 1998). Its main native forest host is *E. marginata* (Kliejunas et al. 2003).

Catasarcus is a group of flightless weevils, with 26 species recorded from Western Australia, and three from South Australia (Plant Health Australia 2001) although there are at least 41 described species and the group is thought to be restricted to these regions (Elliott et al. 1998). Three species are associated with seedlings and older *E. globulus* plantings in Western Australia (Matsuki and Tovar 2012) and *Catasacarcus* are also common pests of *E. gomphocephala* (Elliott et al. 1998). *Catasarcus impressipennis* (Boisduval) was collected only once in Cunningham et al.'s (2005) study, but, along with its congener *C. carinaticeps* Lea, is considered to cause low level occasional damage, mostly in summer, in Western Australia (Matsuki and Tovar 2012), although heavy infestations can strip trees completely, causing retarded growth or death (Elliott et al. 1998). *Catasarcus impressipennis* is also recorded defoliating *Acacia* in South Australia (Plant Health Australia 2001). Their eggs are laid in clusters beneath the soil surface and larvae feed on roots (Elliott et al. 1998). The most abundant foliage-associated native weevil collected in native remnant forest in Western Australia was an unidentified species of *Pascoellus* (Cunningham et al. 2005).

15.4 Hemiptera

15.4.1 Pinkgum Lerp and White Lace Lerp, Cardiaspina densitexta *Taylor and* C. albitextura *Taylor (Hemiptera: Aphalaridae)*

Psyllids or jumping plantlice are a diverse and important component of the Australian insect fauna. Evolutionarily, there are thought to be at least three independent colonisations of psyllids onto Myrtaceae, with around 250 species associated with eucalypts (Queiroz et al. 2012). Species of lerp-forming spondyliaspidine Aphalaridae have radiated together with their eucalypt hosts and are now the most diverse of the Australian psyllid taxa (Austin et al. 2004). The lerp-forming psyllids belonging to the genus *Cardiaspina* are arguably the most damaging insect herbivores of woodland and riverine eucalypts of any taxa across mainland Australia (Taylor 1962). [Lerps are small shelters constructed by nymphs from faecal excretions which solidify on contact with the air; their primarily purpose is considered to be protection of the nymph from desiccation (White 1972; Sharma et al. 2013)]. This is because, during outbreaks, abundances per leaf are high to very high, nymphal feeding causes chlorosis which is followed by necrosis and leaf abscission, the extent of outbreaks can span entire regions (e.g. catchments) and outbreaks are often chronic, persisting for many years, occasionally decades. The two species about which most is known are, coincidentally, those which outbreak in the

Mediterranean-climate regions of eastern Australia, namely *Cardiaspina densitexta* Taylor and *C. albitextura* Taylor. *C. densitexta* outbreaks on *Eucalyptus fasciculosa* (pink gum) in the southern parts of South Australia while *C. albitextura* outbreaks on *E. blakelyi* (Blakely's red gum) and *E. camaldulensis* subspecies *camaldulensis* (river red gum) in the drier Mediterranean-climatic regions of South Australia, Victoria and New South Wales. Since these species are such important defoliators, they have been well studied. The findings of the research into the biology, host utilisation and population ecology of *C. albitextura* are summarised in the book chapters by Morgan and Taylor (1988) and Taylor (1997).

Possibly because the outbreaks of *C. densitexta* have been more confined than those of *C. albitextura* (to the region of endemism of *E. fasciculosa*), this species has previously only been studied in some detail by one entomologist (TCR White) and there are no synthetic works summarising his findings. Feeding by *C. densitexta* nymphs is associated with the appearance of red lesions around lerps which soon become necrotic while un-infested areas of the same leaf remain green and presumably photosynthetically active (White 1970a). The appearance of red lesions (colouration is due to the accumulation of anthocyanins in feeding-damaged tissues) probably follows the development of chlorotic lesions around actively feeding nymphs and may be a response to photo-damage (Steinbauer et al. 2014). Female *C. densitexta* preferentially oviposit on the abaxial surface of expanded leaves towards their base, depositing eggs next to veins (White 1970b). As occurs in the eggs of the majority of psyllid species, each egg has a pedicel which is inserted through the epidermis to attach egg to leaf and to absorb water (White 1968a; Taylor 1992). Egg hatching is synchronised by photoperiodic and thermal cues and occurs in the morning, probably to coincide with cooler ambient temperatures and thereby to allow first instar nymphs to find a place to settle, commence feeding and construct a lerp (White 1968b).

The dispersal of adult *Cardiaspina* has been the subject of some debate previously; Clark (1962) reported that *C. albitextura* do not disperse far from where they eclosed whilst White (1970b) suggested that first (spring) generation adults may be dispersive while second and third (summer and autumn) generations adults are not. In early to mid-November 1971 (late in the Austral spring), White (1973) used nets mounted on a small aeroplane to sample insects at 152 and 305 m above the ground. Small numbers (between 3 and 16 adults) of male and female *C. densitexta* were caught at both altitudes which was taken as evidence that the spring generation was dispersive. White (1973) estimated that the densities of adult *C. densitexta* at 152 m were between 1300 and 11,500 individuals per hectare while at 305 m there were between 2500 and 12,800 individuals per hectare. Remnant stands of pink gum have been seriously defoliated by *C. densitexta* between the years 1914–1922, 1956–1963, 1967–1974 and from 1978 and into the 1980s (Morgan and Bungey 1981). Extensive leaf reddening, subsequent leaf necrosis and abscission was apparent at four locations around Keith, South Australia, between late September 2013 and late March 2014 (Steinbauer unpubl. data). White (1969) related the timing of outbreaks of *C. densitexta* on *E. fasciculosa* to deficits in soil water. Pink gum leaves were suggested to become richer in N when trees were stressed by prolonged, atypical patterns of winter rain and summer drought; during times when foliar nutritional quality improves substantially, greater numbers of *C. densitexta* nymphs survive to adulthood. White's research on Pinkgum lerp, looper caterpillars and locusts eventually led to the formulation of the highly influential (and widely debated) Plant Stress Hypothesis of insect outbreaks (White 1984).

Cardiaspina densitexta has not been the focus of further research since TCR White. However, between 2009 and 2013 a species of *Cardiaspina* whose lerps closely resemble those of *C. densitexta* caused severe defoliation of large areas of *E. moluccana* (grey box) of the Cumberland Plain Woodland in Western Sydney, New South Wales (Steinbauer et al. 2014; Hall et al. 2015). Steinbauer et al. (2014) referred to this species as *Cardiaspina* near *densitexta* but because the location and host represent novel records for *C. densitexta* only sequencing is likely to provide a definitive identification; DNA barcoding is currently in progress. If the *Cardiaspina* on grey box is found to be *C. densitexta* this will be an extremely important finding because it would indicate that long distance dispersal is possible and that this psyllid is not host specific for *E. fasciculosa*. Interestingly, *E. fasciculosa* and *E. odorata* [published host records for *C. densitexta* (Hollis 2004)] and *E. moluccana* belong in *Eucalyptus* subgenus *Symphyomyrtus* section *Adnataria* (EUCLID 2006). Nevertheless, the other host record for *C. densitexta*, namely *E. diversifolia*, belongs in *Eucalyptus* subgenus *Eucalyptus* series *Diversiformes* (EUCLID 2006). White (1970b) reported that, at high densities, *C. densitexta* utilised species of eucalypt other than *E. fasciculosa* but with varying success. The mechanisms of psyllid host specificity for their eucalypt hosts have only recently begun to be studied (Farnier et al. 2014, 2015, Farnier unpubl. data). Current findings suggest that the taxon's ability to discriminate between *Eucalyptus* species pre-alighting may not be sufficiently attuned to negate 'inappropriate landings' (*sensu* Finch and Collier 2000) thereby increasing the opportunity for host mistakes and the utilisation of novel species.

Nothing has been published concerning the occurrence of *Cardiaspina* species on mallee eucalypts. A species of *Cardiaspina* (possibly *squamula* Taylor) was observed on *E. dumosa* in Bronzewing Flora and Fauna Reserve between July 2008 and May 2009 (Fig. 15.1d). During this period, the mean number of nymphs per leaf ranged from 14.4 to 166.1 and the highest count for an individual leaf was 310 nymphs (Steinbauer unpubl. data). In July 2008, red lesions were apparent on all leaves infested with live nymphs but lesions were noticeably larger by September 2008. Overwintering nymphs eclosed in late September 2008 which was immediately followed by significant oviposition on largely undamaged leaves; a few eggs were subsequently observed in late January and more were observed in March 2009 (presumably from first generation adults). The published records for *C. squamula* Taylor do not accord well with the occurrence of the species on *E. dumosa* in Bronzewing Flora and Fauna Reserve. The type specimens for the species were collected from an unidentified species of *Eucalyptus* from Turramurra, New South Wales – a suburb of Sydney (Taylor 1962). A second record (cited in Taylor 1992) is from Derwent Bridge on the island State of Tasmania. Lastly, Hollis (2004) lists *E. viminalis* (manna gum) as a host but provides no authority for this record. *E.*

dumosa belongs in *Eucalyptus* subgenus *Symphyomyrtus* section *Dumaria* whilst *E. viminalis* belongs in section *Maidenaria* (EUCLID 2006). Until such time as specimens of this psyllid can be re-collected from the same host and similar location and sequenced, uncertainty about its identity will remain. (Unfortunately, specimens from 2008 to 2009 were preserved in 70 % ethanol and are no longer suitable for sequencing). It is not known how long before being discovered the trees at Bronzewing had become infested by this species but it is interesting that the population disappeared within 10 months and was never seen again in the same numbers despite trees being surveyed until early December 2013 (all ten study trees were either severely scorched or entirely consumed by bushfire on 17 January 2014). Furthermore, small lerps (probably of first instar nymphs) resembling those on *E. dumosa* were also observed in modest numbers on the neighbouring *E. incrassata* (ridge-fruited or yellow mallee) but most nymphs did not develop beyond the second instar and the leaves exhibited no signs of feeding damage (Steinbauer unpubl. data). It is conceivable that dumosa *Cardiaspina* was a temporary 'spill-over' population from a larger source population arising from another species of eucalypt in the region. This hypothesis is plausible because White (1970b) reported that, during outbreaks of *C. densitexta*, a non-preferred native eucalypt (*E. odorata* var. *angustifolia*) and a non-indigenous eucalypt (*E. cladocalyx*) would be oviposited on, support nymphs through to adulthood and exhibit foliar discolouration. In contrast, White (1970b) also reported that during outbreaks *C. densitexta* would oviposit on *E. diversifolia* (an endemic species), *E. leucoxylon* (an endemic species) and *E. ficifolia* (a non-indigenous species) but most nymphs did not survive beyond the first instar and no discolouration of the leaves of *E. diversifolia* was observed. These observations support the previous suggestion that pre-alighting host discrimination may be poor in psyllids. They also suggest that adults may often accept novel eucalypts for oviposition but that the nutritional suitability of the ingesta is ultimately determined by first instar nymphs.

15.5 Hymenoptera

The plant-feeding Symphyta (sawflies) represent an ancient radiation of the Hymenoptera, a group more biologically diverse than any other hexapod order, and comprising an otherwise disproportionate number of beneficial species (Naumann 1991). Only the larvae feed on leaves, and some species can completely defoliate trees (Elliott et al. 1998). Within Mediterranean forests of Australia, there are two major groups of defoliating sawflies: exposed feeders (in *Lophyrotoma*, *Perga, Pseudoperga, Xyloperga, Cerealces* and *Pergagrapta*) and concealed feeders, the leaf-blister sawflies (*Phylacteophaga*) (Schmidt 2006). Larvae of the latter group are strictly associated with eucalypts (Schmidt and Walter 2014), but the former also have hosts in *Melaleuca* and *Leptospermum* (Naumann 1991). The Myrtaceae are particularly susceptible to leaf mining, despite their chemical and physical defences (Sinclair and Hughes 2008). Many of these sawflies (particularly the pergines, pterygophorines and phylacteophagines) radiated almost exclusively on their myrtaceous hosts (Schmidt et al. 2010), tracking their hosts' radiation until about 25 M years ago (Schmidt and Walter 2014). Sawflies have evolved at least two different methods of dealing with the toxic secondary compounds present in host foliage; the Perginae have unique brushlike mandibular structures that separate leaf oils from ingested leaf material, storing it in pharangeal diverticula and regurgitating it defensively when disturbed, while the Pterygophorinae rely solely on enzymatic detoxification of ingested 1,8-cineole (Schmidt et al. 2010). The leaf-blister sawflies feed on the mesophyll layer between the upper and lower leaf epidermis, creating a raised brown blistered appearance (Loch et al. 2004); their detoxification mechanisms are unknown, but they may either avoid the oil glands (as do jarrah leafminer), tolerate ingested oils (as do paropsine leaf beetles) or detoxify ingested oils (as do some exposed-feeding sawflies) (Schmidt and Walter 2014).

Exposed feeders such as *Perga dorsalis* Leach, a common species in South Australia, have strongly aggregative larvae which cluster together during the day, and feed singly at night (Phillips 1993), maintaining contact by tapping their abdomen on leaves or branches (Ohmart and Edwards 1991); the tightly clustered larval formations facilitate defence, digestion and thermoregulation (Seymour 1974). At high temperatures, this species spreads excreted midgut filtrate from its anus over its body to increase evaporative heat loss (Seymour 1974). *Perga affinis* Kirby, *Pergagrapta* sp., and *Phylacteophaga froggatti* Riek are endemic moderate pests of *E. globulus* plantations in the Green Triangle region, and the latter species is a serious invasive pest in Western Australia plantations (Matsuki and Tovar 2012, and Chap. 17).

The endemic genera *Paraperga*, *Pergula* and *Antiperga* are only known from Western Australia, where *A. enslini* feeds on *Melaleuca* (Schmidt 2006). Four species of *Trichorhachus* are also endemic to Western Australia, where larvae feed on *Conospermum* in native habitat (Naumann 1991). The most south-western distribution described for the cypress pine sawfly, *Zenarge turneri rabus* Moore, a defoliator of native *Callitris hugelii* is just within the boundaries of the Mediterranean region of Victoria (Moore 1962).

15.6 Orthoptera

The wingless grasshopper *Phaulacridium vittatum* (Sjöstedt) is a major defoliator of newly-established *E. globulus* plantations throughout Mediterranean forest regions in Australia (Phillips 1993; Matsuki and Tovar 2012). It normally feeds on herbaceous plants and broadleaved weeds in crops and pastures or grazing paddocks, but when these die off, the grasshoppers will feed on nearby native trees, and young plantations of *Eucalyptus* and *Pinus* (Elliott et al. 1998). Adult *Goniaea vocans* (Leach) (Fig. 15.1e) have been observed by MJS resting on *E. dumosa* in Murray Sunset National Park, south-western Victoria, while nymphs of *G. australasiae* (Leach) have been observed in leaf litter in Bronzewing Flora and Fauna

Reserve. Both Slender gumleaf grasshopper (*G. vocans*) and Gumleaf grasshopper (*G. australasiae*) are probably among the more common members of a suite of nocturnal orthopteran herbivores of mallee and other eucalypt species in both western and eastern parts of the country (Rentz et al. 2003; Steinbauer et al. 2012).

15.7 General Discussion

The marked contrast between the mallee vegetation and woodland forests of the eastern Mediterranean-like climate region and the tall open forests of the southwestern corner of Western Australia probably explains the marked differences in defoliator abundance and diversity between regions, even on a common host grown under similar climatic conditions. The recent movement of defoliator species between regions has been largely uni-directional; several species have moved into Western Australia from the east (see Chap. 17). These species aside, the overlap between regions is small, particularly for the Coleoptera (36 endemic to Green Triangle, 56 endemic to WA and 15 in common to both regions) and Hymenoptera (four endemic to Green Triangle, two endemic to WA and none in common) (from Matsuki and Tovar 2012).

Eucalypt foliage feeders must overcome a number of potential barriers to foliage consumption; these include foliar toughness (or sclerophylly), epicuticular waxes, low nitrogen levels, high tannin levels and other potentially toxic plant secondary metabolites (Cooper 2001). The widely held belief that tannins reduce protein digestion by insect herbivores has recently been discredited because their high gut pH oxidizes and thereby renders them inert (Barbehenn and Constabel 2011). However, the complexities of tannin chemistry and analysis have largely limited the extent to which any classes of or individual compounds have been tested for their biological activity against native herbivores. Recently, Salminen and Karonen (2011) have provided a methodology to estimate the oxidative activity of foliar tannins and other phenolic compounds since oxidative stress is considered the trait most likely to affect insect survival and performance. Application of widely used methodologies will enable Australian researchers to integrate the activity of eucalypt tannins against herbivores into the broader literature concerning effects on insects. On the other hand, phytophagous insects utilising eucalypt foliage exploit some of these traits for host location (e.g. Nahrung et al. 2011), host discrimination and acceptance (e.g. Steinbauer et al. 2004), and overcome them by gregariousness (Nahrung et al. 2001), avoidance (e.g. Mazanec 1983), tolerance (e.g. Ohmart and Larsson 1989), or detoxification (e.g. Schmidt et al. 2010). There is thus a very high diversity of insects that can utilise eucalypts as host plants, and that have co-radiated with these hosts, with estimates of insects feeding on eucalypts likely to be into the thousands (Majer et al. 1997).

Steinbauer et al. (2015a) have emphasized the need to know the longevities of the leaves of eucalypts in Mediterranean-like ecosystems to understand fluctuations in the diversity and abundance of native insect herbivores. There is still surprisingly little quantitative information on the longevities of eucalypt leaves in response to changes in climatic conditions (or tree phenology) despite the importance of leaf type (juvenile or adult) and age on their usage by insect herbivores. While leaf type and age influence toughness for insect folivores, climatic conditions (in particular ambient temperature) have been found to affect concentrations of plant secondary metabolites which is likely to influence annual rates of leaf damage of leaves of the same toughness (Moore et al. 2004; Steinbauer et al. 2015a). Changes in tree quality that affect insect abundance also have the potential to affect higher trophic levels (Recher et al. 1996; Moore et al. 2013; Steinbauer et al. 2015b). As the incidence and severity of tree decline and dieback and insect damage change with increased climate variability, we trust that there will be greater emphasis on conducting research that adopts a bottom-up approach to understanding the trophic pyramids supported by Australian forest trees.

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References

Abbott I (1990) Insect outbreaks in forests of Western Australia. In: Watt AD, Leather SR, Hunter MD, Kidd NA (eds) Population dynamics of forest insects. Intercept Limited, Andover, pp 95–103

Abbott I (1993) Insect pest problems of eucalypt plantations in Australia: 6 Western Australia. Aust For 56:381–384

Abbott I, Burbidge T, Williams M et al (1992) Arthropod fauna of jarrah (*Eucalyptus marginata*) foliage in Mediterranean forest of Western Australia: spatial and temporal variation in abundance, biomass, guild structure and species composition. Aust J Ecol 17:263–274

Abbott I, van Heurck P, Burbidge T et al (1994) Factors influencing the performance of jarrah leafminer (Lepidoptera) within stands of jarrah forest of Western Australia. Aust For 57:165–170

Abbott I, van Heurck P, Burbidge T, Wills A (1995) Cutting out the leafminer. Landscope 11(1):44–47, Spring

Abbott I, Wills A, Burbidge T (1999a) Historical incidence of *Perthida* leafminer species (Lepidoptera) in Southwest Western Australia based on herbarium specimens. Aust J Ecol 24:144–150

Abbott I, Wills A, Burbidge T (1999b) Reinfestation of *Eucalyptus marginata* ground coppice by jarrah leafminer after scorch by autumn or spring fires. Aust For 62:160–165

Abbott I, Wills A, Burbidge T et al (2000) Arthropod faunas of crowns of jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) in mediterranean-climate forest: a preliminary regional-scale comparison. Aust For 63:21–26

Anjos ND, Majer J, Loch AD (2002) Spatial distribution of a chrysomelid leaf beetle (*Cadmus excrementarius* Suffrian) and potential damage in a *Eucalyptus globulus* subsp *globulus* plantation. Aust For 65:227–231

Archibald RD, Bowen BJ, Hardy GSJ et al (2005) Changes to tuart woodland in Yalgorup National Park over four decades. In: Calver M et al (ed) Proceedings 6th national conference of the Australian Forest History Society Inc. Millpress Science Publishers, Rotterdam, pp 363-372

Austin AD, Yeates DK, Cassis G et al (2004) Insects 'Down under' – diversity, endemism and evolution of the Australian insect fauna: examples from selected orders. Aust J Entomol 43:216–234

Barbehenn RV, Constabel CP (2011) Tannins in plant-herbivore interactions. Phytochemistry 72:1551–1565

Beckman R (1986) Jarrah's native pest. Ecos 48:30–31

Berndt LA, Allen GR (2010) Biology and pest status of *Uraba lugens* Walker (Lepidoptera: Nolidae) in Australia and New Zealand. Aust J Entomol 49:268–277

Boland DJ, Brophy JJ, House APN (1991) *Eucalyptus* leaf oils: use, chemistry, distillation and marketing. Inkata Press, Melbourne

Bouwer MC, Slippers B, Wingfield MJ et al (2014) Chemical signatures affecting host choice in the *Eucalyptus* herbivore, *Gonipterus* sp (Curculionidae: Coleoptera). Arthropod Plant Interact 8:439–451

Cai YF, Barber P, Dell B et al (2010) Soil bacterial functional diversity is associated with the decline of *Eucalyptus gomphocephala*. For Ecol Manage 260:1047–1057

Campbell KG (1962) The biology of *Roeselia lugens* (Walk.), the gum-leaf skeletonizer moth, with particular reference to the *Eucalyptus camaldulensis* Dehn. (River red gum) forests of the Murray Valley Region. Proc Linnean Soc NSW 87:316–338

Campbell KG (1969) A note on the biology of *Uraba* (=*Roeselia*) *lugens* Walker, the gum-leaf skeletonizer. J Entomol Soc Aust (NSW) 6:30

Clark LR (1962) The general biology of *Cardiaspina albitextura* (Psyllidae) and its abundance in relation to weather and parasitism. Aust J Zool 10:537–586

Clarke MF, Avitabile SC, Brown L et al (2010) Ageing mallee eucalypt vegetation after fire: insights for successional trajectories in semi-arid mallee ecosystems. Aust J Bot 58:363–372

Common IFB (1981) Some factors responsible for imbalances in the Australian fauna of Lepidoptera. J Lepidopterists' Soc 34:286–294

Common IFB (1990) Moths of Australia. Melbourne University Press, Carlton

Cooper PD (2001) What physiological processes permit insects to eat *Eucalyptus* leaves? Austral Ecol 26:556–562

Cunningham SA, Floyd RB, Weir TA (2005) Do *Eucalyptus* plantations host an insect community similar to remnant Eucalyptus forest? Austral Ecol 30:103–117

de Queiroz DL, Burckhardt D, Majer J (2012) Integrated pest management of eucalypt psyllids (Insecta, Hemiptera, Psylloidea). In: Larramendy ML, Soloneski S (eds) Integrated pest management and pest control – current and future tactics. InTech, pp 385–412. doi:10.5772/1383

Edwards PB (1982) Do waxes on *Eucalyptus* leaves provide protection from grazing insects? Aust J Ecol 7:347–352

Elliott HJ, Ohmart CP, Wylie FR (1998) Insect pests of Australian forests. Inkata Press, Melbourne

EUCLID (2006) Eucalypts of Australia, 3rd edn. CSIRO Publishing, Collingwood

Farnier K, Dyer AG, Taylor GS et al (2015) Visual acuity trade-offs and microhabitat driven adaptation of searching behaviour in psyllids. J Exp Biol 218:1564–1571

Farnier K, Dyer AG, Steinbauer MJ (2014) Related but not alike: not all Hemiptera are attracted to yellow. Front Ecol Evol 2:67

Farr JD (2002) Biology of the gumleaf skeletoniser, *Uraba lugens* Walker (Lepidoptera: Noctuidae), in the Southern jarrah forest of Western Australia. Aust J Entomol 41:60–69

Farr JD, Wills AJ (2012) Field testing Desire® Delta trap and GLS sex pheromone lure system for measuring outbreak and basal populations of *Uraba lugens* Walker (Lepidoptera: Nolidae). Aust For 75:175–179

Farr JD, Swain D, Metcalf F (2004) Spatial analysis of an outbreak of *Uraba lugens* (Lepidoptera: Noctuidae) in the Southwest of Western Australia: does logging, vegetation type or fire influence outbreaks? Aust For 67:101–113

Finch S, Collier RH (2000) Host-plant selection by insects – a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. Entomol Exp Appl 96:91–102

Fox LR, Macauley BJ (1977) Insect grazing on *Eucalyptus* in response to variation in leaf tannins and nitrogen. Oecologia 29:145–162

Gavran M (2014) Australian plantation statistics 2014 update. Technical report No 42. Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra

Gibb AR, Suckling DM, Fielder S et al (2008) Major sex pheromone components of the Australian gum leaf skeletonizer *Uraba lugens*: (10*E*,12*Z*)-hexadecadien-1-yl acetate and (10*E*,12*Z*)-hexadecadien-1-ol. J Chem Ecol 34:1125–1133

Goodger JQD, Woodrow IE (2012) Genetic determinants of oil yield in *Eucalyptus polybractea* R.T.Bake. Trees 26:1951–1956

Grimbacher P, Matsuki M, Collett N et al (2011) Are insect herbivores in *Eucalypt globulus/nitens* plantations a worsening problem? A multi-region spatio-temporal review of Southern Australia. CRC forestry technical report 216, Hobart

Gullan PJ, Cranston PS, Cook LG (1997) The response of gall-inducing scale insects (Hemiptera: Eriococcidae: *Apiomorpha* Rübsaamen) to the fire history of mallee eucalypts in Danggali Conservation Park, South Australia. Trans R Soc South Aust 121:137–146

Hall AAG, Gerlenda AN, Hasegawa S et al (2015) Anatomy of an outbreak: the biology and population dynamics of a *Cardiaspina* psyllid species in an endangered woodland ecosystem. Agric For Entomol. doi:10.1111/afe.12106

Harris C, Young EK (1989) Mallee for firewood. In: Noble JC, Bradstock RA (eds) Mediterranean landscapes in Australia, mallee ecosystems and their management. CSIRO, East Melbourne, pp 379–390

Heads M (2014) Biogeography of Australasia: a molecular analysis. Cambridge University Press, Cambridge

Heather NW (1975) Life history and biology of the leaf bagworm, *Hyalarcta huebneri* (Westwood) (Lepidoptera: Psychidae). J Aust Entomol Soc 14:353–361

Heather NW (1976) An outbreak of the leaf bagworm *Hyalarcta huebneri* (Westwood) (Lepidoptera: Psychidae) in forest plantations of *Pinus radiata* in Queensland. QLD J Agric Anim Sci 33:145–154

Hobbs RJ, Floyd R, Cunningham S et al (2003) Hardwood plantations: quantifying conservation and environmental service benefits. A report of the RIRDC/L&W Australia/FWPRDC joint venture agroforestry program. RIRDC publication No 02/083, Canberra

Hollis D (2004) Australian psylloidea: jumping plantlice and lerp insects. Australian Biological Resources Study, Canberra

Hutchinson MF, McIntyre S, Hobbs RJ, Stein JL, Garnett S, Kinloch J (2005) Integrating a global agro-climatic classification with bioregional boundaries in Australia. Glob Ecol Biogeogr 14:197–212

Kliejunas JT, Burdsall HH Jr, DeNitto GA et al (2003) Pest risk assessment of the importation into the United States of unprocessed logs and chips of eighteen *Eucalypt* species from Australia, vol 137, General technical report FPL-GTR. USDA, Forest Service, Forest Products Laboratory, Madison

Kolesik P (2000) Gall midges (Diptera: Cecidomyiidae) of Australian cypress-pines, *Callitris* spp. (Cupressaceae), with descriptions of three new genera and three new species. Aust J Entomol 39:244–255

Ladiges PY, Bayly MJ, Nelson GJ (2010) East–west continental vicariance in *Eucalyptus* subgenus *Eucalyptus*. In: Williams DM, Knapp S (eds) Beyond cladistics: the branching of a paradigm. University of California Press, Berkeley, pp 267–302

Lawrence JF, Britton EB (1991) Coleoptera (Beetles). In: Naumann I (ed) The insects of Australia. A textbook for students and research workers, vol 2. Melbourne University Press, Carlton, pp 543–683

Li HF (1993) Phytochemistry of *Eucalyptus* spp. and its role in insect-host-tree selection. PhD thesis, University of Tasmania, Hobart

Loch AD (2006) Phenology of *Eucalyptus* weevil, *Gonipterus scutellatus* Gyllenhal (Coleoptera: Curculionidae), and chrysomelid beetles in *Eucalyptus globulus* plantations in South-Western Australia. Agric For Entomol 8:155–165

Loch AD, Floyd RB (2001) Insect pests of Tasmanian blue gum, *Eucalyptus globulus globulus*, in South-Western Australia: history, current perspectives and future prospects. Austral Ecol 26:458–466

Loch AD, Matsuki M (2010) Effects of defoliation by *Eucalyptus* weevil, *Gonipterus scutellatus*, and chrysomelid beetles on growth of *Eucalyptus globulus* in southwestern Australia. For Ecol Manage 260:1324–1332

Loch AD, Matthiessen JN, Floyd RB (2004) Parasitism and seasonal phenology of leafblister sawfly, *Phylacteophaga froggatti* (Hymenoptera: Pergidae), in *Eucalyptus globulus* plantations in south-western Australia. Aust J Entomol 43:88–93

Macauley BJ, Fox LR (1980) Variation in total phenols and condensed tannins in *Eucalyptus*: leaf phenology and insect grazing. Aust J Ecol 5:31–35

Mahon RJ, Miethke PM, Mahon JA (1982) The evolutionary relationships of three forms of the jarrah leaf miner, *Perthida glyphopa* (Common) (Lepidoptera: Incurvariidae). Aust J Zool 30:243–249

Majer JD, Recher HF, Wellington AB et al (1997) Invertebrates of eucalypt formations. In: Williams J, Woinarski J (eds) Eucalypt ecology: individuals to ecosystems. Cambridge University Press, Cambridge, pp 278–302

Majer JD, Recher HF, Ganesh S (2000) Diversity patterns of eucalypt canopy arthropods in eastern and western Australia. Ecol Entomol 25:295–306

Mapondera TS, Burgess T, Matsuki M et al (2012) Identification and molecular phylogenetics of the cryptic species of the *Gonipterus scutellatus* complex (Coleoptera: Curculionidae: Gonipterini). Aust J Entomol 51:175–188

Markham NT, Noble JC (1989) Essential oil production. In: Noble JC, Bradstock RA (eds) Mediterranean landscapes in Australia, Mallee ecosystems and their management. CSIRO, East Melbourne, pp 353–361

Matsuki M, Tovar F (2012) Field guide for *Eucalyptus globulus* plantations in Western Australia and the Green Triangle. IPMG, Manjimup

Matsuki M, Foley WJ, Floyd RB (2011) Role of volatile and non-volatile plant secondary metabolites in host tree selection by Christmas beetles. J Chem Ecol 37:286–300

Mazanec Z (1983) The immature stages and life history of the jarrah leafminer, *Perthida glyphopa* Common (Lepidoptera: Incurvariidae). J Aust Entomol Soc 22:101–108

Mazanec Z (1985) Resistance of *Eucalyptus marginata* to *Perthida glyphopa* (Lepidoptera: Incurvariidae). J Aust Entomol Soc 24:209–221

Mazanec Z (1987) Natural enemies of *Perthida glyphopa* Common (Lepidoptera: Incurvariidae). J Aust Entomol Soc 26:303–308

Mazanec Z (1989) Jarrah leafminer, an insect pest of jarrah. In: Dell B, Havel JJ, Malajczuk N (eds) The jarrah forest: a complex Mediterranean ecosystem. Kluwer, Dordrecht, pp 123–131

Mazanec Z (1996) Key factor analysis of population data for *Perthida glyphopa* Common (Lepidoptera: Incurvariidae). CSIRO Division of Entomology, Technical report No 67, Canberra

Mazanec Z (1999) The influence of the jarrah leafminer *Perthida glyphopa* Common (Lepidoptera: Incurvariidae) and prescribed burning on the girth increment of jarrah *Eucalyptus marginata* Donn ex Smith. Aust For 62:172–181

Mazanec Z, Justin MJ (1986) Oviposition behaviour and dispersal of *Perthida glyphopa* Common (Lepidoptera: Incurvariidae). J Aust Entomol Soc 25:149–159

Mazanec Z, Justin MJ (1994) Fecundity and oviposition by *Perthida glyphopa* Common (Lepidoptera: Incurvariidae). J Aust Entomol Soc 33:223–234

McFarland N (1988) Portraits of South Australian geometrid moths. Allen Press, Lawrence

McQuillan PB (1985) A taxonomic revision of the Australian autumn gum moth genus *Mnesampela* Guest (Lepidoptera: Geometridae, Ennominae). Entomol Scand 16:175–2002

McQuillan PB, Young CJ, Richardson AMM (2001) A revision of the Australian moth genus *Paralaea* Guest (Lepidoptera : Geometridae : Ennominae). Invertebr Taxon 15:277–317

Moore KM (1962) The taxonomy of *Zenarge turneri* Rohwer, the cypress pine sawfly. Proc Linnean Soc NSW 87:116–124

Moore BP (1967) Hydrogen cyanide in the defensive secretions of larval Paropsini (Coleoptera: Chrysomelidae). Aust J Entomol 6:36–38

Moore BD, Wallis IR, Wood JT et al (2004) Foliar nutrition, site quality, and temperature influence foliar chemistry of tallowwood (*Eucalyptus microcorys*). Ecol Monogr 74:553–568

Moore TL, Valentine LE, Craig MD, Hardy GES, Fleming PA (2013) Do woodland birds prefer to forage in healthy *Eucalyptus wandoo* trees? Aust J Zool 61:187–195

Morgan FD, Bungey RS (1981) Dynamics of population outbreaks of Psyllidae (lerp insects) on eucalypts. In: Old KM, Kile GA, Ohmart CP (eds) Eucalypt dieback in forests and woodlands. CSIRO, Melbourne, pp 127–129

Morgan FD, Cobbinah JR (1977) Oviposition and establishment of *Uraba lugens* (Walker), the gum leaf skeletoniser. Aust For 40:44–55

Morgan FD, Taylor GS (1988) The white lace lerp in Southeastern Australia. In: Berryman AA (ed) Dynamics of forest insect populations. Plenum, New York, pp 129–140

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nahrung HF (2004) Biology of *Chrysophtharta agricola* (Coleoptera, Chrysomelidae), a pest of *Eucalyptus* plantations in south-eastern Australia. Aust For 67:59–66

Nahrung HF, Allen GR (2004) Overwintering ecology of *Chrysophtharta agricola*: mechanisms of reproductive diapause induction and termination. Aust J Zool 52:505–520

Nahrung HF, Dunstan PK, Allen GR (2001) Larval gregariousness and neonate establishment of the eucalypt-feeding beetle *Chrysophtharta agricola* (Coleoptera: Chrysomelidae: Paropsini). OIKOS 94:358–364

Nahrung HF, Allen GR, Patel VS (2004) Day-degree development and phenology modelling of the immature stages of *Chrysophtharta agricola* (Chapuis) (Coleoptera: Chrysomelidae), a pest of eucalypt plantations. Aust J Entomol 43:177–183

Nahrung HF, Waugh R, Hayes RA (2009) *Corymbia* species and hybrids: chemical and physical foliar attributes and implications for herbivory. J Chem Ecol 35:1043–1053

Nahrung HF, Waugh R, Hayes RA et al (2011) Influence of *Corymbia* hybridisation on crown damage by three arthropod herbivores. J Trop For Sci 23:383–388

Naumann ID (1991) Hymenoptera (wasps, bees, ants, sawflies). In: CSIRO (ed) The insects of Australia: a textbook for students and research workers, vol 2. Melbourne University Press, Carlton, pp 916–1000

Newman LJ, Clark J (1925) The jarrah leaf miner. (*Tinea* sp.). J Dept Agric West Aust 2:372–378

Newman LJ, Clark J (1926) The jarrah leaf miner, *Tinea* sp. Aust For J 9:95–99

Ogden J (1978) On the dendrochronological potential of Australian trees. Aust J Ecol 3:339–356

Ohmart CP, Edwards PB (1991) Insect herbivory on *Eucalyptus*. Annu Rev Entomol 36:637–657

Ohmart CP, Larsson S (1989) Evidence for absorption of eucalypt essential oils by *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae). Aust J Entomol 28:201–206

Paine TD, Steinbauer MJ, Lawson SA (2011) Native and exotic pests of *Eucalyptus*: a worldwide perspective. Annu Rev Entomol 56:181–201

Parsons RF (1994) *Eucalyptus* scrubs and shrublands. In: Groves RH (ed) Australian vegetation. Cambridge University Press, Cambridge, pp 230–291

Phillips CL (1993a) Insect pest problems of eucalypt plantations in Australia: 5 South Australia. Aust For 56:378–380

Phillips CL (1993b) PIRSA Forestry forest health fact sheets. http://pir.sa.gov.au/forestry/Forest_health_fact_sheets. Accessed Jan 2015

Phillips CL (1996) Insects, diseases and deficiencies associated with eucalypts in South Australia. Primary Industries, Adelaide

Plant Health Australia (2001) Australian Plant Pest Database. http://www.planthealthaustralia.com.au/resources/australian-plant-pest-database/. Accessed Jan 2015

Recher HF, Majer JD, Ganesh S (1996) Eucalypts, arthropods and birds: on the relation between foliar nutrients and species richness. For Ecol Manage 85:177–195

Reid CAM (2006) A taxonomic revision of the Australian Chrysomelinae, with a key to the genera (Coleoptera: Chrysomelidae). Zootaxa 1292:1–119

Reid CAM, Slipinski SA (2001) *Peltoschema* Reitter, a hitherto unrecognised chrysomeline: redescription and synonymy (Coleoptera: Chrysomelidae). Coleopt Bull 55:330–337

Rentz DCF, Lewis RC, Su YN et al (2003) A guide to Australian grasshoppers and locusts. Natural History Publications (Borneo), Kota Kinabalu

Rhainds M, Davis DR, Price PW (2009) Bionomics of bagworms (Lepidoptera: Psychidae). Annu Rev Entomol 54:209–226

Ruthrof KX, Yates CJ, Loneragan WA (2002) The biology of Tuart. In: Keighery BJ, Longman VM (eds) Tuart (*Eucalyptus gomphocephala*) and Tuart communities. Wildflower Society of Western Australia, Nedlands, pp 108–122

Salminen J-P, Karonen M (2011) Chemical ecology of tannins and other phenolics: we need a change in approach. Funct Ecol 25:325–338

Schmidt S (2006) Checklist of the Pergidae (Hymenoptera: Symphyta) of Australasia. In: Blank S, Schmidt S, Taeger A (eds) Recent sawfly research: synthesis and prospects. Goecke Evers, Keltern, pp 627–634

Schmidt S, Walter GH (2014) Young clades in an old family: major evolutionary transitions and diversification of the eucalypt-feeding pergid sawflies in Australia (Insecta, Hymenoptera, Pergidae). Mol Phylogenet Evol 74:111–121

Schmidt S, McKinnon AE, Moore CJ et al (2010) Chemical detoxification vs mechanical removal of host plant toxins in *Eucalyptus* feeding sawfly larvae (Hymenoptera: Pergidae). J Insect Physiol 56:1770–1776

Seymour RS (1974) Convective and evaporative cooling in sawfly larvae. J Insect Physiol 20:2447–2457

Sharma A, Raman A, Taylor G et al (2013) Nymphal development and lerp construction of *Glycaspis* sp. (Hemiptera: Psylloidea) on *Eucalyptus sideroxylon* (Myrtaceae) in central-west New South Wales, Australia. Arthropod Struct Dev 42:551–564

Simmul TL, de Little DW (1999) Biology of the Paropsini (Chrysomelidae: Chrysomelinae). In: Cox ML (ed) Advances in Chrysomelidae. Backhuys Publishers, Leiden

Sinclair RJ, Hughes L (2008) Leaf mining in the Myrtaceae. Ecol Entomol 33:623–630

Specht RL (1981) Mallee ecosystems in Southern Australia. In: di Castri F, Goodall DW, Specht RL (eds) Ecosystems of the world 11. Mediterranean-type shrublands. Elsevier Scientific Publishing Company, Amsterdam, pp 203–231

Steinbauer MJ, Wanjura WJ (2002) Christmas beetles (*Anoplognathus* spp, Coleoptera: Scarabaeidae) mistake peppercorn trees for eucalypts. J Nat Hist 36:119–125

Steinbauer MJ, Matsuki M (2004) Suitability of *Eucalyptus* and *Corymbia* for *Mnesampela privata* (Guenée) (Lepidoptera: Geometridae) larvae. Agric For Entomol 6:323–332

Steinbauer MJ, McQuillan PB, Young CJ (2001) Life history and behavioural traits of *Mnesampela privata* that exacerbate population responses to eucalypt plantations: comparisons with Australian and outbreak species of forest geometrid from the northern-hemisphere. Austral Ecol 26:525–534

Steinbauer MJ, Schiestl FP, Davies NW (2004) Monoterpenes and epicuticular waxes help female autumn gum moth differentiate between waxy and glossy *Eucalyptus* and leaves of different ages. J Chem Ecol 30:1117–1142

Steinbauer MJ, Haslem A, Edwards ED (2012) Using meteorological and lunar information to explain catch variability of Orthoptera and Lepidoptera from 250 W Farrow light traps. Insect Conserv Divers 5:367–380

Steinbauer MJ, Burns AE, Hall A et al (2014) Nutritional enhancement of leaves by a psyllid through senescence-like processes: insect manipulation or plant defence? Oecologia 176:1061–1074

Steinbauer MJ, Wallis IR, Davies NW et al (2015a) Foliar quality of co-occurring mallee eucalypts: balance of primary and secondary metabolites reflects past growing conditions. Chemoecology. doi:10.1007/s00049-015-0187-4

Steinbauer MJ, Sinai KMJ, Anderson A et al (2015b) Trophic cascades in bell miner-associated dieback forests: quantifying relationships between leaf quality, psyllids and *Psyllaephagus* parasitoids. Austral Ecol 40:77–89

Strauss SY (2001) Benefits and risks of biotic exchange between *Eucalyptus* plantations and native Australian forests. Austral Ecol 26:447–457

Strelein GJ (1988) Gum leaf skeletoniser moth, *Uraba lugens*, in the forests of Western Australia. Aust For 51:197–204

Taylor KL (1962) The Australian genera *Cardiaspina* Crawford and *Hyalinaspis* Taylor (Homoptera: Psyllidae). Aust J Zool 10:307–348

Taylor GS (1992) The structure of the eggs of some Australian Psylloidea (Hemiptera). J Aust Entomol Soc 31:109–117

Taylor GS (1997) Effect of plant compounds on the population dynamics of the lerp insect, *Cardiaspina albitextura* Taylor (Psylloidea: Spondyliaspididae) on eucalypts. In: Raman A (ed) Ecology and evolution of plant-feeding insects in natural and man-made environments. International Scientific Publications, New Delhi, pp 37–57

Taylor K, Barber PA, St J Hardy GE et al (2009) Botryosphaeriaceae from tuart (*Eucalyptus gomphocephala*) woodland, including descriptions of four new species. Mycol Res 113:337–353

Tribe GD (2000) Ecology, distribution and natural enemies of the *Eucalyptus*-defoliating tortoise beetle *Trachymela tincticollis* (Blackburn) (Chrysomelidae: Chrysomelini: Paropsina) in southwestern Australia, with reference to its biological control in South Africa. Afr Entomol 8:23–45

Walker PW, Allen GR (2013) Seasonal flight activity, phenology and physiological status of the major establishment pests of *Eucalyptus nitens* plantations, *Heteronyx dimidiata* and *H. crinitus* (Coleoptera: Scarabaeidae: Melolonthinae). Aust J Entomol 52:31–41

Wallace MMH (1970) The biology of the jarrah leaf miner, *Perthida glyphopa* Common (Lepidoptera: Incurvariidae). Aust J Zool 18:91–104

Wardell-Johnson GW, Williams JE, Hill KD et al (1997) Evolutionary biogeography and contemporary distribution of eucalypts. In: Williams J, Woinarski J (eds) Eucalypt ecology: individuals to ecosystems. Cambridge University Press, Cambridge, pp 92–128

White TCR (1968a) Uptake of water by eggs of *Cardiaspina densitexta* (Homoptera: Psyllidae) from leaf of host plant. J Insect Physiol 14:1669–1683

White TCR (1968b) Hatching of eggs of *Cardiaspina densitexta* (Homoptera, Psyllidae) in relation to light and temperature. J Insect Physiol 14:1847–1859

White TCR (1969) An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. Ecology 50:905–909

White TCR (1970a) The nymphal stage of *Cardiaspina densitexta* (Homoptera: Psyllidae) on leaves of *Eucalyptus fasciculosa*. Aust J Zool 18:273–293

White TCR (1970b) Some aspects of the life history, host selection, dispersal, and oviposition of adult *Cardiaspina densitexta* (Homoptera: Psyllidae). Aust J Zool 18:105–117

White TCR (1972) The production of amylose in the faeces of psyllid larvae with special reference to the lerps of *Cardiaspina densitexta*. J Insect Physiol 18:2359–2367

White TCR (1973) Aerial dispersal of adult *Cardiaspina densitexta* (Homoptera: Psyllidae) in South Australia. Trans R Soc South Aust 97:29–31

White TCR (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105

Yen AL (1989) Overstorey invertebrates in the Big Desert, Victoria. In: Noble JC, Bradstock RA (eds) Mediterranean landscapes in Australia, mallee ecosystems and their management. CSIRO, East Melbourne, pp 285–299

Chapter 16
Native Phloem and Wood Borers in Australian Mediterranean Forest Trees

Simon A. Lawson and Valerie J. Debuse

Abstract Native Mediterranean forests in Australia are dominated by two tree genera, *Eucalyptus* and *Acacia*, while *Pinus* and *Eucalyptus* dominate plantation forestry. In native forests, there is a high diversity of phloem and wood borers across several families in the Coleoptera and Lepidoptera. In the Coleoptera, cerambycid beetles (Cerambycidae), jewel beetles (Buprestidae), bark, ambrosia and pinhole beetles (Curculionidae) and pinworms (Lymexelidae) are some of the most commonly found beetles attacking eucalypts and acacias. In the Lepidoptera, wood moths (Cossidae), ghost moths (Hepialidae) and borers in the Xyloryctidae (subfamily Xyloryctinae) are most common. In contrast to native forests, there is a much more limited range of native insects present in Australian plantations, particularly in exotic *Pinus* spp. plantations, although eucalypt plantations do share some borers in common with native forests. This chapter reviews the importance of these borers in Australian forests primarily from an economic perspective (i.e. those species that cause damage to commercial tree species) and highlights a paucity of native forest species that commonly kill trees relative to the large scales regularly seen in North America and Europe.

16.1 Introduction

We examine the key groups of native phloem and wood borers (collectively referred to as ‘borers’) associated with forests in the Mediterranean regions of Australia (as defined in Chap. 1). The focus of this chapter is on insect borers that tunnel into the

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phloem, sapwood and heartwood of living trees for at least part of their lifecycle, but with some reference to saproxylic insects that use dead or dying standing trees or dead fallen wood as hosts where relevant. We also focus on borer species that have economic impacts on Australian forests, reflecting the larger amounts of published literature on these species in comparison to other borers.

Forests in the Mediterranean regions are located in the southwest of Western Australia and the southern parts of South Australia, ranging from the region around Adelaide in the north to Mount Gambier in the south and east into parts of southwestern Victoria. The latter zone comprises the 'Green Triangle' region containing extensive *Eucalyptus globulus* and *Pinus radiata* plantation forests. Two tree groups dominate native Mediterranean region forests in Australia: the eucalypts (including the genera *Eucalyptus*, *Corymbia* and *Angophora*) and the genus *Acacia*. The eucalypts typically form the overstorey layer of Mediterranean region forests, with the exception of *Angophora*, which is more usually present in the mid storey. In contrast, acacias occur in the shrub to mid-storey layers. Mediterranean region forests also include other native tree species such as the conifer *Callitris*. Fire plays an extremely important role in the ecology of these forests (Bradstock and Cohn 2002). Eucalypts are well adapted to frequent fire since they can regenerate from lignotubers and epicormic shoots as well as from seed post-fire. Acacias vary in their sensitivity to fire, depending on the species, so their availability as hosts for borers may vary temporally according to the species mix and the fire regime. Plantation forestry is dominated by *Pinus* and *Eucalyptus* monocultures in these regions. *Pinus* is exotic to Australia, while the predominant eucalypt species grown (Tasmanian blue gum; *E. globulus*) is not endemic to the Mediterranean regions of Australia.

The most common and significant borers of both eucalypts and acacias are cerambycid beetles (Coleoptera: Cerambycidae) and wood moths (Lepidoptera: Cossidae). The cerambycid beetles that are most commonly associated with eucalypts are members of the genus *Phoracantha*, many of which have very wide distributions across Australia (Wang 1995, 1998). Species in this genus spend a substantial part of their life cycles feeding in the phloem/cambium, but also bore into the sapwood and/or heartwood, particularly at pupation. Two subfamilies and genera of cossid moths are also common in these forests: species in the genus *Endoxyla* (Lepidoptera: Cossidae: Zeuzerinae) and *Culama* (Cossidae: Cossinae). *Endoxyla* species either form J-shaped tunnels into the sapwood and heartwood of the stems of their hosts and then feed on the callus that forms at the entry to the hole (Lawson et al. 2002; Monteith 1991), or they feed on the roots of the host (Common 1990). Species in the genus *Culama* feed mainly in the cambium but may also bore into the sapwood/heartwood (Elliott et al. 1998).

In addition to cerambycid beetles, other common coleopteran borers to Mediterranean regions are the ambrosia and pinhole borers (Platypodidae and Curculionidae: Scolytinae), pinworms (Lymexylidae), jewel beetles (Buprestidae) and weevils (Curculionidae). Within the Lepidoptera, xyloryctid wood moths (Xyloryctidae) and ghost moths (Hepialidae) are prevalent in this region (Elliott et al. 1998). Termites (Isoptera) are also a very common feature in Mediterranean region forests and are an important functional component of Australian native forests and woodlands. However, termites are not economically important in Mediterranean forests and so are not included in this review. We discuss economically important borers in the following section, grouped by host tree genera (eucalypts, acacia) and by insect taxonomic classification.

Borers found in Australia's Mediterranean forests are summarised in Table 16.1.

16.2 Impact of Borers in Native and Planted Forests

Borers are major pests of hardwood, softwood and mixed forests in the tropics, subtropics and temperate areas around the globe (Ciesla 2011; Nair 2007; Wylie and Speight 2012). Australia has very few phloem and woodborers that are tree killers on a regular or extensive basis in comparison to North America and Europe (Ohmart 1989). To date, Australia has also been fortunate in not being subject to incursions of invasive borers into our native forests, in comparison with, for example, the USA where the invasion of insects such as the emerald ash borer (*Agrilus planipennnis*) is having devastating impacts on forests (Herms and McCullough 2014). One potential reason for the lack of incursions is the high degree of endemism of tree species in Australian native forests. Only a handful of eucalypt species occur naturally outside Australia, whereas Eurasia and North America share many tree genera, providing a much greater potential for invasives to find suitable hosts when they arrive.

The major threats to Australia involve host range expansion of overseas endemic borers onto plantations of eucalypts and acacias, with subsequent invasion into Australia via pathways such as wood packaging (e.g. pallets and dunnage). Two examples of such host expansions overseas are the cossid moths *Coryphodema tristis* in South Africa and *Chilecomadia valdiviana* in Chile (Adam et al. 2013; Boreham 2006; Degefu et al. 2013; Gebeyehu et al. 2005; Kliejunas et al. 2001; Lanfranco and Dungey 2001), both of which have been recorded extensively damaging *E. nitens* plantations in those countries. Similar threats to Australia exist from southeast Asia, where a number of endemic polyphagous borers have been recorded attacking both eucalypts, including *Sarathrocera lowi*, *Aristobia* spp. (Coleoptera: Cerambycidae) and *Zeuzera coffeae* (Lepidoptera: Cossidae; Thu et al. 2010), and acacias, such as the cerambycid beetle *Xystrocera festiva* on *A. mangium* in the central highlands of Vietnam (Thu PQ pers. comm. 2015). Many of these borers are extreme generalists, with very wide host ranges that enable host-switching under favourable circumstances, such as the presence of extensive areas of plantation monocultures in close proximity to native hosts. Invasions of borers such as these into Australia could have significant detrimental effects on forest ecosystems (including on the diversity of endemic borers and their hosts) and on the viability of eucalypt and acacia plantations.

Table 16.1 Summary of native borers recorded in Mediterranean regions of Australia

Host tree	Order/Family/Species	Region	Damage	Severity
Eucalyptus	***Coleoptera***			
	Cerambycidae			
	Phoracantha acanthocera	WA	Stems	+++
	Phoracantha spp.	WA, SA	Stems	++
	Epithora dorsalis	SA	Stressed trees	++
	Coptocercus ribripes	SA, WA	Dying trees	++
	Hesthesis cingulatus	SA, WA	Stems	++
	Scolytinae, Platypodidae			
	Pinhole borers	WA	Stems	+
	Lymexelidae			
	Atractocerus spp.	WA	Stems	+++
	Buprestidae			
	Cisseis fascigera	WA	Stems, Branches	+
	Bostrichidae			
	Bostrychopsis jesuita	SA, WA	Branches	+
	Curculionidae			
	Rhadinosomus lacordairei	WA	Lower stems	++
	Lepidoptera			
	Cossidae			
	Culama sp.	WA	Stems	+
	Xyloryctidae			
	Cryptophasa unipunctata	WA	Stems	+
	Hepialidae			
	Aenetus spp.	SA, WA	Stems	+
	Abantiades hyalinatus	WA	Roots	+
Acacia	***Coleoptera***			
	Cerambycidae			
	Rhytiphora spp.	SA, WA	Stems, Branches	+
	Buprestidae			
	Agrilus spp.	SA, WA	Branches	+
	Melobasis spp.	SA, WA	Branches	+
	Bostrichidae			
	Bostrychopsis jesuita	SA, WA	Branches	+
	Curculionidae			
	Chrysolopus spectabilis	SA	Root collar, Stem	++
	Lepidoptera			
	Cossidae			
	Endoxyla lituratus	SA, WA	Stems, Branches	+
	Endoxyla leucomochla	SA	Roots	+
	Catoxophylla cyanauges	SA	Unknown	+
	Xyloryctidae			
	Maroga spp.	SA	Stems	+

(continued)

Table 16.1 (continued)

Host tree	Order/Family/Species	Region	Damage	Severity
Callitris	***Coleoptera***			
	Buprestidae			
	Diadoxus erythrurus	SA, WA	Stems	++
Pinus	***Coleoptera***			
	Cerambycidae			
	Cacodacnus planicollis	SA	Decaying stems	+

16.2.1 Borers of Eucalyptus

16.2.1.1 Coleoptera

Cerambycidae

Beetles in the subfamily Cerambycinae, tribe Phoracanthini, form the most prominent group of cerambycid beetles associated with eucalypt forests in Australia, including those forests in the Mediterranean regions. The predominant genus is *Phoracantha*, with more than 40 species described in Australia, 16 of which occur in forests within Mediterranean regions (Wang 1995, 1998; Table 16.2). *Phoracantha* spp. can essentially be divided into two feeding guilds: those that attack and reproduce in living trees and those that reproduce in dead, dying or moribund trees. Prior to the taxonomic revision by Wang (1995), these two groups roughly aligned with the genera *Tryphocaria* and *Phoracantha. Phoracantha semipunctata* and *P. recurva* (Table 16.2) have invaded extensively around the world to become significant pests in many countries where eucalypts have been planted (Paine et al. 2011). In Australia, these two species generally attack stressed, dead or dying trees and have seldom caused damage in native forests or plantations. Other *Phoracantha* species in Australia preferentially attack living trees, with *P. acanthocera*, *P. mastersi* and *P. solida* amongst the most common and damaging of these beetles (Carnegie et al. 2008; Hayes et al. 2014; Lawson et al. 2002; Nahrung et al. 2014).

Two of the most significant *Phoracantha* species that attack living trees in Australian Mediterranean regions are *P. acanthocera* and *P. mastersi*. These two species display dissimilar reproductive and life-history strategies; *P. acanthocera* deposits eggs singly and larvae feed solitarily in the phloem and cambium, and bore extensively into the heartwood while *P. mastersi* deposits many eggs at once and the larvae are gregarious feeders (Wang 1995). The biology of these borers have not been extensively studied, but both have 2–3 year lifecycles (Wang 1995). Adults of *P. acanthocera* are active from October to January and *P. mastersi* from November to March (Wang 1995). Both species have very wide host ranges and can cause considerable degrade to timber value. In the Mediterranean region of Western Australia, *P. acanthocera* has been associated with significant damage and loss of value of production in regrowth forests of karri (*Eucalyptus diversicolor*) and to a lesser extent marri (*Corymbia calophylla*) (Abbott et al. 1991: Farr et al. 2000; Farr

Table 16.2 *Phoracantha* species recorded in Mediterranean regions of Australia (From Wang 1995)

Eucalypt hosts	Species	Region(s)
Dead and dying trees	*P. semipunctata*	WA, SA
	P. recurva	WA, SA
	P. punctate	WA, SA
	P. impavida	WA
Living trees	*P. mastersi*[a]	SA
	P. acanthocera[a]	WA, SA
	P. synonyma	WA, SA
	P. odewahni[a]	WA, SA
	P. lata	SA
	P. rugithoracica	SA
	P. flavopicta	SA
Host status unknown	*P. grallaria*[a]	SA
	P. punctipennis[a]	WA
	P. porosa	SA
	P. tricuspis	SA
	P. obscura	WA, SA

WA Western Australia; *SA* South Australia

[a] Formerly in the genus *Tryphocaria*

2010). Higher incidence of *P. acanthocera*-associated damage was associated with poor quality karri sites. Dry sites in close proximity to jarrah/marri forest and small coupes were also found to be more prone to *P. acanthocera* attack (Farr et al. 2000). Within the more susceptible sites, larger trees were more likely to be attacked.

Phoracantha impavida and *P. semipunctata* have been implicated in dieback of tuart (*E. gomphocephala*) forests in the southwest of Western Australia (Ruthrof et al. 2002; Seaton 2012). Dieback in these forests appears to be a result of a highly complex interaction of long-term rainfall decline, forest fragmentation and altered fire and other forest management practices, with a resultant increase in tree stress and decline in forest health. *P. impavida* and *P. semipunctata* are considered to be only secondarily associated with dieback (i.e they are responding to other factors that initiate dieback) but, nevertheless, are highly damaging agents of decline in these forests. *Phoracantha semipunctata* is known to only attack highly stressed, dying or dead trees in Australia (Elliott et al. 1998).

Cerambycid borers in *E. globulus* plantations in Western Australia and the Green Triangle have not been recorded as significant pests. In both these regions, minor damage to drought-stressed or older plantations has been associated with species of *Phoracantha*, probably *P. semipunctata* (Matsuki and Tovar 2012). This finding is backed up by Smith et al. (2008), who recorded *Phoracantha* spp. borers, including *P. acanthocera*, predominantly damaging trees greater than 6 years of age, especially in drought stressed or overstocked plantations.

A number of other phoracanthine genera occur in the native Mediterranean forests of South Australia and Western Australia. These include species in the genera

Epithora, *Coptocercus*, *Hesthesis*, *Paratesta*, *Steata*, *Phytrocaria*, *Allotisis*, *Atesta*, and *Coleocoptus* (Wang et al. 1996). Among these, *Epithora dorsalis* is known to attack stressed and dying eucalypts in South Australia, particularly *E. obliqua* (Bashford 1994; Elliott et al. 1998). *Coptocercus* spp. commonly occur in eucalypt forests and almost all species reproduce in dead or dying trees, including *Coptocercus ribripes*, which is perhaps the most widely distributed species in South Australia and Western Australia (Elliott et al. 1998). Of the other species, *Hesthesis cingulatus* (Hesthesini) has a wide distribution in both South Australia and Western Australia and is known to attack young eucalypts, occasionally severing young stems (Elliott et al. 1998).

Bark Beetles, Ambrosia Beetles and Pinworms (Platypodinae, Scolytinae and Lymexelidae)

Australia is fortunate in that it lacks the tree-killing bark and wood boring insects that routinely induce large-scale tree mortality in the northern hemisphere. This may be due to the slower evolution of tree-killing behaviour of borers that attack hardwoods as compared to those that attack softwoods (e.g. bark beetles; Ohmart 1989) or differences in the physiological response to attack between conifers and hardwoods. These effects may be exacerbated by the dominance of hardwoods in Australia's forests, as compared to Eurasia and North America where conifers proliferate. While Australia does not have tree-killers on the scale of some other continents, degradation of timber quality associated with boring beetles still occurs, although predominantly in temperate and subtropical forests of eastern Australia rather than in Mediterranean region forests. For example, stem defect in at least 19 species of *Eucalyptus* in Victoria has been linked to the platypodid *Austroplatypus incompertus* (Harris et al. 1976; Kent 2002; Kent 2008; Kent and Simpson 1992). The platypodid *Platypus subgranosus*, in conjunction with the fungal pathogen *Chalara australis*, is associated with southern beech (*Nothofagus cunninghamii*) dieback in Tasmania (Elliott et al. 1987; Kile and Hall 1988; Packham et al. 2008). Little has been reported in the literature regarding specific scolytid and platypodid damage in Australia's Mediterranean forests, but pinhole borer damage has been observed in sawlogs from the jarrah (*E. marginata*) and karri (*E. diversicolor*) forests of southwest Western Australia (Abbott et al. 2003; Donnelly and Davison 2008). Lymexelid pinworm borers (*Atractocerus kreuslerae*, *A. crassicornis*) are prevalent in the southwest region of Western Australia and are a commercially significant pest of eucalypts there (Clark 1925; Elliott et al. 1998). Lymexelid borers attack weakened or dead trees, with the larvae feeding on the ambrosia fungus that itself has been associated with Tuart (*E. gomphocephala*) decline in Western Australia (Fox and Curry 1980; Ruthrof et al. 2002).

We could find no reports of bark and ambrosia beetles associated with acacias in Australia's Mediterranean forests.

16.2.1.2 Other Borers

Buprestidae

The Buprestidae is a large and diverse family in Australia. Larvae of these beetles typically feed in the wood, phloem or root systems of trees or shrubs, but some feed in herbaceous stems or galls, or mine leaves (Atlas of Living Australia (a)). Buprestid species are generally associated with dead or dying trees, with only one species (*Cisseis fascigera*) being implicated as a damaging agent of living trees in eucalypt forests. *Cisseis fascigera* is found in Wandoo (*E. wandoo*) forests in southwestern Western Australia, where decline of Wandoo is a significant issue (Hooper et al. 2010; Hooper and Sivasithamparam 2005).

Bostrichidae

Bostrichid beetles (branch and twig borers) are usually associated with dry or seasoned wood. However, *Bostrychopsis jesuita* have been recorded attacking living trees in the Mediterranean forests of Australia, as well as breeding in stressed, dead or dying trees, including eucalypts and acacias (Brimblecombe 1956). *Bostrychopsis jesuita* is one of the largest and most common bostrichid species found in Australia, having an almost continental distribution (Atlas of Living Australia (b)).

Curculionidae

Curculionid species are rarely recorded attacking hardwoods in Australia. The thin strawberry weevil, *Rhadinosomus lacordairei*, occurs in *E. globulus* plantations in the southwest of Western Australia (Loch 2006), and larvae of this species tunnel in the stems of young eucalypt seedlings in Tasmania, causing death and stem breakage at ground level (Elliott et al. 1998).

16.2.1.3 Lepidoptera

Cossidae

Reports of cossid wood moths from the genus *Endoxyla* (Cossidae: Zeuzerinae) (formerly *Xyleutes*) damaging eucalypts in Mediterranean forests are difficult to find, despite being commonly recorded as damaging pests of eucalypt forests and plantations in north-eastern and south-eastern Australia (Harris 1986; Lawson et al. 2002; Lee et al. 2010; McInnes and Carne 1978; Nichols et al. 2010; Ohmart 1990; Stone 1993; Wylie and Peters 1993). Of the other moths in this family, members of the genus *Culama* (Cossidae: Cossinae) occur commonly across Australia, and have been recorded as secondary pests in eucalypt plantations in eastern Australia

(Carnegie et al. 2008; Elliott et al. 1998; Elliott and DeLittle 1985). A species of *Culama* has been associated with Tuart decline in south-western Western Australia (Ruthrof et al. 2002), but species in this genus have not been recorded as pests in the *E. globulus* plantations of southwest Western Australia or the Green Triangle (Matsuki and Tovar 2012; Smith et al. 2008).

Xyloryctidae

Moths in this family have a variety of feeding strategies. Some species feed almost exclusively on the external surface of the bark within a shelter constructed with webbing, faecal pellets and other material. Other species bore extensively into the wood, and construct webbed shelters that cover the entrance hole and surrounding bark. For example, the stem girdler *Cryptophasa unipunctata* causes damage in the southwestern Western Australia Mediterranean region where it is associated with Tuart (*E. gomphocephala*) dieback (Ruthrof et al. 2002).

Hepialidae

Ghost moths (*Aenetus* spp.) are a widely distributed genus of wood-boring moths found across Australia. Unlike most hepialids, which feed on the roots of a variety of plants, species in this genus are arboreal trunk feeders of several tree genera, including *Eucalyptus*. A number of moth species in this genus have been recorded in Mediterranean regions, including *A. tephroptilus*, *A. dulcis*, *A. scripta* and *A. astathes* in southwestern Western Australia and *A. astathes* in the lower southeast of South Australia, although the hosts of these species is unclear (Atlas of Living Australia (c)). Another hepialid, *Abantiades hyalinatus*, a root feeder, attacks *E. globulus* plantations in Western Australia, although the significance of this damage was not recorded (Matsuki and Tovar 2012; Moore 2014). The Bardee Grub, *Trictena atripalpis* also feeds on roots of eucalypts in the Adelaide region of South Australia (Atlas of Living Australia (d)).

16.2.2 Borers of Acacia

16.2.2.1 Coleoptera

It is remarkable that relatively little has been published on the biology and ecology of Coleopteran borers, including the cerambycids, given the prominence in Australian forests of *Acacia* spp. and the diversity and abundance of Coleoptera. This may partly due to the lower economic value of *Acacia* in comparison to *Eucalyptus*, such that pests generally and borers in particular have not gained as much attention. The exceptions are plantation species such as *A. melanoxylon* (Blackwood) in temperate Tasmania that produces very high quality timber, and *A.*

mangium that is grown for woodchips on the Tiwi Islands in the tropics. Even then, most research has been associated with defoliating pests such as the fireblight beetle *Acacicola orphana* (Chrysomelidae) that damages trees such as *A. mearnsii* (Black wattle; Elliott et al. 1998).

Cerambycidae

There are a large number of cerambycid genera associated with acacias in Australia, but very few of these have caused significant damage, with few or no reports of damage in Mediterranean forests. One of the most important genera associated with acacias in Australia is *Rhytiphora* (Cerambycidae: Lamiinae), which has recently been synonymised with several other genera including *Penthea* and *Platyomopsis* (Slipinski and Escalona 2013). In the tropics and subtropics of Australia, adults of *Rhytiphora* (= *Penthea*) *pardalis* shred the bark of stems and branches of a number of *Acacia* spp. with their mandibles prior to laying eggs in the damaged area where the larvae then feed (Elliott et al. 1998). Other species in this genus (formerly *Platyomopsis*) are known as branch and twig girdlers; adults chew and girdle branches allowing larvae to develop in the distal, dying part of the branch (Hockey and De Baar 1988). *Rhytiphora* spp. are known to occur in the Mediterranean regions of Western Australia and South Australia (Atlas of Living Australia (e)), but little information is available concerning the species involved or their host records, although acacia are likely hosts of some species. Other genera such as *Ancita* and *Pachydissus* are associated with acacias in other parts of Australia (Hockey and De Baar 1988), again more often associated with dead or dying trees.

Buprestidae

A number of buprestid genera have been recorded in association with acacias in Australia, but not specifically from Mediterranean forests (e.g. Bashford 1991; Hawkeswood 1986; Turner and Hawkeswood 1997). *Agrilus* and *Melobasis* are two of the most prominent genera that have been associated with acacias elsewhere in Australia and also occur in Western Australia and South Australia. *Agrilus* in particular is a genus that is cosmopolitan and polyphagous and is known to include pest species in other parts of the world, including the emerald ash borer *Agrilus planipennis* (native to China and invasive in the USA) and the varicose borer *Agrilus sexsignatus* (a pest of *Eucalyptus* and other species in Southeast Asia; Wylie and Speight 2012).

Bostrichidae

As mentioned previously, *B. jesuita* is a highly polyphagous species that can attack a number of hardwood species across Australia, including both eucalypts and acacias in the Mediterranean forests of South Australia and Western Australia. These beetles bore circular tunnels in branches and stems (Brimblecombe 1956). Larvae can develop through to adult in dry wood and are capable of reinfesting seasoned timber making them also a pest of timber in service.

Curculionidae

The most well-known curculionid beetle that attacks acacias in Australia is the Diamond beetle or Botany Bar weevil, *Chrysolopus spectabilis*. This species is widely distributed through eastern Australia as well as in the Mediterranean forests around Adelaide in South Australia (Elliott et al. 1998, Atlas of Living Australia website (g)). Adults attack the stem of the tree just above ground level, chewing roughened spots into the bark into which eggs are laid (Frogatt 1923). Tunnelling by the resultant larvae may girdle the tree (Hawkeswood 1991). Attacks can also occur at branch junctions with the main stem and in the forks of branches. The adults are foliage feeders.

16.2.2.2 Lepidoptera

Cossidae

A number of cossid moths are associated with acacias in Mediterranean and other regions in Australia, but most are external root feeders, and so are not true borers. The best known example of a root feeder is *Endoxyla leucomochla*, the Witjititi grub, which is an important food source for indigenous Australians, particularly in central desert regions of Australia (Common 1990; Zborowski and Edwards 2007). *Endoxyla leucomochla* and another cossid with an acacia host, *Catoxophylla cyanauges*, have been recorded from Murray Bridge and Barmera, within the Mediterranean region of South Australia (Tindale 1953). Females of *Catoxophylla cyanauges* are brachypterous (Tindale 1953). The shell wattle goat moth *Endoxyla lituratus* feeds in the trunks and branches of various *Acacia* spp. and has an extremely wide Australian distribution including South Australia and Western Australia (Elliott et al. 1998). The cossid moth fauna associated with acacias in Australia more generally, and in Mediterranean forests in particular, needs further study.

Xyloryctidae

A number of xyloryctid genera and species have been recorded from the Mediterranean regions of Australia: *Xylorycta stereodesma*, *Clerarcha grammatistis* in Western Australia, and *Maroga* (= *Cryptophasa*) *ochroleuca*, *Telecrates desmochrysa*, *Xylorycta argyrota* and *Catoryctis perichalca* in South Australia (Atlas of Living Australia (f)). *Maroga* spp. have known acacia hosts elsewhere in

Australia, so it is likely that at least some records of this genus in South Australia are associated with acacia. Again, there is a paucity of knowledge of the host relationships of the xyloryctine genera in Australia's Mediterranean forests.

16.2.3 Borers of Other Native Trees

16.2.3.1 Callitris (Native Cypress Pine): Cupressaceae

Coleoptera

Buprestidae

The small cypress jewel beetle *Diadoxus erythrurus* is widely distributed across Australia, including in Mediterranean regions (Atlas of Living Australia (g)). It is known to attack and sometimes kill native cypress pines (*Callitris* spp.) as well as introduced *Cupressus* spp. (Elliott et al. 1998; Frogatt 1925; Hadlington and Gardner 1959). Most damage occurs through log degradation if harvested logs, which are its preferred hosts, are not quickly processed after felling.

16.2.3.2 Pinus spp.

Coleoptera

Cerambycidae

The only native cerambycid beetle to have a significant association with a commercially important exotic tree genus in Australia is the pine witchetty grub *Cacodacnus planicollis* (Cerambycidae: Prioninae). The larvae of this beetle infests decaying stumps and logs in pine plantations in South Australia, and has also been recorded from the Mediterranean region of Western Australia, as well the tropics of far north Queensland (Atlas of Living Australia (h)). Generally, it has a beneficial effect in planted forests by enhancing the rate at which stumps and logs decay, thereby enhancing the availability of nutrients for subsequent rotations. Kliejunas et al. (2006) list its main host in Australia as *Pinus radiata*, and while they rate it as the highest pest risk category (category 1) for introduction into the USA, they did not consider it a strong enough threat to conduct a more detailed import risk analysis.

16.3 Discussion

This review highlights the limited knowledge of native borers in the Mediterranean forests of Australia, and in the forests of Australia more generally. Borers in the higher rainfall and higher productivity forests (both native and plantation) of eastern and south-eastern Australia have received somewhat more attention, although there have been limited detailed studies on the biology, ecology and economic significance of wood borers even in these regions. This is a recurring theme with the study of many insects, with the limited research resources available directed to the study of economically important pests, or those that have significant environmental impacts. The exception identified here is in the southwest of Western Australia, where the bullseye borer, *P. acanthocera*, has been relatively well studied in the karri (*E. diversicolor*) and marri (*C. calophylla*) forests, which have high productivity and are economically important timber species (Abbott 1992; Abbott et al. 1991; Farr et al. 2000). In this region, *P. acanthocera* is associated with significant degrade to wood quality in karri regrowth forests (Abbott et al. 1991; Farr et al. 2000) and occurs at high incidences, ranging from 24 % to 78 % of trees attacked across a number of sites of varying quality. Regrowth karri is managed as even-aged stands (Rayner 1991), mimicking to some extent even-age monoculture plantation forests, and potentially contributing to the enhanced pest status of this borer in these forest by providing an abundance of suitable hosts. While *P. acanthocera* has been identified as a significant borer affecting timber quality in this region, there has been little follow-up research on management to mitigate the hazard with the exception of Abbott et al. (1991), who suggested thinning of regrowth stands. *Phoracantha acanthocera* has a very wide distribution across the continent and has been identified as an important pest in eucalypt plantations and native forests in eastern and south-eastern Australia (e.g. Carnegie et al. 2008; McInnes and Carne 1978; Phillips 1993; Stone 1993; Wylie and Peters 1993).

In the southwest of Western Australia, borers have been associated with two significant tree decline problems with tuart (*E. gomphocephala*) and wandoo (*E. wandoo*). However, the role of borers (and pathogens) in these declines is most likely secondary, with a complex array of other factors, including long-term decline in rainfall, changed disturbance regimes (particularly in relation to fire) and fragmentation of these forest landscapes due to agricultural and urban expansion acting as primary causes (Ruthrof et al. 2002).

Cerambycid borers in particular are thought to respond to tree stress, as has been well documented for *P. semipunctata* outside Australia (Caldeira et al. 2002; Hanks et al. 1999) and to some extent in *E. globulus* plantations in Western Australia (Matsuki and Tovar 2012; Tovar pers. comm.) However, the biology of other *Phoracantha* spp. and cossid wood moths that are obligate feeders of living hosts appears to be more complex, although tree stress may still play a role in increasing susceptibility to attack. Trees growing in Mediterranean regions, with hot dry summers, may thus be more susceptible to these borers, but much more research is required to tease out these causal factors. Recent research focusing on *P. solida*, *P. acanthocera* and *E. cinereus* in the subtropics of eastern Australia is beginning to shed more light on some of these drivers (Debuse et al. 2012; Hayes et al. 2014; Nahrung et al. 2014; Debuse et al. in preparation).

There is little information on borers of economic significance for the Mediterranean forests of South Australia. Of all the Australian states, South

Australia had the smallest native forest resource at the time of European colonisation, which was rapidly utilised for development as the colony grew. The emphasis in South Australia since the late nineteenth century therefore has been to develop plantations to supply the State's timber needs (Boardman 1988). Plantations were dominated by *Pinus radiata* until the 1990s, after which there was an expansion in the *E. globulus* estate. Native borers have not been recorded as significant pests in either of these plantation estates, although a native cerambycid, *C. planicollis* appears to play an important role in the decomposition process of large diameter stumps and slash in pine plantations. *Phoracantha* spp. have also been recorded as minor pests in the *E. globulus* plantations of South Australia, mainly in areas of poor site quality and under drought conditions (Matsuki and Tovar 2012; Smith et al. 2008).

Despite the ubiquity of acacias in Australian native forest landscapes, the fauna of borers associated with acacias is even less well known than for the eucalypts. In part this may be because acacias are less economically important than eucalypts, with only a relatively few species of commercial significance nationally, and none within the Mediterranean forests of Western Australia and South Australia. Some cerambycid beetles, particularly those in the genus *Rhytiphora*, are capable of causing considerable damage to acacias, including tree mortality, but very little is known of the biology and ecology of these species.

The paucity of literature on the biology, ecology and impact of borers on eucalypts and acacias in Australia's Mediterranean forests translates to scant information on the roles the borers play in the ecology of these forests, and how they may interact with fire and other management practices. Recent overseas research indicates that cerambycid beetles in particular may be good bioindicators of forest biodiversity and management practices (Maleque et al. 2009), and this could be a future avenue to investigate their roles in Australian forests. Good tools are now available in the form of generic pheromones/kairomones that can be used to trap a wide range of species (e.g. Hanks et al. 2012), which would assist in both cataloguing the species present in these forests and understanding their relationships to various forest attributes.

One of the more striking features of the native Australian borer fauna is the lack of species capable of causing widespread forest mortality. Outbreaks of bark beetles such as the mountain pine beetle (*Dendroctonus ponderosae*) in the USA and Canada have killed host trees over millions of hectares of forest (Negron and Fettig 2014), while other *Dendroctonus* and *Ips* spp. regularly outbreak over large areas. Australia's forests are dominated by broadleaved hardwood species and while Australia has a diverse fauna of scolytid and platypodid beetles associated with these forests, none have been recorded as tree killers in the way that is common for scolytids in conifer-dominated forests. For some of the bark and ambrosia beetles, co-evolution with pathogenic fungi has been important in developing this capability, although the relative importance of the fungal association in the tree-killing habit has been debated (Six and Wingfield 2011). The tree-killing habit does not appear to have evolved to the same degree in scolytids and platypodids that are associated with hardwoods worldwide, so it is not necessarily surprising that the same is true for Australia. However, some Australian cerambycid beetles, e.g. *P. acanthocera* have been shown to be associated with *Ceratocystis* spp. fungi (Nkuekam et al. 2012; Van Wyk et al. 2007), many species of which are known plant pathogens. Whether these relationships between *Phoracantha* and *Ceratocystis* are obligate or not is not known and should be a focus for future research. A potential risk for Australian forests is accidental introduction of more virulent overseas pathogens, including *Ceratocystis* spp. that could then be vectored by native borers in novel-encounter interactions. For example, a number of new records of pathogens are now being found on eucalypt species overseas (Chen et al. 2013; Van Wyk et al. 2009). Similar associations with pathogens evolving on acacias overseas are also being discovered (Griffin et al. 2015), posing a threat to native Australian acacias, although very little is known in regard to fungi associated with borers on acacias in Australia.

In summary, knowledge of the fauna, biology and ecology of native borers in the natural and planted forests of Australian Mediterranean regions (and Australia more generally) is poor compared to North American and Europe. An improved knowledge of these borers would inform better management of those species that are already significant pests, such *P. acanthocera*, as well as contribute to a better understanding of the role these insects play in forest ecosystems and how these forests are managed for multiple purposes. Finally, greater knowledge of the interactions of these insects and their associated fungal symbionts/pathogens could assist Australia to prepare for introductions of new pathogens that are vectored by native borers and that threaten Australia's forests and their ecosystems.

References

Abbott I (1992) Ecological implications of insect pests in jarrah and karri forests. CALM Occasional Paper Department of Conservation and Land Management Como, Western Australia 2:77–98

Abbott I, Smith R, Williams M et al (1991) Infestation of regenerated stands of karri (*Eucalyptus diversicolor*) by bullseye borer (*Tryphocaria acanthocera*, Cerambycidae) in Western Australia. Aust For 54:66–74

Abbott I, Burbidge T, Strehlow K et al (2003) Logging and burning impacts on cockroaches, crickets and grasshoppers, and spiders in Jarrah forest, Western Australia. For Ecol Manage 174:383–399

Adam E, Mutanga O, Ismail R (2013) Determining the susceptibility of *Eucalyptus nitens* forests to *Coryphodema tristis* (cossid moth) occurrence in Mpumalanga, South Africa. Int J Geogr Inf Sci 27:1924–1938

Atlas of Living Australia (a) website at http://bie.ala.org.au/species/urn:lsid:biodiversity.org.au:afd.taxon:e765175e-8a10-4ab6-9d72-0bce2b1c1d8e. Accessed 27 Jul 2015

Atlas of Living Australia website (b) at http://bie.ala.org.au/species/Bostrychopsis+jesuita. Accessed 27 Jul 2015

Atlas of Living Australia website (c) at http://bie.ala.org.au/species/Aenetus. Accessed 1 Aug 2015

Atlas of Living Australia website (d) at http://bie.ala.org.au/species/Trictena+atripalpis. Accessed 1 Aug 2015

Atlas of Living Australia website (e) at http://bie.ala.org.au/species/Rhytiphora+%28Platyomopsis%29. Accessed 7 Aug 2015

Atlas of Living Australia website (f) at http://bie.ala.org.au/species/XYLORYCTINAE. Accessed 7 Aug 2015

Atlas of Living Australia website (g) at http://bie.ala.org.au/species/urn:lsid:biodiversity.org.au:afd.taxon:0bcf52bd-a25d-4fd4-af58-eac00395a096. Accessed 8 Aug 2015

Atlas of Living Australia website (h) at http://bie.ala.org.au/species/Cacodacnus+planicollis#. Accessed 8 Aug 2015

Bashford R (1991) Wood-boring coleoptera and associated insects reared from *Acacia dealbata* in Tasmania. J Aust Entomol Soc 18:103–109

Bashford R (1994) Life history and mortality of the longicorn *Epithora dorsalis* Macleay (Coleoptera: Cerambycidae) in Tasmania. J Aust Entomol Soc 21:125–136

Boardman R (1988) Living on the edge – the development of silviculture in South Australian pine plantations. Aust For 51:135–156

Boreham GR (2006) A survey of cossid moth attack in *Eucalyptus nitens* on the Mpumalanga highveld of South Africa. South Afr For J 206:23–26

Bradstock RA, Cohn JS (2002) Fire regimes and biodiversity in semi-arid ecosystems. In: Bradstock RA, Williams JE, Gill MA (eds) Flammable Australia: the fire regimes and biodiversity of a continent. Cambridge University Press, Cambridge, p 462

Brimblecombe RA (1956) Destructive wood borers and their damage. Department of Agriculture & Stock, Division of Plant Industry, Brisbane

Caldeira MC, Fernandez V, Tome J et al (2002) Positive effect of drought on longicorn borer larval survival and growth on eucalyptus trunks. Ann For Sci 59:99–106

Carnegie A, Lawson SA, Smith T et al (2008) Healthy hardwoods. A field guide to pests, diseases and nutritional disorders in subtropical hardwoods. Forest and Wood Products Australia, Melbourne, 140 pp

Chen S, Van Wyk M, Roux J et al (2013) Taxonomy and pathogenicity of *Ceratocystis* species on *Eucalyptus* trees in South China, including *C. chinaeucensis* sp. nov. Fungal Divers 58:267–279

Ciesla W (2011) Forest entomology. Wiley-Blackwell, Hoboken, 416 pp

Clark J (1925) Forest pests. The pin-hole borer (*Attractocerus kreuslerae* Pasc.). J Agric West Aust 2:138–142

Common IFB (1990) Moths of Australia. Brill Academic Publication, Leiden, 535 pp

Debuse V, Nahrung H, Smith T et al (2012) Patterns and processes affecting stem boring insects in subtropical hardwood plantations. In: Proceedings of the Australian forest growers national conference 2012, Australian Forest Growers

Degefu DT, Hurley BP, Garnas J et al (2013) Parallel host range expansion in two unrelated cossid moths infesting *Eucalyptus nitens* on two continents. Ecol Entomol 38:112–116

Donnelly D, Davison E (2008) Comparison of the occurrence of rot in sawlogs from regrowth and mature stands of *Eucalyptus diversicolor* (karri). Aust For 71:27–32

Elliott HJ, DeLittle DW (1985) Insect pests of trees and timber in Tasmania. Forestry Commission, Tasmania, Hobart

Elliott HJ, Kile GA, Candy SG et al (1987) The incidence and spatial pattern of *Nothofagus cunninghamii* (Hook.) Oerst. attacked by *Platypus subgranosus* Schedl in Tasmania's cool temperate rainforest. Aust J Ecol 12:125–138

Elliott HJ, Ohmart CP, Wylie FR (1998) Insect pests of Australian forests: ecology and management. Inkata Press, Melbourne, 214 pp

Farr JD (2010) Bullseye borer (*Phoracantha acanthocera*) in karri. Department of Environment and Conservation Western Australia Information Sheet 37/2010

Farr JD, Dick SG, Williams MR et al (2000) Incidence of bullseye borer (*Phoracantha acanthocera*, (Macleay) Cerambycidae) in 20–35 year old regrowth karri in the south west of Western Australia. Aust J Ecol 63:107–123

Fox J, Curry S (1980) Notes on the tuart tree (*Eucalyptus gomphocephala*) in the Perth area. W Aust Nat 14:174–186

Frogatt WW (1923) Forest insects of Australia. Government Printer, Sydney

Frogatt WW (1925) Forest insects no 10. The cypress pine weevil (*Diadoxus erythrurus* White). Aust For J 8:174–177

Gebeyehu S, Hurley BP, Wingfield MJ (2005) A new lepidopteran insect pest discovered on commercially grown *Eucalyptus nitens* in South Africa. S Afr J Sci 101:26–28

Griffin AR, Nambiar ES, Harwood CE et al (2015) Sustaining the future of *Acacia* plantation forestry – a synopsis. S For J For Sci 77:v–viii

Hadlington P, Gardner MJ (1959) *Diadoxus erythuris* (White) (Coleoptera: Buprestidae), attack on fire-damaged *Callitris* spp. Proc Linnean Soc NSW 84:325–331

Hanks LM, Paine TD, Millar JG et al (1999) Water relations of host trees and resistance to the phloem-boring beetle *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). Oecologia 119:400–407

Hanks LM, Millar JG, Mongold-Diers JA et al (2012) Using blends of cerambycid beetle pheromones and host plant volatiles to simultaneously attract a diversity of cerambycid species. Can J For Res 42:1050–1059

Harris JA (1986) Wood moth damage in mountain ash logs. Aust For 49:246–248

Harris JA, Campbell KG, Wright GM et al (1976) Ecological studies on the horizontal borer *Austroplatypus incompertus* (Schedl) (Coleoptera: Platypodidae). J Entomol Soc Aus NSW 9:11–21

Hawkeswood TJ (1986) New larval host records for eight Australian jewel beetles (Coleoptera, Buprestidae). G Ital Entomol 3:173–177

Hawkeswood TJ (1991) Review of the history, biology and host plants of the Australian weevil *Chrysolopus spectabilis* (Fabricius). Spixiana 14:17–25

Hayes RA, Piggott AM, Smith TE et al (2014) *Corymbia* phloem phenolics, tannins and terpenoids: interactions with a cerambycid borer. Chemoecology 24:95–103

Herms DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Ann Rev Entomol 59:13–30

Hockey M, De Baar M (1988) New larval food plants and notes for some Australian Cerambycidae (Coleoptera). Aust Entomol Mag 15:59–66

Hooper RJ, Sivasithamparam K (2005) Characterization of damage and biotic factors associated with the decline of *Eucalyptus wandoo* in southwest Western Australia. Can J For Res 35:2589–2602

Hooper RJ, Wills A, Shearer BL et al (2010) A redescription and notes on biology of *Cisseis fascigera* Obenberger (Coleoptera: Buprestidae) on declining *Eucalyptus wandoo* in southwestern Australia. Aust J Entomol 49:234–244

Kent D (2002) Biology of the ambrosia beetle *Austroplatypus incompertus* (Schedl). Aust J Entomol 41:378–378

Kent DS (2008) Distribution and host plant records of *Austroplatypus incompertus* (Schedl) (Coleoptera: Curculionidae: Platypodinae). Aust Entomol 35:1–6

Kent DS, Simpson JA (1992) Eusociality in the beetle *Austroplatypus incompertus* (Coleoptera: Curculionidae). Naturwissenschaften 79:86–87, 10.1007/BF01131810

Kile GA, Hall MF (1988) Assessment of *Platypus subgranosus* as a vector of *Chalara australis*, causal agent of a vascular disease of *Nothofagus cunningha*mii. N Z J For Sci 18:166–186

Kliejunas JT, Tkacz BM, Burdsall HH Jr et al (2001) Pest risk assessment of the importation into the United States of unprocessed *Eucalyptus* logs and chips from South America. Gen Tech Rep – Forest Prod Lab, USDA For Serv (FPL-GTR-124), 134 pp

Kliejunas JT, Burdsall HH, DeNitto GA et al (2006) Pest risk assessment of the importation into the United States of unprocessed *Pinus* logs and chips from Australia. USDA For Serv FHTET 2006–06, 157 pp

Lanfranco D, Dungey HS (2001) Insect damage in *Eucalyptus*: a review of plantations in Chile. Austral Ecol 26(5):477–481

Lawson SA, Wylie FR, Wylie RL et al (2002) Longicorn beetles (*Phoracantha* spp.) and giant wood moths (*Endoxyla* spp.): emerging threats in tropical and subtropical eucalypt plantations in Queensland, Australia. In: Proceedings of the IUFRO FAO workshop on pest management in tropical forest plantations, Chanthaburi, Thailand 25, 29 May 1998. FORSPA Publication. 2002, No.30, 33 45; 17 ref., 2002. FAO Regional Office for Asia and the Pacific, Bangkok

Lee D, Huth J, Osborne D et al (2010) Selecting hardwood taxa for wood and fibre production in Queensland's subtropics. Aust For 73:106–114

Loch AD (2006) Phenology of Eucalyptus weevil, *Gonipterus scutellatus* Gyllenhal (Coleoptera: Curculionidae), and chrysomelid beetles in *Eucalyptus globulus* plantations in south-western Australia. Agric For Entomol 8:155–165

Maleque MA, Maeto K, Ishii HT (2009) Arthropods as bioindicators of sustainable forest management, with a focus on plantation forests. Appl Entomol Zool 44:1–11

Matsuki M, Tovar F (2012) Field guide for *Eucalyptus globulus* plantations in Western Australia and the green triangle. CRC for Forestry and IPMG, Hobart, 66 pp

McInnes RS, Carne PB (1978) Predation of cossid moth larvae by yellow-tailed black cockatoos causing losses in plantations of *Eucalyptus grandis* in north coastal New South Wales. Aust Wldlf Res 5:101–121

Monteith G (1991) The life and times of the giant wood moth. Wldlf Aust 28:8–10

Moore MD (2014) Two further new species of '*Abantiades*' herrichschaffer (Lepidoptera: Hepialidae) from Western Australia. Aust Entomol 41:217–231

Nahrung HF, Smith TE, Wiegand AN et al (2014) Host tree influences on longicorn beetle (Coleoptera: Cerambycidae) attack in subtropical *Corymbia* (Myrtales: Myrtaceae). Environ Entomol 43:37–46

Nair KS (2007) Tropical forest insect pests: ecology, impact, and management. Cambridge University Press, Cambridge, 424 pp

Negron JF, Fettig CJ (2014) Mountain pine beetle, a major disturbance agent in US Western coniferous forests: a synthesis of the state of knowledge. For Sci 60:409–413

Nichols JD, Smith RGB, Grant J et al (2010) Subtropical eucalypt plantations in eastern Australia. Aust For 73:53–62

Nkuekam GK, Wingfield MJ, Mohammed C et al (2012) *Ceratocystis* species, including two new species associated with nitidulid beetles, on eucalypts in Australia. Antonie Van Leeuwenhoek 101:217–241

Ohmart CP (1989) Why are there so few tree-killing bark beetles associated with angiosperms? Oikos 54:242–245

Ohmart CP (1990) Insect pests in intensively-managed eucalypt plantations in Australia: some thoughts on this challenge to a new era in forest management. Aust For 53:7–12

Packham JM, Elliott HJ, Bashford R (2008) Rate of spread of myrtle wilt disease in undisturbed Tasmanian rainforests. Aust For 71:64–69

Paine TD, Steinbauer MJ, Lawson SA (2011) Native and exotic pests of *Eucalyptus*: a worldwide perspective. Ann Rev Entomol 56:181–201

Phillips CL (1993) Insect pest problems of eucalypt plantations in Australia. 5. South Australia. Aust For 56:378–380

Rayner M (1991) Site index and dominant height growth curves for regrowth karri (*Eucalyptus diversicolor* F. Muell.) in south-western Australia. For Ecol Manage 44:261–283

Ruthrof K, Yates C, Loneragan W (2002) The biology of tuart. In: Keighery BJ, Longman VM (eds) Tuart (*Eucalyptus gomphocephala*) and tuart communities. Wildflower Society of Western Australia, Nedlands, pp 108–122

Seaton S (2012) The interaction of drought and the outbreak of *Phoracantha semipunctata* (Coleoptera: Cerambycidae) on tree collapse in the Northern Jarrah (*Eucalyptus marginata*) forest. Thesis, Murdoch University, Perth

Six DL, Wingfield MJ (2011) The role of phytopathogenicity in bark beetle-fungus symbioses: a challenge to the classic paradigm. Ann Rev Entomol 56:255–272

Slipinski A, Escalona H (2013) Australian longhorn beetles (Coleoptera: Cerambycidae) volume 1: introduction and subfamily lamiinae. CSIRO Publishing, Clayton, 504 pp

Smith D, Smith I, Collett N (2008) A field guide to plantation health surveillance in Victoria. Victoria Department of Primary Industry, Melbourne, 90 pp

Stone C (1993) Insect pest problems of eucalypt plantations in Australia. 2. New South Wales. Aust For 56:363–369

Thu PQ, Griffiths M, Pegg GS et al (2010) Healthy plantations. A field guide to pests and pathogens of *Acacia*, *Eucalyptus* and *Pinus* in Vietnam. Queensland Department of Employment, Economic Development and Innovation, Brisbane, 124 pp

Tindale NB (1953) On some Australian Cossidae including the moth of the witjuti (witchety) grub. Trans Roy Soc S Aust 76:56–65

Turner J, Hawkeswood T (1997) Acacia spectabilis A. Cunn. ex Benth. (Mimosaceae), a new larval host plant for Agrilus australasiae Laporte & Gory (Coleoptera: Buprestidae) from Australia. Mauritiana 16:313–315

van Wyk M, Pegg G, Lawson S et al (2007) *Ceratocystis atrox* sp. nov. associated with *Phoracantha acanthocera* infestations on *Eucalyptus grandis* in Australia. Aust Plant Pathol 36:407–414

Van Wyk M, Wingfield BD, Mohali S et al (2009) *Ceratocystis fimbriatomima*, a new species in the *C. fimbriata* sensu lato complex isolated from *Eucalyptus* trees in Venezuela. Fungal Divers 34:175–185

Wang Q (1995) A taxonomic revision of the Australian genus *Phoracantha* Newman (Coleoptera: Cerambycidae). Invertebr Taxon 9:865–958

Wang Q (1998) The phoracanthine beetles (Coleoptera: Cerambycidae: Ceramby-cinae). Invertebr Taxon 12:667–684

Wang Q, Thornton I, New T (1996) Biogeography of the phoracanthine beetles (Coleoptera: Cerambycidae). J Biogeog 23:75–94

Wylie FR, Peters BC (1993) Insect pest problems of eucalypt plantations in Australia. 1. Queensland. Aust For 56:358–362

Wylie FR, Speight R (2012) Insect pests in tropical forestry. CAB International, Oxford, 376 pp

Zborowski P, Edwards T (2007) A guide to Australian moths. CSIRO Publishing, Clayton, 224 pp

Chapter 17
Invasive Insects in Mediterranean Forest Systems: Australia

Helen F. Nahrung, Andrew D. Loch, and Mamoru Matsuki

Abstract The Mediterranean forest regions of Australia predominantly comprise native mallee scrub, eucalypt woodlands, exotic *Pinus* plantations, and commercial eucalypt plantations. Native forests have, so far, remained largely free of invasive exotic insects. The exotic pines, however, have five well-established and significant invasive pest insects: the bark beetles *Ips grandicollis*, *Hylastes ater*, and *Hylurgus ligniperda* (Coleoptera: Curculiondae), Monterey pine aphid, *Essigella californica* (Hemiptera: Aphididae), and Sirex woodwasp, *Sirex noctilio* (Hymenoptera: Siricidae), with the latter not yet present in Western Australia (WA). The exotic giant pine scale, *Marchalina hellenica* (Hemiptera: Margarodidae), was recently detected on pines in Adelaide and Melbourne and is under an eradication program. Many of the established pest species have had classical biological control programs implemented. European house borer, *Hylotrupes bajulus* (Coleoptera: Cerambycidae), a pest of untreated softwood, is established in areas around Perth, WA, and has been found in dead and live trees, as well as untreated timber. African black beetle, *Heteronychus arator* (Coleoptera: Scarabaeidae) is a major exotic agricultural and forestry pest in wetter parts of the Mediterranean forest regions in WA, where it was first recorded in 1938. Several other exotic polyphagous horticultural pests are occasionally associated with eucalypts. Australia is the origin of major insect pests on *Eucalyptus* species grown in Mediterranean regions across the globe. However, populations of these insects are generally effectively controlled by native species of natural enemies in Australia. At least five species endemic to eastern Australia, *Gonipterus platensis* and *G.* sp. nov. 2, (Coleoptera: Curculionidae), *Paropsisterna m-fuscum* (Coleoptera: Chrysomelidae), *Phylacteophaga froggatti* (Hymenoptera: Pergidae) and *Cardiapsina fiscella* (Hempitera: Psyllidae), have been introduced to Mediterranean regions of WA, where they initially caused exten-

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sive and severe damage to plantations of introduced eucalypt species (predominantly *E. globulus*) in the region. However, the level and extent of damage gradually decreased, and it has been hypothesised that improved control by endemic natural enemies has occurred.

17.1 Introduction

There are two main regions within Australia that have a Mediterranean climate: south-western Australia, encompassing the south-western corner of Western Australia (WA); and southern Australia, including south-eastern parts of South Australia (SA) and south-western Victoria (the "Green Triangle" region), and areas of southern SA (Fig. 17.1). A range of native forests and woodlands occur in these regions, with eucalypts (*Eucalyptus* and *Corymbia*: Myrtaceae) generally being the dominant overstorey species. The greatest concentration of forests occurs in higher

Fig. 17.1 Map of Australia showing the Mediterranean forest regions (*grey*)

rainfall parts of south-western Australia, which includes jarrah (*E. marginata*), marri (*C. calophylla*), karri (*E. diversicolor*), Western Australian blackbutt (*E. patens*) and tuart (*E. gomphocephala*) (Boland et al. 2006). In drier inland areas of south-western Australia, species like wandoo (*E. wandoo*) and salmon gum (*E. salmonophloia*) become more prevalent. Mallee, a shorter and multi-stemmed growth form of some *Eucalyptus* species and other single-stemmed *Eucalyptus* species, become more common in easterly parts of south-western Australia. In addition to eucalypts, *Banksia* spp. (Proteaceae), *Allocasuarina* spp. (Casuarinaceae) and *Nuytsia floribunda* (Loranthaceae), are found in the overstorey and midstorey. Shrubs to small trees in Fabaceae, Myrtaceae, Proteaceae, Ericaceae, Dilleniaceae, Santalaceae, and Goodeniaceae dominate midstorey and understorey. South-western Australia is recognised internationally as an important biodiversity hotspot (Myers et al. 2000), particularly in regard to understorey and heath (Beard et al. 2000). Sugar gum (*E. cladocalyx*) is endemic to southern parts of SA where it typically grows with yellow gum (*E. leucoxylon*), grey box (*E. macrocarpa*) and other species, including *E. baxteri*, *Banksia* spp. and *Allocasuarina* spp. Swamp gum (*E. ovata*), messmate stringybark (*E. obliqua*), and Blackwood (*Acacia melanoxylon*: Fabaceae) are also found among other eucalypt species in forests and woodlands throughout wetter parts of southern Australia.

The main geographic locations for plantations in Mediterranean climatic regions of Australia include south-western Australia, and the ‘Green Triangle’ region, Mount Lofty Ranges and Kangaroo Island in southern Australia (Gavran 2014). Plantation species in these areas are largely the hardwood, Tasmanian blue gum (*Eucalyptus globulus*), which is principally grown on short rotations for pulp, and the softwoods, radiata pine (*Pinus radiata*) and maritime pine (*P. pinaster*), which are grown on longer rotations for timber. Several other eucalypt species (e.g. *E. smithii*, *E. cladocalyx*, *E. saligna* and *E. nitens*) are also grown as plantations in these areas. In total, there are around 490,000 ha of hardwood and 290,000 ha of softwood plantations in the Mediterranean regions of Australia (Gavran 2014). These plantations have gradually accumulated a variety of invasive insects.

In this chapter, we consider four groups of invasive insects: (i) those which have been accidentally introduced to Australia from overseas (mostly onto exotic host plants – Tables 17.1 and 17.2); (ii) Australian endemic insects that have become invasive within Australia following the establishment of hosts (eucalypts) outside their natural range (Table 17.3); (iii) Australian endemic insects that have been accidentally introduced overseas to eucalypts grown in Mediterranean regions as exotics (Table 17.5); and (iv) insects that are not present in Australia but have records of causing significant damage in the Mediterranean forests outside of Australia (Table 17.5). We also discuss insects that have been deliberately released and successfully established as classical biological control agents for exotic pests.

Table 17.1 Exotic insects associated with eucalypts established in Mediterranean forest regions of Australia, their origin and feeding guild

Species	Order: Family	Origin	Year	Feeding guild
Asynonychus cervinus	Coleoptera: Curculionidae	South America	<1939	Defoliator
Atrichonotus taeniatulus	Coleoptera: Curculionidae	South America	<1958	Defoliator
Coccus hesperidum	Hemiptera: Coccidae	Africa/Asia	1931	Sap sucker
Diaspidiotus perniciosus	Hemiptera: Diaspididae	Asia	1958	Sap sucker
Heteronychus arator	Coleoptera: Scarabaedae	Africa	1938	Root/bark feeder,
Naupactus leucoloma	Coleoptera: Curculionidae	South America	<1952	Defoliator
Otiorhynchus cribricollis	Coleoptera: Curculionidae	Europe	1890	Defoliator
Phlyctinus callosus	Coleoptera: Curculionidae	South Africa	<1955	Defoliator
Xyleborinus saxeseni	Coleoptera: Curculionidae	Eurasia	1959	Bark beetle

“Year” refers to the first recorded detection in Mediterranean regions in Australia, but it is not the first record for occurrence on eucalypts

Table 17.2 Exotic insects associated with exotic *Pinus* spp. hosts in Mediterranean forest regions of Australia, their origin and feeding guild

Species	Order: Family	Origin	Year	Feeding guild
Essigella californica	Hemiptera: Aphididae	North America	1999	Sap sucker
Hylastes ater	Coleoptera: Curculionidae	Eurasia	1936	Bark beetle
Hylotrupes bajulus	Coleoptera: Cerambycidae	Europe	2004	Wood borer
Hylurgus ligniperda	Coleoptera: Curculionidae	Europe	1942	Bark beetle
Ips grandicollis	Coleoptera: Curculionidae	North America	1943	Bark beetle
Marchalina hellenica	Hemiptera: Margarodidae	Europe	2014[a]	Sap sucker
Pineus pini	Hemiptera: Adelgidae	Europe	<1962	Sap sucker
Sirex noctilio	Hymenoptera: Siricidae	Eurasia	1977	Wood borer
Scolytus multistriatus	Coleoptera: Curculionidae	Europe	>1975	Bark beetle
Xanthogaleruca (*Pyrrhalta*) *luteola*	Coleoptera: Chrysomelidae	Europe	2010	Defoliator

“Year” refers to the first recorded detection in Mediterranean regions in Australia

[a] Not declared established

Table 17.3 Insects endemic to eastern Australia associated with *Eucalyptus* (mostly *E. globulus*) in Mediterranean forest regions of south-western Australia, their approximate first record and feeding guild

Species	Order: Family	Year	Feeding guild
Phylacteophaga froggatii	Hymenoptera: Pergidae	1978	Defoliator
Gonipterus platensis	Coleoptera: Curculionidae	<1990s	Defoliator
Gonipterus sp 2.	Coleoptera: Curculionidae	mid-2000s	Defoliator
Paropsisterna m-fuscum	Coleoptera: Chrysomelidae	mid-2000s	Defoliator
Cardiaspina fiscella	Hemiptera: Psyllidae	2001	Sap sucker
Ctenarytaina eucalypti	Hemiptera: Psyllidae	<1990s	Sap sucker

17.2 Exotic Invasive Insects in Australia: On Eucalypts

Australia's primary protection against exotic pests and diseases of forests and forest products has been biosecurity regulations and actions aimed at preventing the entry of destructive organisms, and their potential vectors such as seeds, live plant material, logs or sawn timber, wood-based products, and particularly bark (Eldridge and Simpson 1987). Despite the large geographic distance from other countries, best efforts at prevention, and attempts at eradication, several invasive exotic insect species have established in Australian Mediterranean forest regions (Tables 17.1 and 17.2). The most serious are associated with exotic host plant species (Table 17.2).

Few exotic invasive insects have become pests on eucalypts in Australia, possibly because of a lack of pre-existing adaptations to feeding on eucalypts, Australia's history of strong biosecurity regulations limiting numbers of introductions, and possible competitive exclusion by endemic insect herbivores (Paine et al. 2011). Polyphagous exotic insects that are occasional eucalypt-associates: *Coccus hesperidum* (Hemiptera: Coccidae), *Diaspidiotus perniciosus* (Hemiptera: Diaspididae), and *Xyleborinus saxeseni* (Coleoptera: Curculionidae) (Paine et al. 2011) have adventive distributions within Australia that include Mediterranean regions (Atlas of Living Australia 2015). Additionally, at least three species of weevils (Fuller's rose weevil *Asynonychus cervinus*, whitefringed weevil *Naupactus leucoloma*, and garden weevil *Phlyctinus callosus*) cause occasional damage to young *E. globulus* in south-western and southern Australia (Matsuki and Tovar 2012), whereas apple weevil *Otiorhynchus cribricollis* and the small lucerne weevil *Atrichonotus taeniatulus* were collected in low numbers during establishment of young *E. globulus* plantations in south-western Australia (Loch 2006). All exotic insects recorded on eucalypts in Australia are generalists with a diverse host range, are primarily pests of agriculture and horticulture, and in most cases are associated with juvenile eucalypts (Paine et al. 2011). Of the exotic invasive insects, African black beetle, *Heteronychus arator*, (Coleoptera: Scarabaeidae) has caused the most significant damage on plantation eucalypts in Mediterranean regions in Australia.

17.2.1 Heteronychus arator *(African Black Beetle)*

Heteronychus arator is one of the most serious insect pests of newly planted eucalypt seedlings in plantations. This species originated from southern Africa and was first recorded in Australia in the 1930s. This species is now widespread throughout coastal southern Australia. African black beetle typically feeds on roots of grasses but has become a major pest of eucalypt plantations, pastures, turf, grapes, potatoes and other horticultural crops (Matthiessen and Ridsdill-Smith 1991). The adult beetle is the most damaging life stage on eucalypts as it girdles stems of small seedlings just below ground level, which can lead to poor growth and form or even death (Abbott 1993; Loch and Floyd 2001). Larvae feed on roots and organic matter in the soil but are not normally regarded as a pest in plantations. Where widespread damage occurred, expensive replanting was often required in the following year (Bulinski et al. 2006). Even low densities of beetles ($\leq$5–10 m^{-2}) can inflict severe damage, making monitoring and management difficult (Matthiessen and Learmonth 1995). Damage can occur whenever adults are present, from late summer when the next generation of adults emerge until spring when most mating and oviposition occurs (Matthiessen and Ridsdill-Smith 1991). *Heteronychus arator* tends to be more prevalent and cause higher levels of damage in wetter areas and has thus been a more serious issue in plantations in the southern coastal areas in south-western Australia.

Management of *H. arator* in horticulture typically involves incorporation of insecticides into soil to improve insecticide contact with, and control of, beetles (Matthiessen and Learmonth 1995). This approach is not feasible for newly planted eucalypt plantations (Bulinski et al. 2006). As a result, surface application of insecticides has been used to manage *H. arator*, but these tended to be ineffective. In response to this management issue, Bulinski et al. (2006) tested the efficacy of physical barriers in preventing feeding damage. They showed that planting *E. globulus* seedlings in flexible plastic mesh sleeves reduced severe damage and mortality from *H. arator* by over 75 % and led to no observable negative effects on root or tree growth. This success led to widespread adoption of this approach by the eucalypt plantation industry. Consequently, *H. arator* is no longer considered to cause economic damage in south-western Australia (MM, unpublished).

17.3 Exotic Invasive Insects in Australia: On Softwoods

Over 295,000 ha of exotic softwoods are planted in the Mediterranean regions of Australia: predominantly Monterey pine (*P. radiata*), and maritime pine (*P. pinaster*), representing around one-quarter of Australia's total softwood estate (Gavran 2014). These plantations are an important forestry crop but are susceptible to extensive damage from exotic insects introduced from the northern hemisphere (New 1994), and to date, seven have established in one or both of the pine-growing areas in the Mediterranean regions of Australia (Table 17.2). A recent incursion of giant pine scale, *Marchalina hellenica*, was detected on *P. halipensis*, *P. radiata* and *P. pinea* in Adelaide (SA) and Melbourne in late 2014 and a biosecurity response aimed at eradication is underway (DEPI 2015). Most of the established exotic insects are native to Europe.

17.3.1 Sirex noctilio *(Sirex Woodwasp)*

Sirex noctilio (Hymenoptera: Siricidae), *native* to Eurasia and northern Africa, reached eastern Mediterranean forest regions within Australia in 1977, 16 years after its initial establishment in mainland Australia (Haugen 1990). It is likely to have spread to mainland Australia from Tasmania, where it was first detected in 1952. This species, along with its symbiotic fungus *Amylostereum areolatum* (Russulales: Amylostereaceae), was probably introduced to Tasmania from New Zealand, where it was first recorded in 1900 (Bain et al. 2012). *Sirex noctilio* has since spread to all pine-growing areas of the southern hemisphere, although it is not yet present in WA. Moreover, this species has recently become established in North America and has also re-invaded its native habitat in Europe (Boissin et al. 2012). Sirex is attracted to stressed trees (Madden 1968), but can also kill healthy trees through the dual action of its mutualist fungus and phytotoxic mucus, which are introduced during oviposition (Ryan and Hurley 2012). In the Mediterranean regions of Australia, a severe outbreak of *S. noctilio* in the Green Triangle region between 1987 and 1990 killed 5 million trees valued at $AUD10-12 million (Haugen and Underdown 1990). A biological control program based around augmentative inoculation of the bicyclic nematode *Deladenus* (*Beddingia*) *siricidicola* (Nematoda: Neotylenchidae), has been the most effective management method, along with silvicultural management, including thinning and improving stand health (Carnegie and Bashford 2012). *Sirex noctilio* is absent from WA (Carnegie and Bashford 2012), where suitable host species, *P. radiata* and *P. pinaster*, dominate the softwood estate (Gavran 2014), and where climatic modelling predicts it could readily establish if accidentally introduced (Carnegie et al. 2006).

Five exotic parasitoid species were released as biological control agents for *S. noctilio* in the Green Triangle region (Haugen 1990): *Ibalia leucospoides* (Hymenoptera: Ibaliidae), *Megarhyssa nortoni* (Hymenoptera: Ichneumonidae), *Rhyssa hoferi* (Hymenoptera: Ichneumonidae), *R. persuasoria*, and *Schlettererius cinctipes* (Hymenoptera: Ichneumonidae), but both *Rhyssa* spp. failed to establish (Collett and Elms 2009).

17.3.2 Ips grandicollis *(Five-Spined Bark Beetle)*

Ips grandicollis (Coleoptera: Curculionidae) populations in Australia are thought to have originated from two separate introductions from its native range in North America via importation of logs with intact bark (Morgan 1967). It was first detected in SA in 1943 and in WA in 1952 (Morgan 1967). In the Mediterranean regions of Australia, its recorded hosts include the major exotic plantation species *P. radiata* and *P. pinaster*, as well as *P. muricata*, *P. halepensis*, *P. nigra* var *calabrica*, *P. canariensis*, and *P. pinea*. *Ips grandicollis* is a vector for its blue-stain fungal mutualist, *Ophiostoma ips* (Ophiostomatales: Ophiostomataceae) (Stone and Simpson 1987) which is associated with timber downgrade and tree mortality (Yousuf et al. 2014). Feeding and breeding cycles take place in the subcortical tissue of moribund, recently dead and freshly felled trees and logs (Stone 1993). Outbreaks of *I. grandicollis* in Mediterranean regions of Australia have killed up to 30 % of stressed trees and 2.5 % of apparently healthy trees in WA and SA, respectively (Naumann 1987). In addition to causing tree mortality and downgrading of timber, infestation of trees by *I. grandicollis* and *O. ips* can interfere with the efficacy of the biological control of *Sirex noctilio* (Gitau et al. 2013). Silvicultural management methods involve removing debris from plantations and maintaining stand health (Yousuf et al. 2014).

Seven biological control agents were released in Australia, but only two became well-established: *Roptrocerus xylophagorum* (Hymenoptera: Pteromalidae) and *Dendrosoter sulcatus* (Hymenoptera: Braconidae) (Yousuf et al. 2014).

17.3.3 **Hylastes ater** ***(Black Pine Bark Beetle)***

Hylastes ater (Coleoptera: Curculionidae) was first detected in Australia at Mt Burr, SA, in 1936, although by then the population was well established and likely to have been present for some time (Boomsma and Adams 1943). It is of Eurasian origin, but was present in New Zealand since 1929 (Reay et al. 2012). In the Mediterranean regions of Australia, its hosts include *P. radiata*, *P. canariensis*, *P. muricata*, *P. halepensis*, and *P. pinaster*. Typically, it exploits large-diameter thick-barked logs in contact with the ground, stumps and dead trees with thick bark on the root collars, or the main roots just below ground level (Naumann 1987). However, feeding adults can also attack seedlings in nurseries or second-rotation sites (Naumann 1987; Reay and Walsh 2002). Adults have caused >90 % seedling mortality in South Australia (Boomsma and Adams 1943). Biological control appears not to have been attempted for this species in Australia; releases of natural enemies imported from Europe into New Zealand in the 1930s and 1970s were unsuccessful (Reay et al. 2012).

17.3.4 **Hylurgus ligniperda** ***(Golden-Haired Bark Beetle; Red-Haired Bark Beetle)***

Hylurgus ligniperda (Fabricius) (Coleoptera: Curculionidae), of European origin, was first reported from South Australia in 1942 (Swan 1942 in Kierle et al. 1983). However, it is possible that it was the larger, browner and "more-hairy" scolytid beetle mentioned co-occurring with *H. ater* in 1936 by Boomsma and Adams (1943), indicating this species was probably present earlier. It has similar feeding habits to *H. ater*, and when both species occur together, *H. ligniperda* usually dominates (Naumann 1987). In the mid-1980s, an outbreak of *H. ligniperda* in SA killed several hundred *P. radiata*, following a massive population build-up in slash and salvage felling following fires (Naumann 1987). Biological control was not attempted for this species in Australia.

Naumann (1979) and Kliejunas et al. (2006) do not include WA as having *H. ater* or *H. ligniperda*, and we have not found any published WA records for either species. However, the Australian Plant Pest Database: (http://www.planthealthaustralia.com.au/resources/australian-plant-pest-database/) lists WA records for *H. ligniperda* on *P. pinaster* and *P. radiata*, and for *H. ater* on *P. radiata* between 1966 and 1974.

17.3.5 **Essigella californica** ***(Monterey Pine Aphid; California Pine Aphid)***

Essigella californica (Hemiptera: Aphididae) is native to North America and has established in several Mediterranean regions of the world. However, this species is considered a major pest only in Australia (Wharton and Kriticos 2004; Eyles et al. 2011). It spread very rapidly to all pine-growing regions of Australia following its initial detection in 1998. In Australia, *E. californica* only reproduces parthogenetically (Wharton et al. 2004). The aphids attack older *P. radiata* trees in the mid-upper crown, progressing upwards to the terminal shoot and eventually downwards to the lower crown, resulting in very thin crowns and dead tops, facilitating the growth of understorey plants (Stone and Coops 2004).

First releases of a parasitoid wasp, *Diaeretus essigellae* (Hymenoptera: Aphididae), as a biological control agent for *E. californica* began in 2009 (Kimber et al. 2010), and it has established in several regions (Bevan 2014).

17.3.6 **Hylotrupes bajulus** ***(European House Borer)***

Hylotrupes bajulus (Coleoptera: Curculionidae) is native to Europe and North Africa and has established in some Mediterranean regions of the world. It is a pest of coniferous logs (pine and spruce), tunnelling into and weakening construction timber (Slipinski and Escalona 2013). *Hylotrupes bajulus* was originally discovered in untreated pine timber used for feature beams in a private house in the Perth metropolitan area in south-western Australia in 2004 (EHB 2015; Robinson 2008). Since then, this species has been found in other private dwellings and in pine plantations. It was also found in a house approximately 400 km from its initial detection in untreated pine timber transported from the infested area (EHB 2015). An annual survey is carried out to delineate infested areas, and the transport of untreated pine timber out of the infested area is restricted in order to contain distribution of this species. Surveillance for *H. bajulus* is conducted in SA at sites where there are individual and multiple plantings of *Pinus* spp. and at premises where imported seasoned softwood timber and packaging are present (Phillips 2008).

The pine woolly aphid, *Pineus pini* (Hemiptera: Adelgidae) is recorded from south-western Australia (APPD 2015) causing branch deformity in stands of *P. pinaster* and *P. radiata* but is generally only responsible for infrequent damage (Hopmans et al. 2008). Australia is suspected as the source of *P. pini* that was introduced to Zimbabwe in 1962 (Barnes et al. 1976) and an unidentified *Pineus* species intercepted in USA in 2003 (Kliejunas et al. 2006). The ladybirds *Exochomus quadripustulatus* and *Diomus pumilo* were released as biocontrol agents against it (FAO 2013), and both are now naturalised in Australia (Slipinksi 2007).

17.3.7 Other Exotic Insects

Other tree-related invasive insects include the Smaller European Elm Bark Beetle, *Scolytus multistriatus* (Coleoptera: Curculionidae), which established in Australia in the mid-1970s (Naumann 1987). It is a vector of Dutch Elm Disease, which is not yet present in Australia (Elliot et al. 1998). The Elm Leaf Beetle, *Xanthogaleruca* (*Pyrrhalta*) *luteola* (Coleoptera: Chrysomelidae), and its biocontrol agent *Erynniopsis antennata* (Diptera: Tachnidae) are also established in Mediterranean southern Australia (Lefoe 2006; Lefoe et al. 2014).

17.4 Endemic Invasive Insects in Australia

17.4.1 Host Range Expansion

The broad-scale introduction of eucalypts for forestry outside their native ranges within Australia has led to their utilization as hosts by locally occurring native insects (Paine et al. 2011). In particular, *E. globulus* planted in Mediterranean regions has been readily colonised by endemic insect fauna previously not encountering this species (see Chaps. 15 and 16). Movement of insect populations from native forest into eucalypt plantations as novel environments has been considered in an invasive context (Nahrung and Swain 2015). The host and geographic range expansions of local Australian insects via planting of *E. globulus* may also impact native forest insect dynamics: not only may plantations receive insects from native forests, but plantations may also become a conduit for pests into native forests (Strauss 2001; Cunningham et al. 2005). Most examples of host range expansion are of insects moving into eucalypt plantations from native forest (see Chap. 15), but

Cunningham et al. (2005) found adult *Gonipterus platensis* in native forests in south-western Australia and suggested that *E. globulus* plantations provided an ecological bridge for this species to invade native forest. However, extensive searches between 2003 and 2011 in native forest in the same region did not locate any feeding damage by *G. platensis* on native eucalypt species (MM, unpublished data).

Likewise, exotic softwood plantations have also been used as a resource by endemic herbivorous insects expanding their host range. Naumann (1979) lists several native Australian insects that moved onto exotic pines in the Mediterranean regions of Australia, including several moths from the Lymantriidae, Noctuidae, Xylorictidae, Pyralidae, Geometridae, Psychidae and Tortricidae; locusts and grasshoppers, and weevils and scarab beetles. None of these are considered significant pests (Naumann 1979).

17.4.2 Geographic Range Expansion

Despite large numbers of endemic insect species associated with eucalypt plantations and native forests in south-western Australia (Majer et al. 2000; Cunningham et al. 2005), movement of insects associated with eucalypts has been unidirectional (Steinbauer and Nahrung, Chap. 15). At least five eucalypt pest species native to eastern Australia have been accidentally introduced to the Mediterranean regions of south-western Australia (Table 17.3). *Gonipterus platensis* and *Phylacteophaga froggatti* initially caused extensive and severe damage to plantations of introduced eucalypt species (predominantly *E. globulus*, but also *E. smithii*). However, this has subsequently declined in severity and extent (Grimbacher et al. 2011). Three other species have started to expand their distribution ranges more recently.

17.4.3 **Gonipterus** *spp. (Eucalyptus Weevil)*

Once considered to be a single species, the eucalypt weevil, *Gonipterus scutellatus*, is now recognised as a complex of cryptic species (Mapondera et al. 2012). In south-western Australia, *G. platensis* is the main weevil present in *E. globulus* plantations. The species was first observed in *E. globulus* plantations in the 1990s (Loch and Floyd 2001) and by 2005 had spread throughout the plantation area (Mapondera et al. 2012). The original distribution of this species appears to be restricted to Tasmania (Mapondera et al. 2012), where it is uncommon (MM, personal observation). Low genetic diversity in the populations in south-western Australia suggests that *G. platensis* was probably a recent introduction from Tasmania. *Gonipterus platensis* has also been introduced to New Zealand, Canary Island, Hawaii, North America (California), Spain, Portugal and southern and western South America (Mapondera et al. 2012). Both adults and larvae are damaging, but larval feeding is generally regarded to be more serious because their feeding damage coincides with growth of new foliage (Loch 2006; Matsuki and Tovar 2012).

In *E. globulus* plantations in south-western Australia, *G. platensis* has one principal oviposition period in early spring and a second, lesser oviposition period in early summer (Loch 2006). Parasitism rates of *G. platensis* egg masses by a parasitoid *Anaphes nitens* (Hymenoptera: Mymaridae) tend to be extremely low in early spring when the oviposition peak occurs but increase rapidly to nearly 100 % in late spring and early summer (Loch 2008). As *G. platensis* oviposits mainly between August and January, *A. nitens* is likely to experience a host shortage between summer and winter. However, the breakdown of biological control in south-western Australia may also be the result of a host-parasitoid mismatch as *A. nitens* is not recorded from the native distribution range of *G. platensis* (Mapondera et al. 2012), although *G. platensis* is listed as a host for it (Huber and Prinsloo 1990). *Anaphes nitens* was collected from south-western Australia in 1987 from an unidentified host species (Huber and Prinsloo 1990). Considering the taxonomic complexity and new understanding of *Gonipterus* spp., (Mapondera et al. 2012) there is clearly an important need for further research into *Gonipterus*/*Anaphes* host relationships and possible cryptic species within *Anaphes*, to provide better host-parasitoid matching for biological control worldwide.

Larvae of *G. platensis* are parasitised by at least two species of undescribed tachinid flies (Loc 2008; AL & MM, unpublished data). There is a native species, *G. citriophagus*, in the Mediterranean forests in south-western Australia, and it has been hypothesised that these natural enemies of *G. platensis* were present in the native forests in the region.

An undescribed *Gonipterus* species (*G*. nov. sp. 2 in Mapondera et al. 2012) is native to eastern Australia (Mapondera et al. 2012), and this species is likely to have been accidentally introduced to south-western Australia from eastern Australia in the mid-2000s (MM, personal observation). It is now spreading in plantations of *E. globulus* and *E. smithii. Gonipterus* nov. sp. 2 has also been accidentally introduced to Africa, Madagascar, St Helena, Mauritious, Italy and France (Mapondera et al. 2012).

17.4.4 Phylacteophaga froggatti *(Leafblister Sawfly)*

Phylacteophaga froggatti is native to eastern Australia, and was first discovered in south-western Australia in 1978, and spread quickly throughout coastal and subcoastal areas of the region (Curry 1981). Larvae of *P. froggatti* (Hymenoptera: Pergidae) mine the upper surface of eucalypt leaves before pupating in an oval-shaped blister (Farrell and New 1980; Thumlert and Austin 1994). Juvenile leaves in the lower crown of *E. globulus* are preferentially attacked by *P. froggatti*. As a result, damage is generally confined to young plantations where the damage is more likely to be a cosmetic, rather than an economic, problem. In south-western Australia, damage in *E. globulus* plantations by *P. froggatti* has primarily been restricted to areas along the coast. Several eucalypt species native to south-western Australia including *E. marginata*, *C. calophylla*, *E. gomphocephala*, and *E. rudis* are also attacked by *P. froggatti*.

A large number of parasitic wasps have been reared from larvae and pupae of leafblister sawfly in Australia. In Melbourne in south-eastern Australia, Farrell and New (1980) recorded species of *Bracon* and *Cirrospilus* parasitising leafblister sawfly. In the Adelaide region of South Australia, 17 species of parasitic wasps were reared from leafblister sawfly, with *Cirrospilus margiscutellum* (Hymenoptera: Eulophidae) and *Bracon phylacteophagus* (Hymenoptera: Braconidae) being the most common species (Thumlert and Austin 1994). In south-western Australia, Loch et al. (2004) recorded low parasitism rates (<10 %) of *P. froggatti* on *E. globulus* by *C. margiscutellum* and *B. confusus* (Hymenoptera: Braconidae). *Bracon phylacteophagus*, the species responsible for successful biological control of *P. froggatti* in New Zealand (Faulds 1991), does not occur in south-western Australia (Loch et al. 2004). The pest status of *P. froggatti* in south-western Australia therefore appears to have been elevated as a result of ineffective biological control. However, since mid-2000s, damage by *P. froggatti* in plantations of *E. globulus* in south-western Australia has decreased dramatically (Grimbacher et al. 2011), and it is now considered only a moderate to severe occasional pest in *E. globulus* plantations (Matsuki and Tovar 2012). However, it still regularly damages *E. rudis* (a native species of eucalypt that is susceptible to a large number of insect herbivores) especially in and around the Perth metropolitan area.

17.4.5 Paropsisterna (Chrysophtharta) m-fuscum *(Chrysomelid Beetle)*

Paropsisterna m-fuscum (Coleoptera: Chrysomelidae) is native to temperate forests, and the Mediterranean forests in south-eastern Australia (e.g., Morrow and Fox 1980; Fox and Morrow 1981). It has also been collected from *E. dunnii* plantations in subtropical regions of Australia (Nahrung 2006), and causes minor damage in *E. globulus* plantations (Collett and McBeath 2007). Folivorous larvae and adults feed on several *Eucalyptus* species, preferring new growth of juvenile leaves, and is the only species of *Paropsisterna* in the Mediterranean forests in Australia that is consistently found on seedlings (MM, personal observation). This species was accidentally introduced to south-western Australia around 2005 and began to expand its distribution in 2008 (Grimbacher et al. 2011). It has so far been recorded only on *Eucalyptus* species endemic to eastern Australia (mainly *E. globulus*). Species of *Paropsisterna*, including *P. m-fuscum*, in *E. globulus* plantations in south-western Australia are parasitised by tachinid flies (Loch 2008, MM, unpublished data). This species is also an invasive pest on *Eucalyptus* in North America (Chap. 24, and Paine et al. 2010).

17.4.6 **Cardiaspina fiscella** ***(Brown Lace Lerp)***

Cardiaspina fiscella (Hemiptera: Psyllidae) is native to temperate and Mediterranean forests in south-eastern Australia (Taylor 1962) where sup-sucking nymphs and adults feed on several *Eucalyptus* species. The first official record of this species in south-western Australia was in 2001 (Research Working Group 7 2002). This species is currently restricted to *E. robusta* and other eucalypts native to eastern Australia in the vicinity of two ports (Albany and Fremantle). This species was reported from *Corymbia calophylla* (a species endemic to the Mediterranean forests in south-western Australia) (Research Working Group 7 2005), but it was later ascertained that this new host record was due to misidentification of host plants (MM, personal observation). In 2005, *C. fiscella* was found in commercial plantations of *E. saligna* (native to eastern Australia) 70 km from one of the ports (Research Working Group 7 2006). *Cardiaspina fiscella* is an introduced pest of *Eucalyptus* plantations in other continents.

17.4.7 Other Species

Other examples of accidental introduction into WA from eastern Australia include the parasitoid wasp, *Cleruchoides noackae* (Hymenoptera: Mymaridae) which appears to be a recent introduction as a natural enemy of endemic *Thaumastocoris peregrinus* populations on eucalypts in Perth (Nadel et al. 2012) the blue-gum psyllid, *Ctenarytaina eucalypti* (Hempitera: Psyllidae) which was presumably introduced from Tasmania (Abbott 1993); and possibly *Ctenarytaina spatulata* (MM, unpublished data).

17.5 Australia as a Source of Invasive Forest Pests

The number of native Australian insects established as pests outside of Australia continues to increase (Wingfield et al. 2008). Many of these were not significant pests, or were previously unrecorded or rare in Australian forests and plantations prior to their establishment outside of Australia (Paine et al. 2011; Nahrung and Swain 2014). About one-half of the eucalypt-feeding insects of Australian origin that have become established as exotic species worldwide (Paine et al. 2010; Withers 2001) are present in Mediterranean forest ecosystems (Table 17.4). Of these, 40 % are sap-suckers, a guild found previously over-represented in invasive species (Lawton and Brown 1986).

Table 17.4 Australian endemic insects established in Mediterranean forest regions as invasive species

Species	Order: Family	Feeding guild	First record	Mediterranean region
Blastopsylla occidentalis	Hemiptera: Psyllidae	Sap sucker	1983	North America
Cryptoneossa triangula	Hemiptera: Psyllidae	Sap sucker	1995	North America
Ctenarytaina eucalypti	Hemiptera: Psyllidae	Sap sucker	1991	N. & S. America, Europe, South Africa
Ctenarytaina peregrina	Hemiptera: Psyllidae	Sap sucker	2010	Europe,
Ctenarytaina spatulata	Hemiptera: Psyllidae	Sap sucker	1991	N. & S. America, Europe
Epichrysocharis burwelli	Hymenoptera: Eulophidae	Gall-former	1999	North America
Eucalyptolyma maideni	Hemiptera: Psyllidae	Sap sucker	2000	North America
Glycaspis brimblecombei	Hemiptera: Psyllidae	Sap sucker	1998	North America
Gonipterus platensis	Coleoptera: Curculionidae	Defoliator	Unknown	South Africa, Europe, N. & S. America
Gonipterus pulverulentus	Coleoptera: Curculionidae	Defoliator	Unknown	South America
Gonipterus sp. nov. 2	Coleoptera: Curculionidae	Defoliator	1916	Europe, South Africa
Leptocybe invasa	Hymenoptera: Eulophidae	Gall-former	2000	Middle East
Ophelimus maskelli	Hymenoptera: Eulophidae	Gall-former	2000	Europe
Paropsisterna m-fuscum	Coleoptera: Chrysomelidae	Defoliator	2003	North America
Phoracantha recurva	Coleoptera: Cerambycidae	Borer	1949	South Africa, Europe
Phoracantha semipunctata	Coleoptera: Cerambycidae	Borer	1906	South Africa, Europe
Selitrichodes globulus	Hymenoptera: Eulophidae	Gall-former	2008	North America
Thaumastocoris peregrinus	Hemiptera: Thaumastocoridae	Sap sucker	2005	South Africa
Trachymela sloanei	Coleoptera: Chrysomelidae	Defoliator	1976	South Africa
Trachymela tincticollis	Coleoptera: Chrysomelidae	Defoliator	1982	South Africa

"First record" refers to the first record in a Mediterranean region, not necessarily the first exotic record; the first-listed region is the region to which this refers

17.6 Potentially Threatening Insects to the Mediterranean Forests in Australia

An increasing number of insect herbivores exotic to Australia have shifted onto eucalypts planted as ornamental trees or plantations overseas, and may now pose a significant potential biosecurity threat to Australia's native and planted eucalypt forests (Paine et al. 2011). However, Mediterranean forests in Australia are separated by great distances from the Mediterranean forests in other continents. Therefore, the probability of natural colonisation by invasive species into Australia's Mediterranean forests is low. Moreover, dominant plant species in the Mediterranean forests in Australia (e.g., Myrtaceae and Proteaceae) tend to be phylogenetically distant from native plant species in the Mediterranean forests on other continents. Therefore, even if there was an accidental introduction of one or more invasive species into Australia, at least initially, these species are likely to persist on plant species that are exotic to Australia (e.g., ornamental plants or crop plants). Nevertheless, several species have been identified as potential pests in the Mediterranean forests in Australia (Table 17.5). The greatest threats to Australia's eucalypts by invasive insects are highly polyphagous species with hosts from diverse phylogenetic groups, and insects that have moved onto eucalypts grown outside of Australia (Paine et al. 2011). Exchange of live plant material, and extensive travel and trade between Australia and other eucalypt-growing regions of the world, risks the accidental introduction of non-native insects that could establish on eucalypts in Australia.

Australia's Pest and Disease Watch List (http://www.agriculture.gov.au/animal-plant-health/pests-diseases-weeds/plant/forestry) and Plant Health Australia's "Plantation Forest Biosecurity Plan" (http://www.planthealthaustralia.com.au/industries/plantation-forestry) list several herbivores of flowering trees and conifers of invasive potential to the Mediterranean regions of Australia. These species are assessed as priority pests based on their potential to enter, establish and spread in Australia (e.g., environmental factors, host range, vectors), and the cost of control measures.

The pine pests represent similar establishment threats and pathways as those that have already been introduced (Table 17.2), and are already invasive or significant pests in other pine-growing regions. However, the pests of angiosperm forest trees represent potentially more complex invasion events, as they would have to overcome at least two barriers: establishing on evolutionarily unfamiliar host plants and a suite of native natural enemies that may eventually attack the introduced species.

For example, there are several closely-related native species of some of these potential invaders including species of Cossidae, Lymantriidae, and Cerambycidae (Elliot et al. 1998) in Mediterranean forests in Australia, along with their endemic suites of natural enemies. If the exotic species were accidentally introduced to Australia, their populations may eventually be controlled by native natural enemies (Paine et al. 2011). On the other hand, some potential invaders (e.g., *Urocerus gigas*) have no native Australian representatives even within the same family

Table 17.5 List of insect species considered of high invasive potential into Australian Mediterranean forest regions

Species	Order: Family	Guild	Native region
Anoplophora glabripennis	Coleoptera: Cerambycidae	Wood borer	Asia
Arhopalus ferus	Coleoptera: Cerambycidae	Wood borer	Europe
Chilecomadia valdiviana	Lepidoptera: Cossidae	Wood borer	South America
Coryphodema tristis	Lepidoptera: Cossidae	Wood borer	South Africa
*Dendroctonus spp. including D. ponderosae**, *D. valens**, *D. frontalis*	Coleoptera: Curculionidae	Bark beetle	North America
*Hylesia nigricans**	Lepidoptera: Saturniidae	Defoliator	South America
*Ips typographus**	Coleoptera: Curculionidae	Bark beetle	Europe
*Lymantria dispar**	Leptidoptera: Lymantriidae	Defoliator	Eurasia
*Lymantria mononcha**	Leptidoptera: Lymantriidae	Defoliator	Europe
*Monochamus** spp. including *M. alternatus*, *M. galloprovinicialis*, *M. titillator*, *M. scutellatus*	Coleoptera: Chrysomelidae	Wood borer	Asia, Europe, North America
*Orygia thyellina**	Leptidoptera: Lymantriidae	Defoliator	Eurasia
Rhyaciona buoliana	Lepidoptera: Tortricidae	Defoliator	Europe
*Tomicus piniperda**	Coleoptera: Curculionidae	Borer	Eurasia, Africa
*Urocerus gigas**	Hymenoptera: Siricidae	Wood borer	Eurasia

Species marked with a star (*) are listed as "High Priority Pests"

(Naumann 1991), and many proven invaders (e.g., Table 17.2) are not well-represented with native species in Australia (e.g. bark beetles – Elliot et al. 1998).

Of the species listed in Table 17.5, Asian gypsy moth (*Lymantria dispar*) is potentially the most damaging and also the best-studied species.

17.6.1 Lymantria dispar *(Asian Gypsy Moth)*

Lymantria dispar (Lepidoptera: Lymantriidae) is native to Eurasia including the Mediterranean region (Giese and Schneider 1979). Damage is caused by folivorous larvae. This species has an extremely wide host range exceeding 650 tree species (Liebhold et al. 1995). Although trees in the Myrtaceae and Proteaceae are not present in the native distribution range of *L. dispar*, it is able to complete development on at least some myrtaceous species, and at least in laboratory conditions, the larvae performed better on some evolutionarily unfamiliar species in Myrtaceae than on their primary hosts (Matsuki et al. 2001, 2011). Also, the climate in the Mediterranean forests in Australia has been shown to be able to support populations of *L. dispar* (Matsuki et al. 2001). Potential pathways for *L. dispar* into Australia, especially on imported containers, vehicles, and machinery, are well known, with frequent recorded egg-mass interceptions at Australian ports (Paine et al. 2011).

17.7 Patterns, Trends and Conclusions

Here we have considered four major groups of invasive forest pests: exotic insects established in Mediterranean regions of Australia; insects endemic to eastern Australia that have established as exotics in south-western Australia; insects endemic to Australia that have established as exotics in Mediterranean regions overseas; and insects considered of high biosecurity risk to enter, establish and spread within Australia as exotics. The first three groups (proven invaders) all comprise the same three insect Orders: Coleoptera, Hemiptera and Hymenoptera. The fourth group (the potential invaders), however, contains several Lepidoptera and no Hemiptera (Fig. 17.2). The dominance of the Coleoptera among invasive insects is unsurprising considering it represents about one-third of all animal species worldwide, but the under-representation of invasive Lepidoptera – also one of the largest insect orders – is noteworthy.

Nahrung and Swain (2015) concluded that smaller, more-concealed species were more likely to become established as exotic pests of eucalypts. For both groups of exotic invaders considered here (exotic insects established in Australia, and Australian insects established as exotics overseas), over 75 % were small, concealed, or both. Likewise, despite the small sample size for insects invasive between Australian regions, about half also fit this pattern, suggesting that they share pathway traits with exotic invasive insects, and establishment traits with both (Nahrung and Swain 2015). There are a number of border controls between states within Australia designed to prevent interstate pest movement, and the geographic isolation of south-western Australia, coupled with the similarity in invasive patterns suggests that the invasion process between eastern Australia and south-western Australia is similar to that between Australia and overseas. Indeed, all five to six species that are invasive in south-western Australia are also invasive overseas (albeit not all in Mediterranean regions).

Historical movement of plantation pests appears to provide a strong indicator of their future movement; once a pest is established in a new country or region, the likelihood is it will continue to spread (Wingfield et al. 2008). Invasion processes tend to follow a typical pattern of arrival and establishment, spread, and equilibrium (Williamson 1989). Grimbacher et al. (2011) described this general pattern of invasion into eucalypt plantations in the Mediterranean regions of Australia for insects

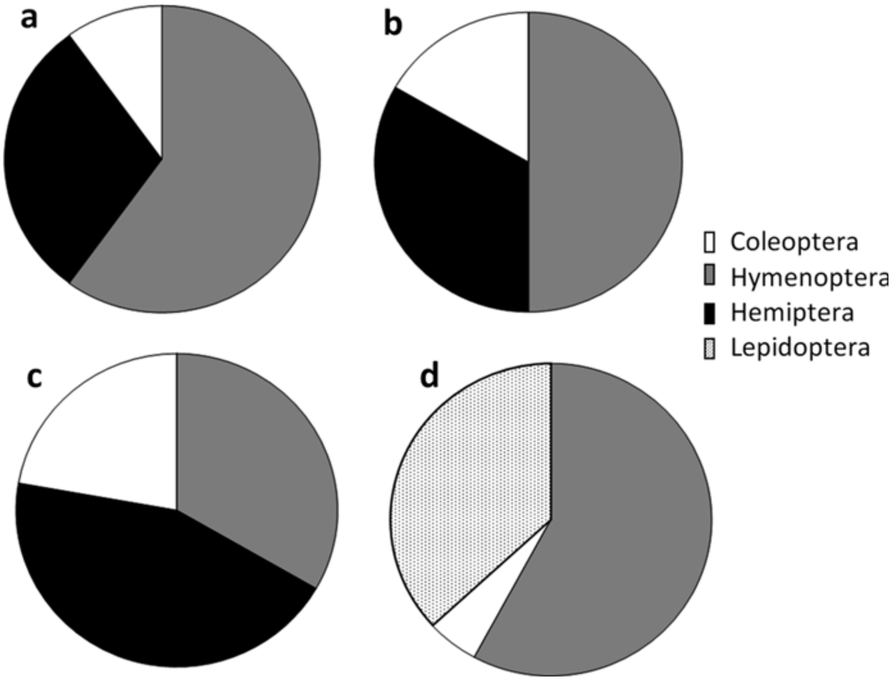

Fig. 17.2 Representation, by Order, of invasive insects in Mediterranean forest regions: (**a**) exotic insect species established in Australia (n = 10); (**b**) Australian endemic insect species invasive within Australia (n = 6); (**c**) Australian endemic insect species established overseas (n = 18); (**d**) exotic insects considered of high biosecurity risk as invasive in Australia (n = 19). Only species primarily associated with forests are included

from eastern Australia, comprising an initial latent period after an accidental introduction, followed by a rapid increase in population size and geographic extent, leading to large areas being colonised and characterised by severe damage throughout the core of new range. Movement into marginal areas is slower, and eventually the pest population stabilises, and damage levels decrease or remain locally restricted to stressed trees. Grimbacher et al. (2011) attributed this stabilisation to the interaction with endemic natural enemy populations becoming more frequent and complex, and suggested that natural enemy populations may have benefited from a decrease in the application of pesticides, and changes in the age structure of the plantation estate. The accumulation of invasive insects from eastern Australia has been gradual, and is an ongoing, dynamic process, as is the accumulation of insects exotic to Australia on exotic hosts, and the movement of Australian endemic insects to eucalypts overseas.

Although exotic pines in Australia, and eucalypts overseas have been planted for similar lengths of time, the rate of establishment of Australian eucalypt insects as exotics in eucalypt plantations in overseas Mediterranean regions has been far greater than the establishment of exotic insects into Mediterranean pine plantations in Australia over the past 30 years (Fig. 17.3).

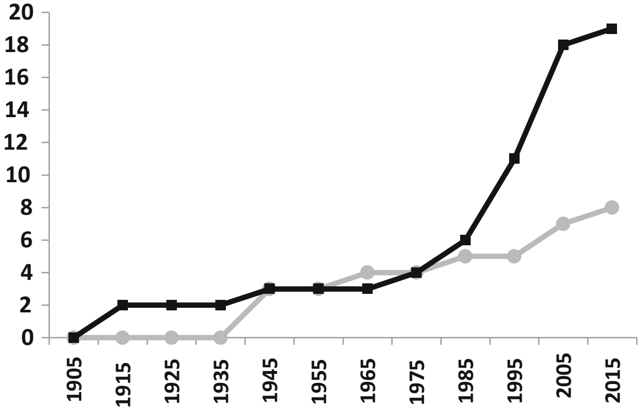

Fig. 17.3 Number of species (y-axis) accumulated in Mediterranean forest regions as exotic insects moving into Australia (*grey*), and of eucalypt insects endemic to Australia establishing overseas (*black*). Only species that are primarily associated with forest trees are included

The invasion of exotic insects onto pines in Australia, therefore, does not appear to have followed the two phases of movement described by Paine et al. (2011) that has occurred for eucalypt pests moving overseas from Australia. Since the suites of insects are similar at ordinal and guild levels (Fig. 17.2, Tables 17.2 and 17.4), this difference may reflect success in Australia's biosecurity measures compared with regions overseas, or simply the vastly smaller areas of plantations in Mediterranean Australia compared with Mediterranean regions overseas. Regardless of historical patterns, current unprecedented rates of travel and trade, coupled with funding declines for biosecurity, loss of expertise in taxonomy, and impacts of climate change on species' distributions, the introduction, establishment and spread of invasive insects into, out of, and within, Mediterranean forest regions of Australia will continue and may well increase.

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References

Abbott I (1993) Insect pest problems of eucalypt plantations in Australia. 6. Western Australia. Aust For 56:381–384

APPD Australian Plant Pest Database. http://www.planthealthaustralia.com.au/resources/australian-plant-pest-database/. Accessed Jan 2015

Atlas of Living Australia. http://www.ala.org.au/. Accessed Jan 2015

Bain J, Sopow SL, Bulman L (2012) The sirex woodwasp in New Zealand: history and current status. In: Slippers B, de Groot P, Wingfield MJ (eds) The sirex woodwasp and its fungal symbiont. Springer, Dordrecht, pp 167–173

Barnes RD, Jarvis RF, Schweppenhause MA et al (1976) Introduction, spread and control of the pine woolly aphid, *Pineus pini* (L.), in Rhodesia. South Afr For J 96:1–11

Beard JS, Chapman AR, Gioia P (2000) Species richness and endemism in the Western Australian flora. J Biogeogr 27:1257–1268

Bevan P (2014) http://www.dpi.nsw.gov.au/aboutus/news/all/2014/dpi-study-shows-biocontrol-for-pine-aphid-is-taking-hold

Boissin E, Hurley B, Wingfield MJ et al (2012) Retracing the routes of introduction of invasive species: the case of the Sirex noctilio woodwasp. Mol Ecol 21:5728–5744

Boland DJ, Brooker MIH, Chippendale GM et al (2006) Forest trees of Australia, 5th edn. CSIRO Publishing, Melbourne

Boomsma CD, Adams AJS (1943) The pine bark beetle (*Hylastes ater*) at Mount Burr, South Australia. Aust For 7:33–37

Bulinski J, Matthiessen JN, Alexander R (2006) Development of a cost-effective, pesticide-free approach to managing African black beetle (*Heteronychus arator*) in Australian *Eucalyptus* plantations. Crop Prot 25:1161–1166

Carnegie AJ, Bashford R (2012) Sirex woodwasp in Australia: current management strategies, research and emerging issues. In: Slippers B, de Groot P, Wingfield MJ (eds) The sirex woodwasp and its fungal symbiont. Springer, Dordrecht, pp 175–201

Carnegie AJ, Matsuki M, Haugen DA et al (2006) Predicting the potential distribution of *Sirex noctilio* (Hymenoptera: Siricidae), a significant exotic pest of *Pinus* plantations. Ann For Sci 63:119–128

Collett NG, Elms S (2009) The control of sirex wood wasp using biological control agents in Victoria, Australia. Agric For Entomol 11:283–294

Collett NG, McBeath J (2007) Managing insect pests in *Eucalyptus globulus* (Labill.) plantations in Victoria using insecticide tablets at establishment. Aust For 70:53–60

Cunningham SA, Floyd RB, Weir TA (2005) Do *Eucalyptus* plantations host an insect community similar to remnant *Eucalyptus* forest? Austral Ecol 30:103–117

Curry SJ (1981) Native wasps hit introduced tree pest. J Agric West Aust 22:61–62

DEPI (2015) State Government of Australia. http://www.depi.vic.gov.au/agriculture-and-food/pests-diseases-and-weeds/pest-insects-and-mites/giant-pine-scale. Accessed Jan 2015

EHB (2015) Website on European House Borer http://www.ehb.wa.gov.au/index.htm. Accessed Jan 2015

Eldridge RH, Simpson JA (1987) Development of contingency plans for use against exotic pests and diseases of trees and timber: 3. Histories of control measures against some introduced pests and diseases of forests and forest products in Australia. Aust For 50:24–36

Elliot HJ, Ohmart CP, Wylie FR (1998) Insect pests of Australian forests. Inkata Press, Melbourne

Eyles A, Robinson AP, Smith D et al (2011) Quantifying stem growth loss at the tree-level in a *Pinus radiata* plantation to repeated attack by the aphid, *Essigella californica*. For Ecol Manage 261:120–127

FAO (2013) Forestry pest profiles: *Pineus pini* http://www.fao.org/forestry/37415-040d412f6c6416c70d216a4768cc60a91.pdf. Accessed Jan 2015

Farrell GS, New TR (1980) Some aspects of the biology of the eucalypt mining sawfly *Phylacteophaga froggatti* Riek (Hymenoptera: Pergidae). Aust J Zool 28:83–90

Faulds W (1991) Spread of *Bracon phylacteophagus*, a biocontrol agent of *Phylacteophaga froggatti*, and impact on host. N Z J For Sci 21:185–193

Fox LA, Morrow PA (1981) Specialization: species property or local phenomenon. Science 211:887–893

Gavran M (2014) Australian plantation statistics 2014 update, ABARES technical report 14.2, Canberra

Giese RI, Schneider ML (1979) Cartographic comparisons of Eurasian gypsy moth distribution (*Lymandria dispar* L., Lepidoptera: Lymantriidae). Entomol News 90:1–16

Gitau CW, Carnegie AJ, Nicol HI et al (2013) Incidence of *Ips grandicollis* (Coleoptera: Scolytinae) in trap trees prepared for biological control of *Sirex noctilio* (Hymenoptera: Siricidae) in Australia: influence of environment and silviculture. For Ecol Manage 310:865–874

Grimbacher P, Matsuki M, Collett N et al (2011) Are insect herbivores in Eucalyptus globulus/nitens plantations a worsening problem? A multi-region spatio-temporal review of southern Australia. CRC for For Tech Rep 216. Hobart, Tasmania

Haugen DA (1990) Control procedures for *Sirex noctilio* in the Green Triangle: review from detection to severe outbreak (1977–1987). Aust For 53:24–32

Haugen DA, Underdown MG (1990) *Sirex noctilio* control program in response to the 1987 Green Triangle outbreak. Aust For 53:33–40

Hopmans P, Collett NC, Smith IW et al (2008) Growth and nutrition of *Pinus radiata* in response to fertilizer applied after thinning and interaction with defoliation associated with *Essigella californica*. For Ecol Manage 255:2118–2128

Huber JT, Prinsloo GL (1990) Redescription of *Anaphes nitens* (Girault) and description of two new species of *Anaphes* Haliday (Hymenoptera: Mymaridae), parasites of *Gonipterus scutellatus* Gyllenhal (Coleoptera: Curculionidae) in Tasmania. Aust J Entomol 29:333–341

Keirle RM, Johnson IG, Magor VE (1983) Winter storage of *Pinus radiata* logs in forest and sawmill at Tumut, New South Wales. Aust For 46:210–215

Kimber W, Glatz R, Caon G et al (2010) *Diaeretus essigellae* Starý and Zuparko (Hymenoptera: Braconidae: Aphidiini), a biological control for Monterey pine aphid, *Essigella californica* (Essig) (Hemiptera: Aphididae: Cinarini): host-specificity testing and historical context. Aust J Entomol 49:377–387

Kliejunas JT, Burdsal HH, DeNitto GA et al (2006) Pest risk assessment of the importation into the United States of unprocessed *Pinus* logs and chips from Australia. U.S. Department of Agriculture, Forest Service, Forest Products Laboratory, Madison

Lawton JH, Brown KC (1986) The population and community ecology of invading insects. Philos Trans R Soc Lond B314:607–617

Lefoe G (2006) Management of elm pests and diseases in Australia. Horticulture Australia Limited, Sydney

Lefoe G, Dominiak B, Worsley P et al (2014) Elm leaf beetle *Xanthogaleruca luteola* (Muller) dispersal across south eastern Australia (1989–2011). Plant Protec Quart 29:61–65

Liebhold AM, Gottschalk KG, Muzika R et al (1995) Suitability of North American tree species to the Gypsy Moth: a summary of field and laboratory tests. USDA Gen Tech Rep NE-211, USDA, For Serv, Delaware

Loch AD (2008) Parasitism of the Eucalyptus weevil, *Gonipterus scutellatus* Gyllenhal, by the egg parasitoid, *Anaphes nitens* Girault, in *Eucalyptus globulus* plantations in southwestern Australia. Biol Control 47:1–7

Loch AD (2006) Phenology of *Eucalyptus* weevil, *Gonipterus scutellatus* Gyllenhal (Coleoptera: Curculionidae), and chrysomelid beetles in *Eucalyptus globulus* plantations in southwestern Australia. Agric For Entomol 8:155–165

Loch AD, Floyd RB (2001) Insect pests of Tasmanian blue gum, *Eucalyptus globulus globulus*, in southwestern Australia: history, current perspectives and future prospects. Austral Ecol 26:458–466

Loch AD, Matthiessen JN, Floyd RB (2004) Parasitism and seasonal phenology of leafblister sawfly, *Phylacteophaga froggatti* (Hymenoptera: Pergidae), in *Eucalyptus globulus* plantations in south-western Australia. Aust J Entomol 43:88–93

Madden JL (1968) Physiological aspects of host tree favourability for the woodwasp, *Sirex noctilio* F. Proc Ecol Soc Aust 3:147–149

Majer JD, Recher HF, Ganesh S (2000) Diversity patterns of eucalypt canopy arthropods in eastern and Western Australia. Ecol Entomol 25:295–306

Mapondera TS, Burgess T, Matsuki M et al (2012) Identification and molecular phylogenetics of the cryptic species of the *Gonipterus scutellatus* complex (Coleoptera: Curculionidae: Gonipterini). Aust J Entomol 51:175–188

Matsuki M, Tovar F (2012) Field guide for *Eucalyptus globulus* plantations in Western Australia and the Green Triangle. CRC Forestry/University of Tasmania, Hobart

Matsuki M, Kay M, Serin J et al (2001) Potential risk of accidental introduction of Asian gypsy moth (*Lymantria dispar*) to Australasia: effects of climatic conditions and suitability of native plants. Agric For Entomol 3:30–320

Matsuki M, Kay N, Serin J et al (2011) Variation in the ability of larvae of phytophagous insects to develop on evolutionarily unfamiliar plants: a study with gypsy moth *Lymantria dispar* and *Eucalyptus*. Agric For Entomol 13:1–13

Matthiessen JN, Learmonth SE (1995) Impact of the soil insects African black beetle, *Heteronychus arator* (Coleoptera: Scarabaeidae) and whitefringed weevil, *Graphognathus leucoloma* (Coleoptera: Curculionidae), on potatoes and effects of soil insecticide treatments in south-western Australia. Bull Entomol Res 85:101–111

Matthiessen JN, Ridsdill-Smith TJ (1991) Populations of African black beetle, *Heteronychus arator* (Coleoptera: Scarabaeidae) in a Mediterranean climate region of Australia. Bull Entomol Res 81:85–91

Morgan FD (1967) Ips grandicollis in south Australia. Aust For 31:137–155

Morrow PA, Fox LR (1980) Effects of variation in *Eucalyptus* essential oil yield on insect growth and grazing damage. Oecologia 45:209–219

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nadel RL, Wingfield MJ, Scholes MC et al (2012) Mitochondrial DNA diversity of *Cleruchoides noackae* (Hymenoptera: Mymaridae): a potential biological control agent for *Thaumastocoris peregrinus* (Hemiptera: Thaumastocoridae). BioControl 57:397–404

Nahrung HF (2006) Paropsine beetles (Coleoptera: Chrysomelidae) in south-eastern Queensland hardwood plantations: identifying potential pest species. Aust For 69:270–274

Nahrung HF, Swain AJ (2015) Strangers in a strange land: do coloniser traits in novel environments differ between aliens and natives? Biol Invasions 17:699–709

Naumann FG (1979) Beetle communities in eucalypt and pine forests in north-eastern Victoria. Aust For Res 9:277–293

Naumann FG (1987) Introduced bark beetles on exotic trees in Australia with special reference to infestations of *Ips grandicollis* in pine plantations. Aust For 50:166–178

Naumann ID (1991) Hymenoptera (wasps, bees, ants, sawflies). In: Naumann ID (ed) The insects of Australia: a textbook for students and research workers, vol 2. Melbourne University Press, Carlton, pp 916–1000

New TR (1994) Exotic insects in Australia. Gleneagles Publishing, Adelaide

Paine TD, Millar JG, Daane KM (2010) Accumulation of pest insects on eucalyptus in California: random process or smoking gun? J Econ Entomol 103:1943–1949

Paine TD, Steinbauer MJ, Lawson SA (2011) Native and exotic pests of *Eucalyptus*: a worldwide perspective. Annu Rev Entomol 56:181–201

Phillips CL (2008) Forest health surveillance in South Australia. Aust For 71:196–201

Reay SD, Walsh PJ (2002) The incidence of seedling attack and mortality by *Hylastes ater* (Coleoptera: Scolytidae) in second rotation *Pinus radiata* forests in the central North Island, New Zealand. N Z J For 47:19–23

Reay SD, Glare TR, Brownbridge M (2012) *Hylastes ater* (Curculionidae: Scolytinae) affecting *Pinus radiata* seedling establishment in New Zealand. Psyche J Entomol, Article ID 590619, 9 p

Research Working Group 7 – Forest Health (2002) Annual pest and disease status report for Australia and New Zealand 2001–2002

Research Working Group 7 – Forest Health (2005) Annual pest and disease status report for Australia and New Zealand 2004–2005

Research Working Group 7 – Forest Health (2006) Annual pest and disease status report for Australia and New Zealand 2005–2006

Robinson R (2008) Forest health surveillance in Western Australia: a summary of major activities from 1997 to 2006. Aust For 71:202–211

Ryan K, Hurley BP (2012) Life history and biology of *Sirex noctilio*. In: Slippers B, de Groot P, Wingfield MJ (eds) The sirex woodwasp and its fungal symbiont. Springer, Dordrecht, pp 15–30

Slipinksi A (2007) Australian ladybird beetles (Coleoptera: Coccinellidae): their biology and classification. ABRS, Canberra

Slipinski A, Escalona HE (2013) Australian longhorn beetles (Coleoptera: Cerambycidae). Volume 1. Introduction and subfamily lamiinae. CSIRO Publishing, Collingwood

Stone C (1993) Survey of arthropods from billets of *Pinus* following infestation by *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) in northeastern New South Wales. Aust J Entomol 32:289–296

Stone C, Coops NC (2004) Assessment and monitoring of damage from insects in Australian eucalypt forests and commercial plantations. Aust J Entomol 43:283–292

Stone C, Simpson JA (1987) Influence of *Ips grandicollis* on the incidence and spread of bluestain fungi in *Pinus elliottii* billets in north-eastern New South Wales. Aust For 50:86–94

Strauss SY (2001) Benefits and risks of biotic exchange between Eucalyptus plantations and native Australian forests. Austral Ecol 26:447–457

Taylor KL (1962) The Australian Genera *Cardiaspina* Crawford and *Hyalinaspis* Taylor, (Homoptera: Psyllidae). Aust J Zool 10:307–348

Thumlert TA, Austin AD (1994) Biology of *Phylacteophaga froggatti* Riek (Hymenoptera: Pergidae) and its parasitoids in South Australia. Trans R Soc South Aust 118:99–113

Wharton TN, Kriticos DJ (2004) The fundamental and realized niche of the Monterey Pine aphid, *Essigella californica* (Essig)(Hemiptera: Aphididae): implications for managing softwood plantations in Australia. Divers Distrib 10:253–262

Wharton T, Coope P, Floyd R (2004) Life stage development of *Essigella californica* (Aphidoidea: Lachnidae: Cinarinae). Ann Entomol Soc Am 97:697–700

Williamson M (1989) Mathematical models of invasion. In: Drake JA, Mooney HA, di Castri F et al (eds) Biological invasions: a global perspective. Wiley, Chichester

Wingfield MJ, Slippers B, Hurley BP et al (2008) Eucalypt pests and diseases: growing threats to plantation productivity. South For J For Sci 70:139–144

Withers TM (2001) Colonization of eucalypts in New Zealand by Australian insects. Austral Ecol 26:467–476

Yousuf F, Gurr GM, Carnegie AJ et al (2014) Biology of the bark beetle *Ips grandicollis* Eichhoff (Coleoptera: Scolytinae) and its arthropod, nematode and microbial associates: a review of management opportunities for Australia. Aust Entomol 53:298–316

Chapter 18
Native Bark Beetles and Wood Borers in Mediterranean Forests of California

Christopher J. Fettig

Abstract Several species of bark beetles (Coleoptera: Curculionidae, Scolytinae), and to a much lesser extent wood borers (primarily Coleoptera: Buprestidae and Cerambycidae), are capable of causing conifer mortality in Mediterranean forests of California, U.S. This mortality is an important part of the ecology of these ecosystems, but the economic and social implications can be significant when outbreaks occur. I review the ecology, impact and management of the more notable species, including western pine beetle, *Dendroctonus brevicomis* LeConte, mountain pine beetle, *D. ponderosae* Hopkins, Jeffrey pine beetle, *D. jeffreyi* Hopkins, red turpentine beetle, *D. valens* LeConte, California fivespined ips, *Ips paraconfusus* Lanier, pine engraver, *I. pini* (Say), pinyon ips, *I. confusus* LeConte, fir engraver, *Scolytus ventralis* LeConte, cedar bark beetles, *Phloeosinus* spp., and several wood borers.

18.1 Introduction

Bark beetles (Coleoptera: Curculionidae, Scolytinae), a large and diverse group of insects consisting of >550 species in North America (Wood 1982b), are commonly recognized as important disturbance agents in conifer forests. While some 200 species are native to California (Wood 1982b), only a handful is capable of causing tree mortality in Mediterranean forests (Table 18.1). Trees of all species, ages and size classes may be colonized and killed, but each bark beetle species exhibits unique host preferences, life history traits, and impacts. For example, some species, such as *Ips*, are considered secondary agents that typically colonize stressed, dead or dying trees while others, such as the western pine beetle, *Dendroctonus ponderosae* LeConte, are capable of killing healthy trees (Furniss and Carolin 1977). In most cases, the resultant tree mortality goes unnoticed until a large infestation or outbreak occurs, which generally requires several years of favorable weather conducive to beetle survival and population growth, and an abundance of susceptible host trees (Bentz et al. 2010).

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Table 18.1 Notable conifer-infesting bark beetles and wood borers in Mediterranean forests of California

Common name	Scientific name	Primary host(s)
California fivespined ips	*Ips paraconfusus*	*Pinus coulteri*, *P. lambertiana*, *P. ponderosa*, *P. radiata*, *P. torreyana*
California flathead borer	*Phaenops californica*	*P. jeffreyi*, *P. lambertiana*, *P. ponderosa*
Cedar bark beetles	*Phloeosinus spp.*	*Calocedrus decurrens*, *Sequoia sempervirens*, *Sequoiadendron giganteum*
Fir engraver	*Scolytus ventralis*	*Abies concolor*
Flatheaded fir borer	*Phaenops drummondi*	*A. concolor*
Jeffrey pine beetle	*Dendroctonus jeffreyi*	*P. jeffreyi*
Mountain pine beetle	*Dendroctonus ponderosae*	*P. contorta*, *P. lambertiana*, *P. ponderosa*
Pine engraver	*Ips pini*	*P. contorta*, *P. jeffreyi*, *P. lambertiana*, *P. ponderosa*
Pinyon ips	*Ips confusus*	*P. monophylla*, *P. quadrifolia*
Red turpentine beetle	*Dendroctonus valens*	*P. jeffreyi*, *P. lambertiana*, *P. ponderosa*, *P. radiata*
Western pine beetle	*Dendroctonus brevicomis*	*P. coulteri*, *P. ponderosa*

Adult bark beetles maintain limited energy reserves (Atkins 1966), and are highly susceptible to predation, starvation and adverse weather conditions when searching for hosts. Therefore, it is important that bark beetles locate the correct habitat, correct tree species, and the most susceptible trees within these species with efficiency (Byers 1995; Borden 1997). The dominant theory for many species, such as the well-studied mountain pine beetle, *Dendroctonus ponderosae* Hopkins, suggests pioneering beetles (i.e., those that initiate host selection and colonization) use a combination of random landings and visual orientations followed by direct assessment of hosts based on olfactory and/or gustatory cues (Raffa and Berryman 1982, 1983). Given the cues received during these processes, the host is either rejected or accepted. If accepted, pioneering beetles bore through the outer bark and into the phloem where gallery construction occurs upon which many species release aggregation pheromones that enhance attraction of conspecifics to the target tree (Wood 1982a).

Successful host colonization requires overcoming tree defenses, which can only be accomplished by recruitment of a critical minimum number of beetles to *mass attack* vigorous hosts and overwhelm their defenses (i.e., the more "healthy" the tree the more beetles required to overcome tree defenses; Fettig et al. 2007a). Most conifers are capable of mobilizing large amounts of oleoresin following wounding, which constitutes their primary defense against colonization by bark beetles (Franceschi et al. 2005), although resin chemistry (Reid and Purcell 2011) and the development of hypersensitive responses are also important (Lieutier 2004). Bark beetles that initiate host selection are often killed by drowning or immobilization in resin that collects at the entrance hole (*pitch tube*), which in combination with the presence of boring dust is commonly used to identify trees that have been recently attacked (Fig. 18.1). The number of pitch tubes and amount of boring dust is indicative of the number of beetles attacking the tree, while the size of pitch tubes indicates the vigor of the host at the time of attack. Vigorous hosts often produce large pitch tubes that are largely free of phloem material (Fig. 18.1, left), indicating the tree is likely to survive. Monoterpenes released from pitch tubes often enhance attraction to the host tree, however for most *aggressive* species (i.e., those capable of causing large amounts of tree mortality) attraction to host volatiles has not been demonstrated in the absence of aggregation pheromone components (e.g., Moeck et al. 1981). Following mating, eggs are laid in the phloem and larvae excavate feeding tunnels in this tissue and/or the outer bark (Furniss and Carolin 1977). Bark beetles carry a variety of phoretic organisms including bacteria, fungi, yeasts, mites, and nematodes. Relationships ranged from mutualistic to antagonistic. The best studied group are the symbiotic blue-stain fungal associates in the family Ophiostomataceae, which upon inoculation into the tree serve as important food sources for bark beetles, and may also negatively impact tree health (Paine et al. 1997; Six and Wingfield 2011), although tree mortality occurs primarily through girdling of the phloem and cambium tissues.

Following pupation, adult beetles of the next generation tunnel outward through the bark and initiate flight in search of new hosts (Fig. 18.2). The time required to complete a generation (*voltinism*) varies among bark beetle species, among populations within a species, and among individuals within a population. For example,

Fig. 18.1 Bark beetles, such as this female *Dendroctonus brevicomis*, that initiate host colonization are often killed by drowning or immobilization in resin that collects at the entrance hole (*pitch tube*, *Left*), which in combination with the presence of boring frass (*Right*, in this case resulting from *D. ponderosae*) is commonly used to identify trees that have been recently colonized by bark beetles. Monoterpenes released from pitch tubes enhance attraction to the host tree, however for most *aggressive* bark beetle species attraction to host volatiles has not been demonstrated in the absence of aggregation pheromone components (Borden 1997) (Photo credits: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

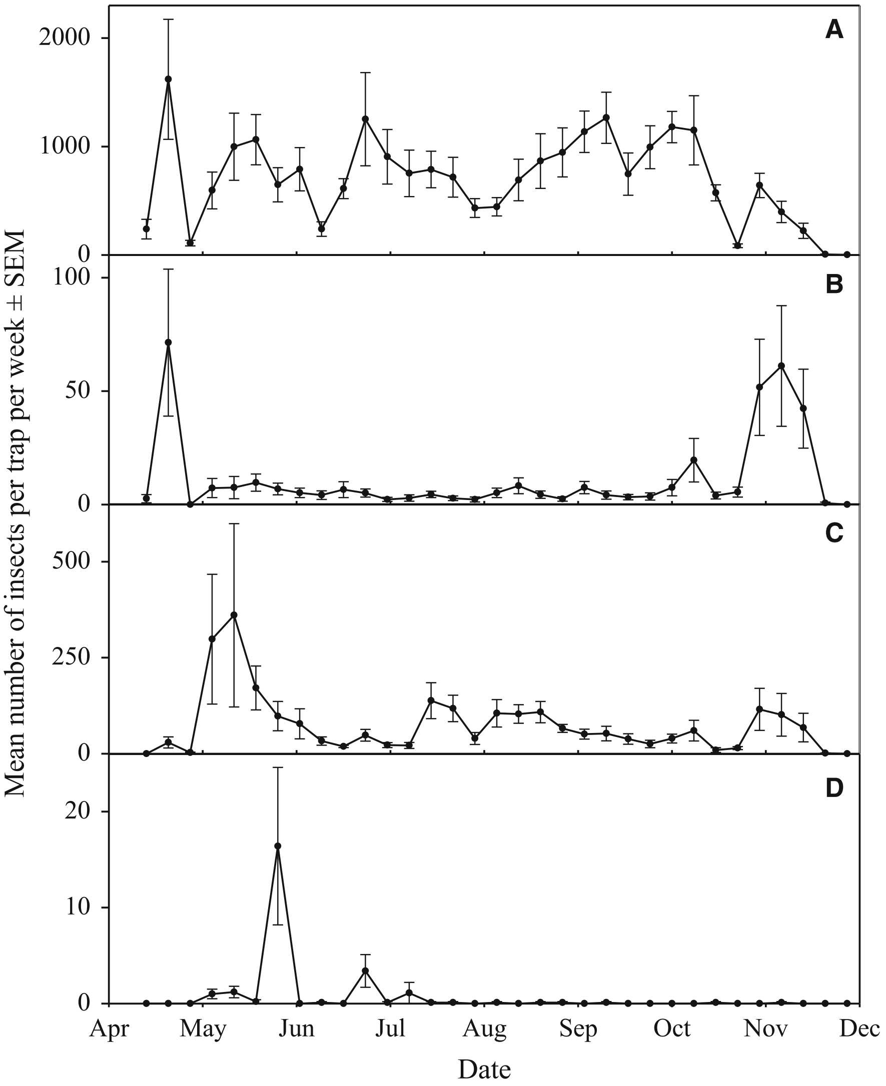

Fig. 18.2 The flight periodicity of (**A**) *Dendroctonus brevicomis*, (**B**) *D. ponderosae*, (**C**) *Ips paraconfusus*, and (**D**) *I. pini* at 823 m elevation, Georgetown Ranger District, Eldorado National Forest, California, 1992–1994 (Modified from Fettig et al. (2005a), and based on captures in baited, multiple-funnel traps)

species such as *D. brevicomis* may complete more than one generation per year, while others, such as the *D. ponderosae*, may take up to 3 years to complete a single generation depending on the temperature profile at a particular locale, among other factors. Because bark beetles are highly sensitive to thermal conditions conducive to population survival and growth, and drought stress influences host tree vigor, recent outbreaks of several bark beetle species have been correlated with shifts in temperature and precipitation (Bentz et al. 2010). As such, many experts agree that anthropogenic-induced climate change will intensify the impacts of bark beetle outbreaks in the future (Fettig et al. 2013a). Hosts native to the Mediterranean forests of California are likely to be particularly vulnerable.

Substantial basic and applied research has been devoted to the development of tools and tactics for mitigating undesirable levels of tree mortality attributed to bark beetles. *Direct control* involves short-term tactics designed to address current infestations by manipulating beetle populations, and often includes the use of insecticides, semiochemicals (i.e., chemicals released by one organism that elicit a response, usually behavior, in another organism), sanitation harvests that remove infested trees, or a combination of these treatments. Natural enemies, such as predators and parasitoids, are important in regulating bark beetle populations at endemic levels (Miller et al. 1987), but none have been successfully developed as biocontrol agents for bark beetles in western North America. Synthetic formulations of entomopathogenic microorganisms, such as fungi, are being developed for some species (Fettig and Hilszczański 2015). Often aerial surveys are conducted with helicopters and/or fixed-wing aircraft to identify and delineate infestations prior to more detailed ground surveys being conducted to determine if direct control measures are warranted. *Indirect control* is preventive, and designed to reduce the probability and severity of future bark beetle infestations by manipulating stand, forest and/or landscape conditions by reducing the number of susceptible hosts through thinning, prescribed burning, and altering age classes and species compositions. Unlike direct control, the focus of indirect control is on the susceptibility of residual forest structure and composition to future infestations (Fettig and Hilszczański 2015), and represents an important component of proper forest management. In short, reducing tree competition improves tree growth and defensive mechanisms while often disrupting pheromone plumes, thus negatively affecting the beetle's ability to locate and successfully mass attack host trees (Fettig et al. 2007a). *Risk and hazard rating systems* have been developed for several species of bark beetles native to Mediterranean forests of California to provide land managers and others with a means of identifying stand conditions that are likely to foster initiation and/or spread of infestations (Fettig and Hilszczański 2015), but are rarely used.

The impact of wood borers pales in comparison to that of bark beetles in most forests, but some species are capable of causing tree mortality. Eggs of most species are laid in slits created by females in the outer bark or within bark crevices. The larvae initially mine the cambium and phloem, and then extend their tunneling into the sapwood and occasionally the heartwood. The time required to complete a generation varies from months to years depending on the species and other factors. Two families are of significance. The Buprestidae compromise a large group of ~700 species in North America, many of them indigenous to the western U.S. (Furniss and Carolin 1977). The larvae have a flattened thorax (hence the common name, *flatheaded borers*) while the adults are often brightly-colored with a metallic-type luster (*metallic borers*). The Cerambycidae have a swollen thorax (*roundheaded borers*) while the adults have very long antennae (*longhorned beetles*). Some wood borers pupate in the xylem, while others create a *chip cocoon* in the inner bark. Different species arrive at different times after a tree is stressed or killed, likely due to changes in the chemical composition of trees that influence host finding, selection and colonization behaviors (Kelsey and Joseph 2003). Wood borers serve a very important ecological function by helping to facilitate wood decomposition and nutrient cycling (Edmonds and Eglitis 1989).

Tree mortality resulting from colonization of native bark beetles and wood borers is an important part of the ecology of Mediterranean forests. Some level of tree mortality is desirable and often results in a mosaic of age classes and tree species compositions that increase resistance and resilience to multiple disturbances, including bark beetle infestations (Fettig 2012). This differs from the impacts associated with large infestations or outbreaks, which may negatively affect several ecological goods and services, including timber and fiber production, water quality and quantity, fish and wildlife populations, recreation, grazing capacity, biodiversity, endangered species, carbon sequestration and storage, and cultural resources, among many others. It is important to note that the ecology and impact of these insects is influenced by other biotic, abiotic, and anthropogenic (e.g., management activities and land use patterns) disturbances that also directly influence successional pathways.

In California, Mediterranean climates are distributed throughout much of the Coast Range, the Sacramento Valley, along the western slope of the Sierra Nevada, and in the Transverse and Peninsular Ranges of southern California (Kauffmann 2003). As such, I discuss the biology, ecology and management of bark beetles and wood borers native to conifer forests in these regions. Given the number of species involved, I focus exclusively on those that cause the majority of tree mortality (Table 18.1). In this context, many species are ignored that are also vital to the proper functioning of these ecosystems. Others, such as the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, are notable forest pests elsewhere in western North America (Furniss and Carolin 1977), but have limited and/or infrequent impacts in Mediterranean forests of California and are ignored.

18.2 Life History and Management of Bark Beetle and Wood Borers

18.2.1 Western Pine Beetle, Dendroctonus brevicomis

Dendroctonus brevicomis is recognized as a significant cause of *P. ponderosa* mortality in much of the western U.S., and particularly in Mediterranean forests of California. The only other host in California is Coulter pine, *P. coulteri* D. Don, a species indigenous to the Transverse and Peninsular Ranges of southern California. In the early and mid-twentieth century, substantial research was conducted on *D. brevicomis* due to its impacts in mature *P. ponderosa* stands in California, Oregon and Washington, U.S. Much of the knowledge gained was published in a seminal work titled "Biology and Control of the Western Pine Beetle" by noted USDA Forest Service scientists J.M. Miller and F.P. Keen (1960), which I encourage the reader to review for more detailed information. Today, *D. brevicomis* continues to exert significant impacts on forests in California and elsewhere. For example, the mountain ranges of southern California experienced an outbreak of *D. brevicomis* in the early 2000s that resulted in 73.5 % and 78 % mortality of large-diameter (>43.2 cm diameter at breast height, dbh) *P. ponderosa* and *P. coulteri*, respectively (Walker et al. 2006). In some areas, tree mortality exceeded 80 % (Fig. 18.3).

Dendroctonus brevicomis generally exhibits a preference for larger diameter (>50 cm dbh) trees (Fig. 18.4), but under certain conditions may colonize and kill apparently-healthy trees of all ages and size classes. Female *D. brevicomis* initiate host colonization by tunneling through the outer bark and into the phloem and outer

Fig. 18.3 Tree mortality (bare and faded crowns) resulting from a notable *Dendroctonus brevicomis* outbreak in southern California. In 2000, *D. brevicomis* was first noticed colonizing *Pinus coulteri* at elevated levels in the San Jacinto Mountains on the San Bernardino National Forest (USDA Forest Service 2000). Activity peaked in 2002–2003 in both *P. coulteri* and *P. ponderosa*, and rapidly declined thereafter. Severe drought stress (i.e., precipitation was the lowest in recorded history during 2001–2002) was important in facilitating the outbreak, but elevated ozone and nitrogen deposition were likely predisposing factors (Jones et al. 2004). Estimates of commercial sawlogs and other fiber (all trees killed) salvaged (*above*) or harvested (e.g., during fuels reduction projects) ranged from 115,312 to 566,788 green metric tons (mt) per year during 2004–2008 (CJF, unpublished) (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

Fig. 18.4 A *Pinus ponderosa* snag that was killed by *Dendroctonus brevicomis* several years earlier (*Left*). Close examination of the lower bole, where the bark has sloughed, shows the characteristic "S"-shaped galleries produced by this species. The shape, distribution and orientation of galleries are commonly used to distinguish among bark beetle species. *Dendroctonus brevicomis* enters the bark during the second larval instar (there are four instars) and completes development within the mid-bark layer. Woodpeckers, especially the genus *Picoides* (Farris and Zack 2005), remove the outer bark of such trees to forage for larvae, pupae and adults (*Right*) (Photo credits: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

xylem where they rupture resin canals. As a result, oleoresin exudes and collects on the bark surface, as is commonly observed with other bark beetle species. During the early stages of attack, females release *exo*-brevicomin, which in combination with the host monoterpene myrcene released from pitch tubes is attractive to conspecifics (Bedard et al. 1969). Frontalin, produced by males (Kinzer et al. 1969), enhances attraction and mass attack ensues (Wood 1972; Bedard et al. 1985). These volatiles are commercially produced and effective attractants (Wood et al. 1976). Verbenone is produced during latter stages of the attack sequence by several pathways, and is thought to reduce intraspecific competition, and in some cases interspecific competition, by altering adult behavior to minimize overcrowding of developing brood within the host (Byers and Wood 1980; Byers et al. 1984). There are typically two to four generations per year (Furniss and Carolin 1977).

Tactics for managing *D. brevicomis* infestations are limited to tree removals (thinning) that reduce stand density and host susceptibility (Fig. 18.5), sanitation harvests, and applications of insecticides to protect individual trees. Verbenone was the focus of early work designed to develop a semiochemical-based tool for mitigating undesirable levels of *P. ponderosa* mortality attributed to *D. brevicomis*, but alone is ineffective for protecting individual trees (Gillette et al. 2006) or forest

Fig. 18.5 Thinning has long been advocated as a preventive measure to alleviate or reduce the amount of bark beetle-caused tree mortality (Fettig et al. 2007a). Among other factors, thinning reduces host availability; reduces competition among trees for nutrients, water, and other resources thereby increasing vigor; and affects microclimate decreasing the effectiveness of chemical cues used in host finding, selection and colonization (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

stands (Fettig et al. 2009a). Based on early work by Paine and Hanlon (1991), Bertram and Paine (1994) found that applications of verbenone and ipsdienol significantly reduced both numbers of *D. brevicomis* landing on *P. ponderosa* and the densities of attacking beetles, but tree mortality rates were not determined. In more recent years, Fettig et al. (2008a, 2009b, 2012a, b) developed a four-component blend [acetophenone, (*E*)-2-hexen-1-ol + (*Z*)-2-hexen-1-ol, and (−)-verbenone; Verbenone Plus] that has been demonstrated effective for protecting individual *P. ponderosa* and *P. ponderosa* stands from mortality attributed to *D. brevicomis*, but has yet to be commercialized.

18.2.2 Mountain Pine Beetle, Dendroctonus ponderosae

Dendroctonus ponderosae is the best studied of all bark beetles in North America, presumably a result of the significant impacts it exerts in several different hosts and forest types. The species colonizes at least 15 *Pinus* native to North America (Negrón and Fettig 2014), but in Mediterranean forests of California *P. ponderosa*,

Fig. 18.6 Like other *Dendroctonus*, female *D. ponderosae* initiate host colonization (*Left*). Notice the distinctive vertical galleries that often end in a "J"; the deceased adult (within *red circle*); and the presence of bluestain introduced upon colonization by the beetle (*Right*). Some studies have shown that fungi associated with *D. ponderosae* and other bark beetles are capable of directly causing mortality (e.g., on *P. ponderosa* seedlings, Owen et al. 1987), but others have failed to demonstrate such an effect (Photo credits: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

lodgepole pine, *Pinus contorta* Dougl. ex Loud. (Fig. 18.6), and sugar pine, *P. lambertiana* Dougl., are preferred hosts. At higher elevations in the Sierra Nevada, significant levels of mortality have been attributed to *D. ponderosae* in whitebark pine, *Pinus albicaulis* Engelm, a tree species of concern that has been considered for listing as a threatened and endangered species (Federal Register 2011). The lifecycle of *D. ponderosae* is generally considered univoltine, but a mixture of univoltine and semivoltine (i.e., less than univoltine) life cycles commonly occur (Bentz et al. 2014), even within the same tree. In southern California, three generations may be completed in 2 years (San Bernardino National Forest, 2100 m elevation; Bentz et al. 2014), but truly bivoltine populations (i.e., two generations per year) have not been documented.

Most large-scale infestations of *D. ponderosae* occur in *P. contorta* forests in a near contiguous pattern and often across extensive areas. To that end, recent outbreaks have been severe and long lasting, with >27 million hectares impacted in western North America (BC Ministry of Forests, Lands and Natural Resource Operations 2012; USDA Forest Service 2012). As a result, significant research has been executed on *D. ponderosae* in the last decade in both Canada and the U.S., much of which was recently reviewed in a special issue titled "Mountain Pine

Beetle, a Major Disturbance Agent in US Western Coniferous Forests: A Synthesis of the State of Knowledge" (Negrón and Fettig 2014). I encourage the reader to consult this publication for more detailed information on *D. ponderosae*.

In *P. contorta* forests, *D. ponderosae* tends to initially colonize the largest trees with progressively smaller trees being attacked over time (Klein et al. 1978). Larger-diameter *P. contorta* (e.g., >23 cm dbh) provide for a higher reproductive potential and probability of beetle survival (Reid and Purcell 2011; Graf et al. 2012) because of the greater quantity of phloem available on which larvae feed. Based on research conducted in Oregon, Mitchell and Preisler (1991) reported that small-diameter *P. contorta* were not colonized unless they were near currently-infested larger trees, and that larger trees (≥23 cm dbh) were colonized with greater frequency than could be accounted for by a random attack model. Working in British Columbia, Canada, Safranyik et al. (1974) reported that *P. contorta* ≤25 cm dbh serve as *D. ponderosae* sinks, whereas those >25 cm dbh serve as sources producing more beetles than required to overcome host defenses. Whitehead et al. (2004) and Whitehead and Russo (2005) showed thinning *P. contorta* stands to a uniform residual inter-tree spacing of at least 4 m or ~400–625 trees/ha is effective for mitigating levels of tree mortality attributed to *D. ponderosae*.

In *P. ponderosa*, *D. ponderosae* tends to colonize trees in the small to mid-diameter classes (Olsen et al. 1996), but this may be an artifact of these forests being less dense, less continuous, and exhibiting a higher diversity of stand ages and tree sizes than *P. contorta* forests (Fettig et al. 2014). Working in the Colorado Front Range, U.S., Negrón and Popp (2004) reported the probability of *P. ponderosa* stands becoming infested by *D. ponderosae* is 0.71 when *P. ponderosa* basal area (cross-sectional area of trees at 1.37 m in height) is >17.1 m^2/ha and decreases to 0.21 when basal area is ≤17.1 m^2/ha. Interestingly, these values are similar to those reported by Larsson et al. (1983) for *P. ponderosa* forests in Oregon. In northeastern California, Egan et al. (2010) reported that higher levels of tree mortality occurred in unthinned *P. ponderosa* compared to pre-commercially thinned stands. Fiddler et al. (1989) showed that thinning significantly reduced the amount of *P. ponderosa* mortality caused by *D. ponderosae* in California. No tree mortality occurred in stands of <9 m^2/ha of basal area, which agrees with the optimal stocking level of 11 m^2/ha described by Oliver (1979, 1995). Mortality was reduced in thinned plots regardless of the level of thinning. In Mediterranean forests of California, where *D. brevicomis* and *D. ponderosae* often coexist in forests dominated by *P. ponderosa*, the role of *D. ponderosae* is usually secondary to that of *D. brevicomis*, particularly in larger-diameter trees (Fettig et al. 2010a). The two species occasionally colonize the same tree.

Progar et al. (2014) synthesized information related to the chemical ecology of *D. ponderosae*. In short, aggregation pheromones *trans*-verbenol and *cis*-verbenol are the primary compounds produced in the insect's hindgut (Miller and Lafontaine 1991). c*is*-Verbenol, produced by female *D. ponderosae*, increases the attraction of females to *exo*-brevicomin, but its effect is less than that of *trans*-verbenol (Miller and LaFontaine 1991). Attraction is enhanced by the presence of host volatiles α-pinene (Pitman et al. 1968) and myrcene (Borden et al. 1987), among others.

Male *D. ponderosae* release *exo*-brevicomin, which is a primary attractant of females, further augmenting mass attack (Amman and Lindgren 1995). Males also produce frontalin, which attracts females at low concentrations (Ryker and Libbey 1982). Several of these volatiles are commercially produced and effective attractants. During the latter stages of colonization, increasing amounts of verbenone are produced inhibiting additional *D. ponderosae* from infesting the target tree, thus limiting the number of infesting beetles to a density that increases the likelihood of brood survival (Amman and Lindgren 1995). Newly arriving *D. ponderosae* then reorient to adjacent trees where the cycle of colonization is repeated.

Fettig et al. (2014) analyzed the effectiveness of treatments for preventing and mitigating undesirable levels of tree mortality attributed to *D. ponderosae*. Tactics include silvicultural treatments that reduce stand density (thinning) and host susceptibility, sanitation harvests, applications of insecticides to protect individual trees (Fig. 18.7), and applications of semiochemicals including aggregation pheromones deployed in trap out or trap tree methods (i.e., where beetles are collected and later destroyed) and inhibitors used to disrupt colonization of individual trees or stands. Unlike *D. brevicomis*, verbenone is effective for reducing levels of tree mortality attributed to *D. ponderosae*, but efficacy varies (*see* Progar et al. 2014 for related factors), and studies indicate verbenone is ineffective for reducing levels of tree mortality attributed to *D. ponderosae* in *P. ponderosa* (Bentz et al. 1989; Gibson et al. 1991; Negrón et al. 2006). While several formulations of verbenone are registered in the U.S., pouches are most commonly used and stapled at maximum reach to individual trees (Fig. 18.8, left) or applied in a grid pattern when stand protection is the objective. Recently, a new biodegradable formulation of verbenone that is applied directly to the tree bole has been developed and demonstrated effective for protecting *P. contorta and P. lambertiana* from mortality attributed to *D. ponderosae* (Fettig et al. 2015) (Fig. 18.8, right).

18.2.3 Jeffrey Pine Beetle, Dendroctonus jeffreyi

Jeffrey pine beetle, *Dendroctonus jeffreyi* Hopkins, only colonizes Jeffrey pine, *P. jeffreyi* Grev. & Balf., a species that ranges from the Klamath Mountains in southwestern Oregon, throughout much of the Sierra Nevada and the Transverse and Peninsular Ranges in southern California, to the Sierra San Pedro Mártir of Baja California, Mexico. In Mediterranean forests of California, *D. jeffreyi* usually colonizes individual trees and its activity often goes unnoticed, but group kills of 20–30 trees are not uncommon (Smith et al. 2009). Large outbreaks may occur during periods of extended drought, but are typically associated with *P. jeffreyi* forests in other climatic zones. Paine et al. (1999) reported that 1–heptanol and n-heptane were attractive to *D. jeffreyi*, and a 5:95 blend is an effective trap lure (Strom et al. 2013). Frontalin, produced by males (Hall et al. 2002), reduces trap catches and

Fig. 18.7 A common method of protecting conifers from mortality attributed to bark beetles is to saturate all surfaces of the tree bole with an insecticide. Usually only high-value, individual trees growing in unique environments (e.g., campgrounds) or under unique circumstances are treated (Fettig et al. 2013b) (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

may have utility for tree protection (Strom et al. 2013). There are one to two generations per year (Furniss and Carolin 1977).

Tactics for managing *D. jeffreyi* infestations are limited, and much of what is implemented is based on research executed in other bark beetle-host systems, typically *D. brevicomis* in *P. ponderosa*. Sanitation harvests and applications of insecticides to individual trees are commonly recommended (Smith et al. 2009). The USDA Forest Service is conducting a long-term study to determine the effectiveness of thinning for reducing stand susceptibility to *D. jeffreyi*, but results are thus far inconclusive due to few trees being colonized and killed by *D. jeffreyi* (Fettig et al. 2012c) (Fig. 18.9).

Fig. 18.8 The antiaggregant verbenone has been evaluated as a tool for mitigating tree mortality attributed to bark beetles for several decades. The most common application method includes the use of pouch release devices stapled at maximum reach to individual trees prior to beetle flight (*Left*), or applied in a grid pattern to achieve uniform coverage when stand protection is the objective. Bead, flake and sprayable formulations have also been evaluated, but are not widely used. Fettig et al. (2015) recently developed a novel formulation of verbenone (SPLAT® Verb, ISCA Technologies Inc., Riverside, CA) that has shown a high degree of efficacy for protecting *P. contorta* from *D. ponderosae*. Rather than a single release device, SPLAT® Verb is an amorphous, flowable controlled-release emulsion that is also biodegradable (*Right*), which allows for significant labor cost savings by not having to retrieve release devices from the field after use (Photo credits: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

This area is included in a scientific study to determine the optimum tree density to minimize Jeffrey pine beetle *(Dendroctonus jeffreyi)* caused mortality in pure Jeffrey pine stands.

The long term goal of this study is to develop a set of thinning guidelines which will limit unacceptable levels of Jeffrey pine mortality caused by Jeffrey pine beetle. This investigation is lead by Dr Patrick Shea of the Pacific Southwest Research Station, Sheri Smith, North East Zone Entomologist for the Forest Service and Truckee Ranger District timber management personnel.

The experiment plots were established in 1997 and timber designation was accomplished by the Truckee Ranger District timber marking crew. Twelve (12) plots, each 25 acres in size were established. The blocks consist of plots thinned to 3 different densities (basal area of 80 square feet per acre, 120 square feet per acre and 180 square feet per acre) and control blocks averaging more than 200 square feet of basal area per acre.

Commercial thinning was executed by including this study area in the Canyons Timber Sale. Excess trees were harvested in 1998 by Hood Logging under the supervision of John Hood, Field Representative for Hood Logging. Special care was given to not damage trees or create excess soil disturbance.

Slash cleanup and removal of submerchantable material was accomplished by the Truckee Ranger District timber management personnel in 1999. Submerchantable trees were cut and skidded to a central landing location with ATV's where they were piled for disposal (fuelwood utilization, chipping, and burning).

Annually Jeffrey pine beetle-related mortality will be recorded. The measure of success for this project will be the maintenance of Jeffrey pine beetle caused mortality at acceptable levels, particularly during periods of drought stress and the development of thinning guidelines.

For more information contact the Truckee Ranger District Office located at 10342 Hwy 89N, Truckee, California or (530) 587 - 3558

Fig. 18.9 The USDA Forest Service is conducting several studies to determine the effectiveness of different silvicultural treatments to reduce the susceptibility of forests to bark beetle infestations, the results of which are used to inform practitioners of proper management techniques. The study above was initiated in 1997. Treatments include thinning from below (i.e., initiating in the smallest diameter classes) to a residual target basal area of 18.4 m^2/ha, 27.6 m^2/ha or 41.3 m^2/ha, and an untreated control (*see* Fettig et al. 2012c) (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

18.2.4 Red Turpentine Beetle, Dendroctonus valens

Red turpentine beetle, *Dendroctonus valens* LeConte, is a common bark beetle species found throughout much of North America. This species colonizes all *Pinus* within its native range, and perhaps several other tree species (Furniss and Carolin 1977). Attacks are usually confined to basal portions of stressed, weakened, or dead and dying trees, and rarely cause mortality of healthy trees (Fig. 18.10). *Dendroctonus valens* was accidentally introduced into China from North America in the 1980s, and has caused significant levels of tree mortality in Chinese red pine, *P. tabuliformis* Carr. (Yan et al. 2005). There is concern that genetic changes in the fungus associated with *D. valens*, which likely contributed to the invasive success of the beetle–fungal complex in China, could pose an increased threat to North American forests if *D. valens* was re-introduced back into North America from China (Lu et al. 2011). The lifecycle is univoltine throughout much of the range including mid-elevations of the Sierra Nevada, but two to three generations per year may occur in warmer areas (Furniss and Carolin 1977).

Fig. 18.10 A robber fly (Diptera: Asilidae) predating upon *Dendroctonus valens* on the bark of *Pinus ponderosa* in California. *Dendroctonus valens* is the largest bark beetle in North America. Attacks are usually confined to the basal portions of stressed, weakened, or dead and dying trees (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

Hobson et al. (1993) reported significant increases in *D. valens* trap catch attributable to 3-carene and α-pinene when added to β-pinene. Combinations of these three kairomones comprise an effective bait. More recently, it was demonstrated that female *D. valens* produce frontalin (Zhang and Sun 2006), which likely functions as both a sex and aggregation pheromone (Liu et al. 2013). Verbenone is present in the frass (Grégoire et al. 1991) and hindgut of *D. valens* (Yan et al. 2004), and has been demonstrated to reduce numbers of attacks on individual trees (Sun et al. 2003; Gillette et al. 2006; Fettig et al. 2008a). Working in the central Sierra Nevada, Fettig et al. (2006a) showed that California five-spined ips, *I. paraconfusus* LeConte, attack densities in logging slash were inversely related to *D. valens* attacks on adjacent freshly-cut stumps, and later demonstrated that components of the *I. paraconfusus* aggregation pheromone were inhibitory to *D. valens* (Fettig et al. 2005b). Levels of inhibition were increased with the addition of verbenone (Fettig et al. 2007b). However, due to the species limited pest status in North America, efforts there to develop a semiochemical-based tool for tree protection have been limited.

Management strategies are rarely implemented for *D. valens* in North America. Care should be taken to avoid damaging residual trees during harvest operations (Fig. 18.11), which may produce populations that attack nearby healthy trees, as

Fig. 18.11 During harvest operations, care should be taken to avoid damaging residual trees as populations of *Dendroctonus valens* may buildup in these hosts and then colonizing adjacent healthy trees. This can facilitate colonization by more aggressive species, such as *Dendroctonus brevicomis* (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

trees weakened by *D. valens* are more likely to be colonized and killed by more aggressive species (Furniss and Carolin 1977). The impact of *D. valens* in Mediterranean forests of California may become more significant due to the increased use of prescribed fire, which makes trees more susceptible to colonization by *D. valens* (Fettig et al. 2008b).

18.2.5 California Fivespined Ips, **Ips paraconfusus**

Ips paraconfusus was synonymous with pinyon ips, *Ips confusus* LeConte, until 1970 (Lanier 1970). As such, the reader must exert caution when consulting the early literature concerning these species. *Ips paraconfusus* occurs from southern Oregon to southern California and east to the crest of the Sierra Nevada and Cascade mountain ranges (Furniss and Carolin 1977). Recently, populations were recorded in Washington (Murray et al. 2013). All *Pinus* occurring within the range of *I. paraconfusus* are susceptible to colonization, especially *P. ponderosa*. Like other *Ips*, endemic populations of *I. paraconfusus* infest forest debris, widely scattered individual trees or small groups of trees. Top-killing of *P. ponderosa* is common, and often followed by *D. brevicomis* colonization of the main stem (Furniss and Carolin 1977). Occasionally, outbreaks result in mortality of large numbers of trees, but are usually associated with improper slash management (Fig. 18.12) or drought. *Ips paraconfusus* is also a vector of the fungus *Fusarium circinatum* Nirenberg & O'Donnell (Fox et al. 1991) that causes pitch canker disease in Monterey pine, *P. radiata* D. Don., and other *Pinus*, and represents a serious threat to *Pinus* production in Mediterranean forests worldwide (Wingfield et al. 2008). Male *I. paraconfusus* construct a nuptial chamber in the phloem and attract multiple females, typically three, yielding the classic "Y-shaped" gallery pattern. Males produce three aggregation pheromone components, ipsenol, ipsdienol, and *cis*-verbenol, which comprised the first pheromone to be fully described for any bark beetle species (Silverstein et al. 1966). There are two to five generations per year (Furniss and Carolin 1977).

Management strategies implemented for *I. paraconfusus* are similar to those recommended for other *Ips*. Early work by Buckhorn (1957) in Oregon demonstrated that tree mortality attributed to *Ips* was greatest when slash was generated between February and July. Conversely, the *safe period* for producing slash was August through December. During this time, host material declines in suitability over time as phloem moisture is reduced (Sartwell 1970). Most slash management treatments promote desiccation of slash and/or rendering slash unsuitable for colonization by chipping, cutting, lopping-and-scattering, or piling-and-burning (DeGomez et al. 2008). Slash that is infested by *I. paraconfusus* and related species can usually be successfully treated by solarization, a process that involves covering slash piles with clear plastic and securely anchoring the plastic to the ground. To be effective, solarization must result in temperatures that are high enough (>45 °C) to kill developing brood within slash prior to emergence. Insecticides may be applied to protect individual, high-value trees, but are rarely used. Shea and Neustein (1995) used baited

Fig. 18.12 Outbreaks of *Ips paraconfusus* are often associated with improper slash management (*Left*) or drought. Under most circumstances, slash should be treated to promote desiccation and/or to render it unsuitable for colonization by *Ips paraconfusus* and conspecifics by chipping, lopping-and-scattering (*Right*), burning or other treatments (DeGomez et al. 2008). If properly applied, this will reduce the risk of populations increasing in slash (i.e., where there is little or no host resistance) and then colonizing adjacent trees (Photo credits: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

traps to reduce the impact of *I. paraconfusus* in stands of Torrey pine, *Pinus torreyana* Parry ex Car., however, semiochemical-based tools for tree protection have not been commercialized for this species.

18.2.6 Pine Engraver, Ips pini

Pine engraver, *Ips pini* (Say), has a transcontinental distribution, and is one of the most common bark beetles in North America (Kegley et al. 1997). The species generally colonizes slash, saplings, and weakened trees. Top killing of *P. ponderosa* is common (Fig. 18.13, left), and often facilitates colonization by more aggressive bark beetles. Colonization rates are negatively correlated with tree diameter in *P. ponderosa* (Kolb et al. 2006), and trees 5–20 cm dbh are most frequently colonized. Infestations of *I. pini* are often short-lived, but may increase in scale and duration when suitable host material is plentiful and populations grow sufficient to kill apparently-healthy trees. Males construct a nuptial chamber in the phloem and produce ipsdienol and lanierone, which attracts multiple females (Fig. 18.13, right). These semiochemicals make an effective bait, but efficacy varies geographically (Lanier et al. 1972; Seybold et al. 1992, 1995). California populations are attracted to high ratios of (−)-ipsdienol, and lanierone has no effect on attraction (Miller et al. 1997). There are one to two generations per year (Furniss and Carolin 1977).

Fig. 18.13 Top killing of *Pinus ponderosa* by *Ips pini* is common (*Left*). Male *I. pini* construct a central nuptial chamber in the phloem and produce ipsdienol and lanierone, which attracts multiple females, typically 3–6. This results in a unique gallery pattern characteristic of the species (*Right*) (Photo credits: T. DeGomez, University of Arizona, with permission)

Similar to *I. paraconfusus*, guidelines for managing *I. pini* include separating slash production in time and space; generating slash during periods of beetle inactivity; limiting the size of treatment blocks; and treating slash through solarization, burning, chipping, lop-and-scattering and/or direct removal from the site (DeGomez et al. 2008). Insecticides may be applied to protect individual, high-value trees. While there is evidence that several semiochemicals are inhibitory to *I. pini* (Miller et al. 1995; Huber et al. 2001), none are used operationally for tree protection in California.

18.2.7 Pinyon Ips, Ips confusus

Notable outbreaks of *I. confusus* frequently occur in the Great Basin, U.S., and are usually associated with forest densification and drought (Kleinman et al. 2012). The species is mentioned here because although most of the mortality attributed to *I. confusus* in California occurs in other climatic zones, both single leaf pinyon, *P. monophylla* Torr. & Frem., and Parry pinyon, *P. quadrifolia* Parl. ex Sudw., grow to some degree in Mediterranean forests and are occasionally colonized and killed by *I. confusus* (Fig. 18.14). Males produce three aggregation pheromone components,

Fig. 18.14 *Pinus monophylla* killed (fading crowns) by *Ips confusus* (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

ipsenol, ipsdienol, and *cis*-verbenol (Young et al. 1973; Birch et al. 1977), which constitute an effective bait. In a somewhat unique adaptation, *I. confusus* adults overwinter in large numbers at the base of trees. There are two to four generations per year (Furniss and Carolin 1977).

Guidelines for managing *I. confusus* are similar those for other *Ips* (DeGomez et al. 2008). Insecticides may be applied to protect individual, high-value trees, but are rarely used (Fettig et al. 2006b), and caution should be exerted if harvesting of pinyon nuts is planned.

18.2.8 Fir Engraver, Scolytus ventralis

Fir engraver, *Scolytus ventralis* LeConte, frequently colonizes *Abies*, particularly white fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., in Mediterranean forests of California. Trees of all sizes may be attacked and killed (Fig. 18.15), but outbreaks are typically associated with trees stressed by drought, defoliation (e.g., by Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough)), root pathogens or other factors (Berryman and Ferrell 1988; Ferrell et al. 1994). Large numbers of trees may be killed by *S. ventralis* following prescribed fire (Schwilk et al. 2006; Fettig and McKelvey 2014), particularly in the smaller-diameter classes (Table 18.2), but these treatments are usually implemented to promote *Pinus* over

Fig. 18.15 *Scolytus ventralis* frequently colonizes *Abies*, and produces a very distinctive gallery pattern that scores the sapwood. Infestations are typically associated with trees stressed by drought, defoliation, and/or root pathogens (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

Abies and therefore this mortality may not interfere with management objectives. There is one generation per year throughout much of the range (Furniss and Carolin 1977). Our understanding of the chemical ecology of *S. ventralis* is poor. Macías-Sámano et al. (1998) hypothesized that both sexes of *S. ventralis* aggregate on a tree in response to odors emitted by the tree, which intensify when females bore into the bark further liberating host odors. The lack of identification of a strong attractant has, to some degree, limited other aspects of research on *S. ventralis*.

Tactics for managing *S. ventralis* are limited to tree removals (thinning) that reduce stand density and presumably host susceptibility (although specific studies have not been conducted to determine the influence of thinning on *S. ventralis*), and sanitation harvests (Berryman and Ferrell 1988).

18.2.9 Cedar Bark Beetles, **Phloeosinus** *spp.*

The genus *Phloeosinus* contains some 25 species in North America, which generally colonize the twigs, branches and stems of trees weakened by drought or other

Table 18.2 Numbers of trees killed by bark beetles by diameter class (mid-point of 10 cm diameter classes) and treatment (*LoD* low structural diversity, *HiD* high structural diversity) in 12 experimental plots ranging in size from 77 to 144 ha 10 years following prescribed burns (*B*), California (From Fettig and McKelvey 2014)

Treatment	Dbh Class	*Dendroctonus brevicomis*	*Dendroctonus ponderosae*	*Dendroctonus jeffreyi*	*Ips* spp.	*Scolytus ventralis*	Total
HiD + B	24.1	190	448	7	129	1354	2128
	34.3	198	227	11	28	537	1001
	44.5	102	59	2	1	157	321
	54.7	66	10	2	2	27	107
	>59.7	250	28	2	1	14	295
	All	806	772	24	161	2089	3852
HiD	24.1	119	450	1	2	1071	1643
	34.3	89	175	1	0	626	891
	44.5	33	37	2	0	200	272
	54.7	27	10	0	0	29	66
	>59.7	100	13	0	0	17	130
	All	368	685	4	2	1943	3002
LoD + B	24.1	65	221	5	252	1151	1694
	34.3	86	104	3	60	549	802
	44.5	18	13	1	2	66	100
	54.7	0	4	0	0	*	4
	>59.7	*	*	0	*	0	0
	All	169	342	9	314	1766	2600
LoD	24.1	12	68	4	6	586	676
	34.3	27	30	1	1	381	440
	44.5	11	3	0	0	67	81
	54.7	1	0	0	0	*	1
	>59.7	0	2	0	0	1	3
	All	51	103	5	7	1035	1201
Total		1394	1902	42	484	6833	10,655

Asterisks denote the host was not present

factors (Furniss and Carolin 1977). Several hosts are colonized in Mediterranean forests of California, including coast redwood, *Sequoia sempervirens* (D. Don) Endl., giant sequoia, *Sequoiadendron giganteum* (Lindl.) J. Buchh., incense cedar, *Calocedrus decurrens* (Torr.) Florin, and Monterey cypress, *Cupressus macrocarpa* Hartw. While generally not considered an important cause of tree mortality, severe droughts in the Sierra Nevada during the 1980s and then again in the early 2000s resulted in significant branch flagging and some tree mortality attributed to the western cedar bark beetle, *Ph. punctatus* LeConte (USDA Forest Service 2003). In addition, some *Phloeosinus* spp. vector the fungus *Seiridium cardinal* (Wag.), which may result in cypress canker, a disease that is of increasing importance worldwide (Graniti 1998). Management strategies are rarely implemented for these species.

18.2.10 Wood Borers

In Mediterranean forests of California, two wood-boring species, the California flatheaded borer, *Phaenops californica* (Van Dyke), and flatheaded fir borer, *Phaenops drummondi* (Kirby) (Coleoptera: Buprestidae), occasionally cause noticeable levels of tree mortality. *Phaenops californica* is native to western North America (Lyon 1970), but perhaps exerts its greatest impact in California where it colonizes *P. ponderosa* and *P. jeffreyi* in addition to other *Pinus*. Typically, stressed, dead or dying trees are colonized (Fig. 18.16). However, *Ph. californica* may colonize and kill apparently-healthy trees, and repeated attacks may facilitate those of more aggressive species, such as *D. brevicomis* or *I. pini*. The life cycle is quite variable, and

Fig. 18.16 In many cases, bark beetles serve as keystone species facilitating colonization of trees by other organisms. For example, Stephen and Dahlsten (1976) collected >100 species of insects on the bark surface of *Pinus ponderosa* shortly after being colonized by *Dendroctonus brevicomis*. In particular, wood borers help facilitate decomposition and nutrient cycling (Photo credit: C. Fettig, Pacific Southwest Research Station, USDA Forest Service)

may take from several months to several years to complete (Lyon 1970). *Phaenops drummondi* has a transcontinental distribution and colonizes a wide variety of hosts in Pinaceae. However, its impact is most significant in the western U.S. where it readily colonizes *A. concolor* and is often a common associate of *S. ventralis*. There is one generation per year (Furniss and Carolin 1977). Management strategies are rarely implemented for either species.

While wood borers may not be considered an important source of tree mortality overall, Fettig et al. (2008a) reported that wood borers were directly contributing to tree mortality in fire-injured *P. ponderosa* during the second year following prescribed fires in California, but similar effects were not observed in related studies (e.g., Fettig et al. 2010a, b). Lumber degrade and introduction of wood decay fungi may be of concern if salvage is planned. Some wood borers (e.g., *Monochamus* spp., Coleoptera: Cerambycidae) are vectors of a wilting disease caused by pine wood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer) Nickel (Linit 1988). Infection affects water transport in susceptible (non-native) *Pinus*, often rapidly resulting in tree death.

18.3 Conclusions

In the Mediterranean forests of California, most (>90 %) bark beetle and wood borer species are beneficial while several others are capable of occasionally causing undesirable levels of tree mortality (Table 18.1). However, this mortality is essential to the proper functioning of these ecosystems and influences ecological succession, community structure, nutrient cycling, and habitat creation (Franklin et al. 1987). For example, snags created by the activity of bark beetles and wood borers provide critical habitat for insects and many other species of wildlife (Fig. 18.16), including amphibians, reptiles, birds and mammals (Bull et al. 1997). Furthermore, while infestations of some species may affect timber and fiber production, and indirectly a wide range of ecosystem goods and services, the mortality of individual or small groups of trees provides fine-scale spatial heterogeneity in composition and structure thereby increasing forest resilience and resistance to a multitude of disturbances (Fettig 2012). This differs from the negative impacts associated with large-scale infestations or outbreaks that homogenize the landscape and may merit intervention.

References

Amman GD, Lindgren BS (1995) Semiochemicals for management of mountain pine beetle: status of research and application. In: Salom SM, Hobson KR (eds) Application of semiochemicals for management of bark beetle infestations-proceedings of an informal conference. USDA Forest Service General Technical Report INT-GTR-318, Ogden, pp 14–22

Atkins MD (1966) Behavioral variation among scolytids in relation to their habitat. Can Entomol 98:285–288

Bedard WD, Tilden PE, Wood DL et al (1969) Western pine beetle: field response to its sex pheromone and a synergistic host terpene, myrcene. Science 164:1284–1285

Bedard WD, Lindahl KQ Jr, Tilden PE, Wood DL (1985) Behavior of the western pine beetle during host colonization. J Chem Ecol 11:1249–1261

Bentz BJ, Lister CK, Schmid JM et al. (1989) Does verbenone reduce mountain pine beetle attacks in susceptible stands of ponderosa pine? USDA Forest Service Research Note RM-RN-495, Fort Collins

Bentz BJ, Régnière J, Fettig CJ et al (2010) Climate change and bark beetles of the western United States and Canada: direct and indirect effects. Bioscience 60:602–613

Bentz B, Vandygriff J, Jensen C et al (2014) Mountain pine beetle voltinism and life history characteristics across latitudinal and elevational gradients in the western United States. For Sci 60:434–449

Berryman AA, Ferrell GT (1988) The fir engraver beetle in western states. In: Berryman AA (ed) Dynamics of forest insect populations: patterns, causes, implications. Plenum Press, New York, pp 556–577

Bertram SL, Paine TD (1994) Influence of aggregation inhibitors (verbenone and ipsdienol) on landing and attack behavior of *Dendroctonus brevicomis* (Coleoptera: Scolytidae). J Chem Ecol 20:1617–1629

Birch MC, Tilden PE, Wood DL et al (1977) Biological activity of compounds isolated from air condensates and frass of the bark beetle, *Ips confusus*. J Insect Physiol 23:1373–1377

Borden JH (1997) Disruption of semiochemical-mediated aggregation in bark beetles. In: Cardé RT, Minks AK (eds) Insect pheromone research, new directions. Chapman & Hall, New York, pp 421–437

Borden JH, Ryker LC, Chong L et al (1987) Response of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), to five semiochemicals in British Columbia lodgepole pine forests. Can J For Res 17:118–128

British Columbia (BC) Ministry of Forests, Lands and Natural Resource Operations (2012) Facts about B.C.'s mountain pine beetle. http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/Updated-Beetle-Facts_April2013.pdf. Accessed 9 Feb 2015

Buckhorn WJ (1957) Scheduling of cutting or thinning operations in immature stands of ponderosa pine to minimize damage by the Oregon pine ips. USDA Forest Service Research Note PNW-RN-142, Portland

Bull EL, Parks CG, Torgersen RR (1997) Trees and logs important to wildlife in the interior Columbia River basin. USDA Forest Service General Technical Report PNW-GTR-391, Portland

Byers JA (1995) Host tree chemistry affecting colonization in bark beetles. In: Cardé RT, Bell WJ (eds) Chemical ecology of insects 2. Chapman & Hall, New York, pp 154–213

Byers JA, Wood DL (1980) Interspecific inhibition of the response of the bark beetles *Dendroctonus brevicomis* and *Ips paraconfusus* to their pheromones in the field. J Chem Ecol 6:149–164

Byers JA, Wood DL, Craig J, Hendry LB (1984) Attractive and inhibitory pheromones produced in the bark beetle, *Dendroctonus brevicomis*, during host colonization: regulation of inter- and intraspecific competition. J Chem Ecol 10:861–877

DeGomez T, Fettig CJ, McMillin JD et al. (2008) Managing slash to minimize colonization of residual leave trees by *Ips* and other bark beetle species following thinning in southwestern ponderosa pine. AZ1448. University of Arizona, College of Agriculture and Life Sciences, Tucson

Edmonds RL, Eglitis A (1989) The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. Can J For Res 9:853–859

Egan JM, Jacobi WR, Negrón JF et al (2010) Forest thinning and subsequent bark beetle-caused mortality in northeastern California. For Ecol Manag 260:1832–1842

Farris KL, Zack S (2005) Woodpecker-snag interactions: an overview of current knowledge in ponderosa pine systems. USDA Forest Service General Technical Report PSW-GTR-198, Albany

Federal (U.S.) Register (2011) Proposed rules, Tuesday July 19, 2011. 76:42631–42654

Ferrell GT, Otrosina WJ, DeMars CJ (1994) Predicting susceptibility of white fir during a drought-associated outbreak of the fir engraver, *Scolytus ventralis*, in California. Can J For Res 24:302–305

Fettig CJ (2012) Forest health and bark beetles. In: North M (ed) Managing Sierra Nevada forests. USDA Forest Service General Technical Report PSW-GTR-237, Albany, pp 13–22

Fettig CJ, McKelvey SR (2014) Resiliency of an interior ponderosa pine forest to bark beetle infestations following fuel-reduction and forest-restoration treatments. Forests 5:153–176

Fettig CJ, Hilszczański J (2015) Management strategies for bark beetles in conifer forests. In: Vega FE, Hofstetter RW (eds) Bark beetles: biology and ecology of native and invasive species. Springer, London, pp 555–584

Fettig CJ, Borys RR, Dabney CP et al (2005a) Disruption of red turpentine beetle attraction to baited traps by the addition of California fivespined ips pheromone components. Can Entomol 137:748–752

Fettig CJ, Shea PJ, Borys RR (2005b) Spatial and temporal distributions of four bark beetle species (Coleoptera: Scolytidae) along two elevational transects in the Sierra Nevada. Pan Pacific Entomol 81:6–19

Fettig CJ, Allen KK, Borys RR et al (2006a) Effectiveness of bifenthrin (Onyx™) and carbaryl (Sevin® SL) for protecting individual, high-value trees from bark beetle attack (Coleoptera: Curculionidae: Scolytinae) in the western United States. J Econ Entomol 99:1691–1698

Fettig CJ, McMillin JD, Anhold JA et al (2006b) The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. For Ecol Manag 230:55–68

Fettig CJ, Klepzig KD, Billings RF et al (2007a) The effectiveness of vegetation management practices for prevention and control of bark beetle outbreaks in coniferous forests of the western and southern United States. For Ecol Manag 238:24–53

Fettig CJ, McKelvey SR, Dabney CP, Borys RR (2007b) The response of *Dendroctonus valens* (Coleoptera: Scolytidae) and *Temnochila chlorodia* (Coleoptera: Trogossitidae) to *Ips paraconfusus* (Coleoptera: Scolytidae) pheromone components and verbenone. Can Entomol 139:141–145

Fettig CJ, Dabney CP, McKelvey SR, Huber DPW (2008a) Nonhost angiosperm volatiles and verbenone protect individual ponderosa pines from attack by western pine beetle and red turpentine beetle (Coleoptera: Curculionidae, Scolytinae). West J Appl For 23:40–45

Fettig CJ, Borys RR, McKelvey SR, Dabney CP (2008b) Blacks Mountain Experimental Forest: bark beetle responses to differences in forest structure and the application of prescribed fire in interior ponderosa pine. Can J For Res 38:924–935

Fettig CJ, McKelvey SR, Borys RR et al (2009a) Efficacy of verbenone for protecting ponderosa pine stands from western pine beetle (Coleoptera: Curculionidae, Scolytinae) attack in California. J Econ Entomol 102:1846–1858

Fettig CJ, McKelvey SR, Dabney CP et al (2009b) Response of *Dendroctonus brevicomis* to different release rates of nonhost angiosperm volatiles and verbenone in trapping and tree protection studies. J Appl Entomol 133:143–154

Fettig CJ, Borys RR, Dabney CP (2010a) Effects of fire and fire surrogate treatments on bark beetle-caused tree mortality in the Southern Cascades, California. For Sci 56:60–73

Fettig CJ, McKelvey SR, Cluck DL et al (2010b) Effects of prescribed fire and season of burn on direct and indirect levels of tree mortality in ponderosa and Jeffrey pine forests in California, USA. For Ecol Manag 260:207–218

Fettig CJ, McKelvey SR, Dabney CP, Huber DPW (2012a) Responses of *Dendroctonus brevicomis* (Coleoptera: Curculionidae) in behavioral assays: implications to development of a semiochemical-based tool for tree protection. J Econ Entomol 105:149–160

Fettig CJ, McKelvey SR, Dabney CP et al (2012b) Efficacy of "Verbenone Plus" for protecting ponderosa pine trees and stands from *Dendroctonus brevicomis* (Coleoptera: Curculionidae) attack in British Columbia and California. J Econ Entomol 105:1668–1680

Fettig CJ, Hayes CJ, Jones KJ et al (2012c) Thinning Jeffrey pine stands to reduce susceptibility to bark beetle infestations in California, U.S.A. Agric For Entomol 14:111–117

Fettig CJ, Reid ML, Bentz BJ et al (2013a) Changing climates, changing forests: a western North American perspective. J For 111:214–228

Fettig CJ, Grosman DM, Munson AS (2013b) Advances in insecticide tools and tactics for protecting conifers from bark beetle attack in the western United States. In: Trdan S (ed) Insecticides – development of safer and more effective technologies. InTech, Rijeka, pp 472–492

Fettig CJ, Gibson KE, Munson AS, Negrón JF (2014) Cultural practices for prevention and mitigation of mountain pine beetle infestations. For Sci 60:450–463

Fettig CJ, Munson AS, Reinke M, Mafra-Neto A (2015) A novel semiochemical tool for protecting *Pinus contorta* from mortality attributed to *Dendroctonus ponderosae* (Coleoptera: Curculionidae). J Econ Entomol. 108:173–182

Fiddler GO, Hart DR, Fiddler TA, McDonald PM (1989) Thinning decreases mortality and increases growth of ponderosa pine in northeastern California. USDA Forest Service Research Paper PSW-RP-194, Berkeley

Fox JW, Wood DL, Koehler CS, O'Keefe ST (1991) Engraver beetles (Scolytidae: *Ips* species) as vectors of the pitch canker fungus, *Fusarium subglutinans*. Can Entomol 123:1355–1367

Franceschi VR, Krokene P, Christiansen E, Krekling T (2005) Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytol 167:353–376

Franklin J, Shugart H, Harmon M (1987) Tree death as an ecological process. Bioscience 37:550–556

Furniss RL, Carolin VM (1977) Western forest insects. USDA Forest Service Miscellaneous Publication, Washington, DC

Gibson KE, Schmitz RF, Amman GD, Oakes RD (1991) Mountain pine beetle response to different verbenone dosages in pine stands of western Montana. USDA Forest Service Research Paper INT-RP-444, Ogden

Gillette NE, Stein JD, Owen DR et al (2006) Verbenone-releasing flakes protect individual *Pinus contorta* from attack by *Dendroctonus ponderosae* and *Dendroctonus valens* (Coleoptera: Curculionidae, Scolytinae). Agric For Entomol 8:243–251

Graf M, Reid ML, Aukema BH, Lindgren BS (2012) Association of tree diameter with body size and lipid content of mountain pine beetles. Can Entomol 144:467–477

Graniti A (1998) Cypress canker: a pandemic in progress. Annu Rev Phytopathol 36:91–114

Grégoire JC, Baisier M, Drumont A et al (1991) Volatile compounds in the larval frass of *Dendroctonus valens* and *Dendroctonus micans* (Coleoptera: Scolytidae) in relation to oviposition by the predator, *Rhizophagus grandis* (Coleoptera: Rhizophagidae). J Chem Ecol 17:2003–2019

Hall GM, Tittiger C, Blomquist GJ et al (2002) Male Jeffrey pine beetle, *Dendroctonus jeffreyi*, synthesizes the pheromone component frontalin in anterior midgut tissue. Insect Biochem Mol Biol 11:1525–1532

Hobson KR, Wood DL, Cool LC et al (1993) Chiral specificity in responses by the bark beetle *Dendroctonus valens* to host kairomones. J Chem Ecol 19:1837–1846

Huber DPW, Borden JH, Stastny M (2001) Response of the pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae), to conophthorin and other angiosperm bark volatiles in the avoidance of non-hosts. Agric For Entomol 3:225–232

Jones ME, Paine TD, Fenn ME, Poth MA (2004) Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. For Ecol Manag 200:67–76

Kauffmann E (2003) Climate and topography. In: Parisi M (ed) Atlas of biodiversity of California. California Department of Fish and Game, Sacramento, pp 12–15

Kegley SL, Livingston RL, Gibson KE (1997) Pine engraver, *Ips pini* (Say), in the western United States. USDA Forest Service FIDL 122, Portland

Kelsey RG, Joseph G (2003) Ethanol in ponderosa pine as an indicator of physiological injury from fire and its relationship to secondary beetles. Can J For Res 33:870–884

Kinzer GW, Fentiman AF, Page TF et al (1969) Bark beetle attractants: identification, synthesis and field bioassay of a new compound isolated from *Dendroctonus*. Nature 221:477–478

Klein WH, Parker DL, Jensen CE (1978) Attack, emergence, and stand depletion trends of the mountain pine beetle in a lodgepole pine stand during an outbreak. Environ Entomol 112:185–191

Kleinman SJ, DeGomez TE, Snider GB, Williams KE (2012) Large-scale pinyon ips (*Ips confusus*) outbreak in southwestern United States tied with elevation and land cover. J For 110:194–200

Kolb TE, Guerard N, Hofstetter RW, Wagner MR (2006) Attack preference of *Ips pini* on *Pinus ponderosa* in northern Arizona: tree size and bole position. Agric For Entomol 8:295–303

Lanier GN (1970) Biosystematics of North American *Ips* (Coleoptera: Scolytidae): Hopping's group IX. Can Entomol 102:1139–1163

Lanier GN, Birch MC, Schmitz RF, Furniss MM (1972) Pheromones of *Ips pini* (Coleoptera: Scolytidae): variation in response among three populations. Can Entomol 104:1917–1923

Larsson S, Oren R, Waring RH, Barrett JW (1983) Attacks of mountain pine beetle as related to tree vigor of ponderosa pine. For Sci 29:395–402

Lieutier F (2004) Host resistance to bark beetles and its variations. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe. Kluwer, Dordrecht, pp 135–180

Linit MJ (1988) Nematode-vector relationships in the pine wilt disease system. J Chem Ecol 20:227–235

Liu Z, Xu B, Miao Z, Sun J (2013) The pheromone frontalin and its dual function in the invasive bark beetle *Dendroctonus valens*. Chem Senses 38:485–495

Lu M, Wingfield MJ, Gillette N, Sun J-H (2011) Do novel genotypes drive the success of an invasive bark beetle–fungus complex? Implications for potential reinvasion. Ecology 92:2013–2019

Lyon RL (1970) California flatheaded borer. USDA Forest Service FIDL 24, Washington, DC

Macías-Sámano JE, Borden JH, Gries R et al (1998) Primary attraction of the fir engraver, *Scolytus ventralis*. J Chem Ecol 24:1049–1075

Miller JM, Keen FP (1960) Biology and control of the western pine beetle. USDA Forest Service Miscellaneous Publication 800, Washington, DC

Miller DR, LaFontaine JP (1991) *cis*-Verbenol: an aggregation pheromone for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). J Entomol Soc Br Columbia 88:34–38

Miller MC, Moser JC, McGregor M et al (1987) Potential for biological control of native North American *Dendroctonus* beetles (Coleoptera: Scolytidae). Ann Entomol Soc Am 80:417–428

Miller DR, Borden JH, Lindgren BS (1995) Verbenone: dose-dependent interruption of pheromone-based attraction of three sympatric species of pine bark beetles (Coleoptera: Scolytidae). Environ Entomol 24:692–696

Miller DR, Gibson KE, Raffa KF et al (1997) Geographic variation in response of pine engraver, *Ips pini*, and associated species to pheromone, lanierone. J Chem Ecol 23:2013–2031

Mitchell RG, Preisler HK (1991) Analysis of spatial patterns of lodgepole pine attacked by outbreak populations of the mountain pine beetle. For Sci 37:1390–1408

Moeck HA, Wood DL, Lindahl KQ Jr (1981) Host selection behavior of bark beetles (Coleoptera: Scolytidae) attacking *Pinus ponderosa*, with special emphasis on the western pine beetle, *Dendroctonus brevicomis*. J Chem Ecol 7:49–83

Murray TA, Kohler GR, Willhite EA (2013) *Ips paraconfusus* Lanier (Coleoptera: Curculionidae): new records of the California fivespined ips from Washington State and the Columbia River Gorge in Oregon. Coleop Bull 67:28–31

Negrón JF, Fettig CJ (2014) Mountain pine beetle, a major disturbance agent in US western coniferous forests: a synthesis of the state of knowledge. For Sci 60:409–413

Negrón JF, Popp JB (2004) Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. For Ecol Manag 191:17–27

Negrón JF, Allen K, McMillin J, Burkwhat H (2006) Testing verbenone for reducing mountain pine beetle attacks in ponderosa pine in the Black Hills, South Dakota. USDA Forest Service Research Note RMRS-RN-31, Fort Collins

Oliver WW (1979) Fifteen-year growth patterns after thinning a ponderosa pine-Jeffrey pine plantation in northeastern California. USDA Forest Service Research Paper PSW-RP-141, Berkeley

Oliver WW (1995) Is self-thinning in ponderosa pine ruled by *Dendroctonus* bark beetles? In: Eskew LG (compl) Forest health through silviculture: proceedings of the 1995 national silviculture workshop, USDA Forest Service General Technical Report RM-GTR-267, Fort Collins, pp 213–218

Olsen WK, Schmid JM, Mata SA (1996) Stand characteristics associated with mountain pine beetle infestations in ponderosa pine. For Sci 42:310–327

Owen DR, Lindahl KQ, Wood DL, Parmeter JR Jr (1987) Pathogenicity of fungi isolated from *Dendroctonus valens*, *D. brevicomis*, and *D. ponderosae* to ponderosa pine seedlings. Phytopathology 77:631–636

Paine TD, Hanlon CC (1991) Response of *Dendroctonus brevicomis* and *Ips paraconfusus* (Coleoptera: Scolytidae) to combinations of synthetic pheromone attractants and inhibitors verbenone and ipsdienol. J Chem Ecol 17:2163–2176

Paine TD, Raffa KF, Harrington TC (1997) Interactions among scolytid bark beetles, their associated fungi, and live host conifers. Annu Rev Entomol 42:179–206

Paine TD, Millar JG, Hanlon CC, Hwang JS (1999) Identification of semiochemicals associated with Jeffrey pine beetle, *Dendroctonus jeffreyi*. J Chem Ecol 25:433–453

Pitman GB, Vité JP, Kinzer GW, Fentiman AF Jr (1968) Bark beetle attractants: *trans*-verbenol isolated from *Dendroctonus*. Nature 218:168

Progar RA, Gillette N, Fettig CJ, Hrinkevich K (2014) Applied chemical ecology of the mountain pine beetle. For Sci 60:414–433

Raffa KF, Berryman AA (1982) Gustatory cues in the orientation of *Dendroctonus ponderosae* (Coleoptera: Scolytidae) to host trees. Can Entomol 114:97–104

Raffa KF, Berryman AA (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecol Monogr 53:27–49

Reid ML, Purcell JRC (2011) Condition-dependent tolerance of monoterpenes in an insect herbivore. Arthropod Plant Interact 5:331–337

Ryker LC, Libbey LM (1982) Frontalin in the male mountain pine beetle. J Chem Ecol 8:1399–1409

Safranyik L, Shrimpton DM, Whitney HS (1974) Management of lodgepole pine to reduce losses from the mountain pine beetle. Canadian Forest Service Forest Technical Report 1, Victoria

Sartwell C (1970) *Ips pini* attack density in ponderosa pine thinning slash as related to felling date in eastern Oregon. USDA Forest Service Research Note PNW-RN-131, Portland

Schwilk DW, Knapp EE, Ferrenberg SM et al (2006) Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. For Ecol Manag 232:36–45

Seybold SJ, Teale SA, Wood DL et al (1992) The role of lanierone in the chemical ecology of *Ips pini* (Coleoptera: Scolytidae) in California. J Chem Ecol 18:2305–2329

Seybold SJ, Ohtsuka T, Wood DL, Kubo I (1995) Enantiomeric composition of ipsdienol: a chemotaxonomic character for North American populations of *Ip*s spp. in the *pini* subgeneric group (Coleoptera: Scolytidae). J Chem Ecol 21:995–1016

Shea PJ, Neustein M (1995) Protection of a rare stand of Torrey pine from *Ips paraconfusus.* In: Salom SM, Hobson KR (eds) Application of semiochemicals for management of bark beetle infestations: proceedings of an informal conference, USDA Forest Service General Technical Report INT-GTR-318, Ogden, pp 39–43

Silverstein RM, Rodin JO, Wood DL (1966) Sex attractants in frass produced by male *Ips confusus* in ponderosa pine. Science 154:509–510

Six DL, Wingfield MJ (2011) The role of phytopathogenicity in bark beetle–fungus symbioses: a challenge to the classic paradigm. Ann Rev Entomol 56:255–272

Smith SL, Borys RR, Shea PJ (2009) Jeffrey pine beetle. USDA Forest Service FIDL 11, Portland

Stephen FM, Dahlsten DL (1976) The arrival sequence of the arthropod complex following attack by *Dendroctonus brevicomis*. Can Entomol 108:283–304

Strom BL, Smith SL, Brownie C (2013) Attractant and disruptant semiochemicals for *Dendroctonus jeffreyi* (Coleoptera: Curculionidae: Scolytinae). Environ Entomol 42:323–332

Sun JH, Gillette NE, Miao ZW et al (2003) Verbenone interrupts attraction to host volatiles and reduces attack by *Dendroctonus valens* LeConte (Coleoptera: Scolytidae) on *Pinus tabuliformis* in China. Can Entomol 135:721–732

USDA Forest Service (2003) Forest pest conditions in California – 2003. www.fs.fed.us/r5/spf/publications/pestconditions/. Accessed 2 Mar 2015

USDA Forest Service (2010) Forest pest conditions in California – 2010. www.fs.fed.us/r5/spf/publications/pestconditions/. Accessed 25 Feb 2015

USDA Forest Service (2012) Areas with tree mortality from bark beetles: summary for 2000–2011, Western U.S

Walker R, Rosenberg M, Warbington R et al. (2006) Inventory of tree mortality in southern California Mountains (2001–2004) due to bark beetle impacts. http://www.frap.fire.ca.gov/projects/mast/reports.html. Accessed 9 Feb 2015

Whitehead RJ, Russo GL (2005) "Beetle-proofed" lodgepole pine stands in interior British Columbia have less damage from mountain pine beetle. Canada Forest Service Information Report BC-X-402, Victoria

Whitehead RJ, Safranyik L, Russo G et al. (2004) Silviculture to reduce landscape and stand susceptibility to the mountain pine beetle. In: Shore TL, Brooks JE, Stone JE (eds) Mountain pine beetle symposium: challenges and solutions. Canadian Forest Service Information Report BC-X-399, Victoria, pp 233–244

Wingfield MJ, Hammerbacher A, Ganley RJ et al (2008) Pitch canker caused by *Fusarium circinatum* – a growing threat to pine plantations and forests worldwide. Aust Plant Pathol 37:319–334

Wood DL (1972) Selection and colonization of ponderosa pine by bark beetles. In: van Emden HF (ed) Insect/plant relationships, vol 6. Blackwell Scientific Publications, Oxford, pp 101–117

Wood DL (1982a) The role of pheromones, kairomones and allomones in the host selection and colonization behavior of bark beetles. Ann Rev Entomol 27:411–446

Wood SL (1982b) The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Nat Mem 6:1–1359

Wood DL, Browne LE, Ewing B et al (1976) Western pine beetle: specificity among enantiomers of male and female components of an attractant pheromone. Science 192:896–898

Yan ZL, Fang YL, Sun JH, Zhang ZN (2004) Identification and electroantennal olfactory and behavioral tests of hindgut-produced volatiles of the red turpentine beetle, *Dendroctonus valens* LeConte (Coleoptera: Scolytidae). Acta Entomol Sinica 47:695–700

Yan Z-G, Sun J, Owen D, Zhang Z (2005) The red turpentine beetle, *Dendroctonus valens* LeConte (Scolytidae): an exotic invasive pest of pine in China. Biodivers Conserv 14:1735–1760

Young JC, Silverstein RM, Birch MC (1973) Aggregation pheromone of the beetle *Ips confusus*: isolation and identification. J Insect Physiol 19:2273–2277

Zhang LW, Sun JH (2006) Electrophysiological and behavioral responses of *Dendroctonus valens* (Coleoptera: Curculionidae: Scolytinae) to candidate pheromone components identified in hindgut extracts. Environ Entomol 35:1232–1237

Chapter 19
Native Diseases of California Mediterranean Forest Angiosperms

A. James Downer

Abstract Disease is an interaction with host plants and their environment and a biotic agent (pathogen) which changes host physiology resulting in symptoms of changes in growth, reproduction or longevity. While the pathogenic agent can be in the form of bacteria, mollicute, nematode, parasitic algae, parasitic seed plant, virus, or fungus, not all of these agents result in the formation of diseases that significantly limit populations of woody plants. Fungi are dominant pathogens of Mediterranean Forests. Fungi cause disease in all parts of woody plants but their impact can be summarized by examining the disease they cause in the major organs of trees. This chapter discusses important diseases of the foliage, shoots, periderm (cankers) and woody systems (main stem) and root systems of trees. In each section, a detailed description of the disease category is given along with descriptions of symptoms, diagnostics and etiology of the pathogens. Each disease category is accompanied by an introductory section that reviews environmental conditions that facilitate disease development. Adaptations of fungi to the Mediterranean climate of California are mentioned throughout the chapter.

19.1 Introduction

California is one of the most diverse states in terms of its floristic provinces and the Mediterranean regions are extensive, including many lowland coastal zones from the beyond the Mexican border all the way to Oregon (Jepson 1993). Important forest (tree) angiosperms are in the genera: *Acer*, *Alnus*, *Arbutus*, *Cornus*, *Fraxinus*, *Juglans*, *Lithocarpus*, *Populus*, *Platanus*, *Quercus*, *and Salix*. Species in these genera are susceptible to plant pathogens that infect leaves, stems wood or xylem and roots causing disease. These diseases may occur as single infections or epiphytotics, when environmental conditions predispose trees to infection by virulent pathogens present in their environment. Many native diseases are caused by pathogens that have evolved in the Mediterranean climates to follow rain and drought events. The

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role of global climate change while uncertain has likely had effects on disease outbreaks in many host pathogen systems around the globe (Sturrock et al. 2011). Climate warming and associated weather changes such as droughts significantly increased disease potential in Mediterranean forests, especially abiotic disorders caused by drought and heat stress (Allen et al. 2010). Climate change has caused significant destruction of Aspen in Colorado (Worrall et al. 2010). The effects of a warming climate are global, and the Western United states and its Mediterranean regions are a smaller but much affected region of this larger effect. The result is to drive plants to greater elevation or latitude in order to survive the effects of insects and pathogens that attack them in the newly affected regions.

While severe abiotic conditions (temperature and moisture extremes) can alone be the cause of tree mortality, they also can predispose trees to pathogens and thus stimulate biotic disease progression. The added stress of low rainfall and high temperatures tends to increase the amount of canker diseases in most hardwoods. Reduced photosynthesis from early leaf drop, less shoot extension and smaller leaves leads to less cambial growth resulting in limited development of xylem (wood) and wound response tissue. Less wood volume results in fewer stored carbohydrates and thus these stressed trees have less tolerance for attack by other pathogens and their lives are thus shortened.

Trees as members of woodlands and forests are susceptible to a variety of pathogens (Hepting 1971). While there are also a number of parasitic seed plants causing significant amounts of disease on native trees, these as well as native viral, bacterial and nematode pathogens are less important than fungal pathogens in most California Mediterranean forest trees. Fungi are the most destructive pathogens causing widespread disease of all angiosperm woody plants. Host ranges of pathogens may be large, attacking multiple genera or narrow and restrictive to a single taxon. The resulting diseases can affect any part of an individual tree and if disease conditions are right, populations of trees within an ecosystem. It is reasonable therefore to categorize disease in terms of the various parts of a tree that are affected.

Native pathogens evolved with native trees and are integral components of forest systems (Hansen and Goheen 2000) and have mechanisms that enable their survival and reproduction, thus disease severity is usually limited. Genes for virulence and avirulence are often recognized by pathogen and host. As a result, environmental conditions, usually rainfall or drought and heat, predisposes forest trees to greater disease development or can prevent disease altogether. Many pathogens time the production of fruiting bodies and thus spore releases leading to infections in conjunction with winter or late spring rains typical in California's Mediterranean climate. Even during drought years (likely associated with climate change), there is usually enough water and wind to splash spores and cause infection cycles. During wet periods, anthracnose, blight and other leaf affecting diseases can become so severe that trees are defoliated until Mediterranean dry summer ensues at which time most of these diseases disappear and the pathogen "oversummers" until wet conditions occur again in the following year. While climate change will likely affect pathogen distribution, it is fairly certain that not all pathogens will be increased, drought and increased temperatures are not favorable for all organisms and disease severity may in some cases decrease as climate shifts occur (Desprez-Loustau et al. 2007).

19.2 Leaf/Foliage Diseases

Thousands of fungi cause symptoms on leaves of native trees (Table 19.1). To simplify this section diseases that are significant and common on the hosts listed are presented. These diseases are caused by fungi that are usually restricted to leaves but occasionally move onto young stems or distort the apical meristem thus resulting in growth abnormalities. The group is dominated by powdery mildew diseases. These are obligate biotrophic fungi that require living hosts to form conidia, their asexual spores. They are polycyclic, usually with a teleomorphic (sexual) stage formed in an ascomata (cleistothecium) in fallen leaves. Ascospores serve as primary inoculum during the spring growth flush. Infections on leaves rapidly form conidia (sometimes referred to as *Oidium*) that continue to cause infections as long as new leaves are formed. As foliar growth slows, leaves mature, and temperatures increase, powdery mildew infections decrease.

Many other fungi also may cause necrotic spots on foliage, especially on Oak, Willow and Poplar (Farr et al. 1994). While they are not insignificant in their occurrence or ecology, they are too numerous to catalogue here. I present two interesting

Table 19.1 Leaf invading fungi of selected trees

Host	Pathogen	Symptoms/signs
Alder, (*A. rhombifolia*)	*Melampsoridium hiratsukanum*	Orange pustules
Oak (*Q. agrifolia*)	*Cystotheca lanestris* (*Harkn.*) *Sacc. 1911*	Witches' broom symptoms on Coast Live Oak
Oak, Sycamore	*Erysiphe penicillata* (*Wallr.*) *Link 1824*	Distorted and stunted leaves
Sycamore	*Phyllactinia alnicola* U. Braun 2012;	White patches on distorted leaves
Oak (*Q. lobata*)	*P. angulata* (*E.S. Salmon*) *S.* Blumer 1933	Distorted leaves
Poplar	*Erysiphe polygoni DC. 1821*	Distorted and mildewed leaves
Poplar/cottonwood	*Melampsora medusae* Thum. 1878	Orange pustules below and yellow on upper leaf surfaces
Maple	*Rhytisma punctatum* (Pers.) Fr. 1823	Blackened lesions on leaves
Sycamore	*Stigmina platani* (Fuckel) Sacc. 1880	Mature foliage blackened by spores
Willow	*Erysiphe adunca* (Wallr.) Fr. 1829	White patchy spots on foliage

Fig. 19.1 (**a**) *Rhytisma puctata* on Big Leaf Maple (*Acer macrophyllum*) (**b**) *Apiognomonia errabunda* on *Quercus agrifolia* (**c**) *Cystotheca lanestris* on *Q. agrifolia* (**d**) *Apiognomonia veneta* on *Platanus racemosa* (**e**) *Erysiphe adunca* on *Salix* spp.

examples on maple and Sycamore that are restricted primarily to leaves; Tar spot and Stigmina leaf spot (Fig. 19.1).

Another group that is ubiquitous in all ecosystems including the Mediterranean climates are the rust fungi. These typically occur on Willow, Alder, Poplar, Cottonwood, and shrubs in the family malvaceae. Rusts like powdery mildews are also obligate biotrophic fungi, but may or may not have alternate hosts and a variety of spore stages including sexual and asexual spores. Teleospores are the dominant sexual spores and are dark colored, orange colored uredospores are commonly seen on willow and Alder (Bloomquist et al. 2014) and ribes or gooseberry.

19.2.1 Symptoms and Diagnosis

Powdery mildew is most often observed in its conidial stage which is usually a white powdery covering over the surface of the leaves. During early stages of infection prior to development of conidia, there may be few signs, but symptoms of distorted foliage, puckering of leaves or slowed growth may occur. Powdery mildews infect young expanding leaves and shoot tips. Since infection can be heavy depending on the load of primary and secondary inoculum, there is a tendency to distort the primary growth of the shoot tips and the developing leaves. These distortions result in cupping and deformation of young leaves (Fig. 19.1: Sycamore leaves) and sometimes in complete prevention of leaf expansion. Apical dominance is affected in oak and the combination of loss of dominance and decreased leaf size leads to the development of witches' broom symptoms in *Quercus agrifolia*. Broom symptoms result in loss of chlorophyll and stunting of trees overall when they are extensive throughout a canopy. Conidia form on the brooms so they are usually white or light colored and contrast with the dark green foliage. Broom symptoms are less common on the deciduous oaks.

Since powdery mildews are obligate biotrophs, they rely on living hosts to form their anamorphic spore stages (mildew). While most native trees can sustain mildew without consequence to their own reproduction, trees growing in fog belts or moist coastal areas can become defoliated by these pathogens and weakened to the point of susceptibility to other pathogens or insects. As mildewed leaves fall to the forest floor, these fungi form their sexual stage and produce asci and ascospores in a cleistothecium. This stage of development often occurs after leaf fall and ascospores released in the spring from litter layers can be blown onto new growth as the primary source of inoculum.

Tar spot is a foliar leaf spot formed on maples and is characterized by raised black ascomata that are striking in contrast to the surrounding foliage. Little is known about conditions of disease development in California. Stigmina leaf spot is a disease of aging leaves of California Sycamore. Spores develop on leaf surfaces eventually covering leaves to the point that the entire canopy of affected trees will darken. While dramatic, the disease has little long term consequence as leaves will senesce and the disease may not reappear until years later. However, when it occurs, disease caused by *Stigmina plantani* is considered more destructive than sycamore anthracnose (Wolf 1938).

19.2.2 Etiology of Leaf/Foliage Diseases

Leaf infecting fungi are mostly in the group Ascomycetes. Since many leaf invading fungi form anamorphic stages in leaves while still on the tree, the Deuteromycotina (imperfect fungi) classifications was created many years ago. With the advent of molecular tools, many of these fungi are being reclassified to reflect the parentage of the name given to their teleomorph. Resulting changes within the powdery mildews have clarified genera involved, and names now mostly reflect their teleomorph stages. Classification by conidial stages is largely defunct.

19.3 Diseases of Foliage Shoots and Small Branches/ Anthracnose Diseases

Anthracnose diseases affect leaves and young shoots of affected trees and shrubs (Table 19.2). These pathogens are Ascomycete fungi with a conidial stage that usually forms in an acervulus (Manion 1981). Fruiting bodies are generally formed by the anamorphic stages as acervuli or pycnidia on small twigs or branches while the teleomorphic stages are found in perithecia in cankers on larger twigs or branches. Ascomata are generally immersed, solitary, lacking stromata or in a simple stroma (Sogonov et al. 2008). Primary inoculum is from either conidia or ascospores that reside in dead twigs in the canopy of the tree. Rain splash is required to disseminate spores onto healthy new shoots where germination occurs, usually in the late spring months (February through April). Disease increases as secondary infections occur on new shoots. When rains cease in late spring or early summer, most affected trees produce new growth free of the disease. Wilted and necrotic twigs lose their leaves and fruiting bodies formed in the dead tissues "over summer" until the disease cycle starts again when rains occur around the time of new shoot emergence and Spring rains.

These diseases are regulated by moisture. In drought years or years when rains do not occur at the time trees break dormancy, disease incidence is slight or absent. If disease occurs frequently after shoot growth initiates, it will be severe, often to

Table 19.2 Hosts of anthracnose diseases

Host	Pathogen	Portion of the tree affected and symptoms
Ash	*Discula umbrinella* (Berk. & Broome) M. Morelet 1973	Leaves. Necrotic blotches
Alder	*Gnomoniella tubaeformis* (*Tode*) *Sacc. 1882* *Plagiostoma alneum* (*Fr.*) *Arx 1951*. (*syn. Gnomonia alnea*)	Spots on leaves
Maple	*Aureobasidium apocryptum*(Ellis & Everh.) Herm.-Nijh. 1977	Leaves, necrotic blotches
Oak	*Apiognomonia errabunda* (Roberge ex Desm.) Hohn. 1918	Leaves and small shoots. Vein following necrosis
Sycamore	*Apiognomonia veneta* (*Sacc.&Speg.*) *Hohn. 1920*	Leaves and small to medium sized shoots. Vein following necrosis
Walnut	*Ophiognomonia leptostyla* (Fr.) Sogonov 2008	Leaves and small twigs. Distorted necrotic lesions

the point of total defoliation. While defoliation events can be dramatic in a stand of native trees so can the recovery of these trees as dry weather of summer tends to regulate the disease.

19.3.1 Symptoms and Diagnosis

Anthracnose diseases occur on Sycamore, Coast Live Oak (and other oaks), alder and ash, Dogwood, Maple and Walnut. Anthracnose can cause a range of blight symptoms on various hosts such as bud blight, leaf blight or twig and shoot blights (Berry 1985). While individual symptoms on leaves vary from non-specific necrosis (*Fraxinus*) to vein following necrosis in leaves (Oak and Sycamore) all infections tend to distort affected foliage (Fig. 19.1). Newly expanding leaves are most susceptible so they often do not reach maturity or form normal leaf shapes if they become infected. Foliage infections rapidly spread to the petiole and small twigs, other leaves giving the disease a blight-like appearance as it progresses. Symptoms often appear on the lowest foliage of a tree or group of trees and spread to the upper canopy. This is likely from rain splash downward through the canopy. Foliage on lower portions of the canopy has the most spores splashed on new growth, this results in the lower canopy defoliating before the upper canopy. In many cases, foliage uppermost in the canopy remains disease free because spores are not splashed on it.

19.3.2 Etiology Anthracnose Diseases

Most anthracnose fungi are in the Ascomycota and particularly the family Gnomoniaceae. Many of the anamorphic stages of these fungi (often in the *Discula* genus) have been identified as members of *Gnomonia* or *Apiognomonia*. Some confusion about the type species *A. veneta* being synonymous with *A. errabunda* was resolved by Sogonov et al. (2007) who declared them separate but very similar species. Recent molecular comparisons of the genera *Gnomonia* and *Apiognomonia* consider all hosts in the genus *Gnomonia* to be members of the Betulaceae, while hosts of *Apiognomonia* cover diverse taxonomic host groups.

19.4 Canker Diseases

Many canker diseases are caused by facultative ascomycete parasitic fungi (Table 19.3). Disease cycles vary according to the biology of the pathogen but many are polycyclic having an ascospore perfect stage and a conidial phase. Often the two stages have distinct names i.e. *Diplodia quercina* (anamorph) is actually

Table 19.3 Hosts and pathogens of canker causing diseases

Host	Disease name	Pathogen name	Portion of tree affected	Associated insect vector/ symbiont
Black Walnut	Thousand cankers disease	*Geosmithia morbida* M. Kolarik, E. Freeland, C. Utley & Tisserat 2010	Branches and the main stem	*Pityophthorus juglandi*
Madrone	Madrone canker	*Neofusicoccum mangiferae* (syd. & P. Syd.) Crous, Slippers, & AJL Phillips 2006	Small shoots to the main stem	
Oak	Foamy canker disease	*Geosmithia pallida.*	Main stem and large branches	*Pseudopityopthorous pubipenis*
Oak	Hypoxylon canker	*Annulophypoxylon thousarianum* (Lev.) Y.M. Ju, J.D. Rogers & H.M. Hsieh 2005.	Sapwood or the main stem or large branches	
Oak	Branch canker	*Botryosphaeria stevensii* Shoemaker, 1974	Twigs to small branches	
Oak	Oak decline	*Diplodia mutila* (Fr.) Mont. 1834 (see also *Botryosphaeria stevensii*); *Diplodia agrifolia* S.C. Lynch & A. Eskalen, 2012 *Diplodia corticola* A.J.L. Phillips, A.Alves & J. Luque 2004	Twigs and small branches	Not established
Chaparral plants: California Bay Laurel, Ceanothus, Holly Leaf Cherry, Mountain Mahogany, Madrone, Manzanita, Oak, Redbud, Sumac	Branch Canker/ dieback	*Botryosphaeria dothidea*(*Moug.*) *Ces. & De Not. 1863*	Twigs and branches of trees and main stems of wood shrubs	Not established

Botryosphaeria stevensii. Typically the anamoprh is the more commonly viewed stage and teleomorph rarely observed. Fruiting bodies are produced in tissue as pycnidia (anamorph) or perithecia (teleomorph) usually in a stromata of black tissue. Fruiting bodies are usually produced in killed tissue which may be quite dry. Spores reside in dried twigs or branches or main stems until environmental conditions favor dispersal.

Many of canker diseases are increased by heat and drought stress (Schoeneweiss 1975). Widespread disease in oak followed the drought in 1976 in Northern California (Swiecki and Bernhardt 2006). Drought occurred in 4 of 5 years preceding a *Botryosphaeria dothidea* outbreak in Southern California (Brooks and Ferrin 1994). Following drought years, the Mediterranean climate in California often provides a brief burst of moisture in the winter or late spring which is sufficient for spore release, dispersal and germination in native plant communities. Many of these ascomycete twig invading fungi are facultative parasites that remain dormant throughout most of the year and respond rapidly to rainfall events which are also timed to new growth of their hosts.

Another factor involved in the development of canker diseases is the relationship between insects and the trees they attack. In many cases ambrosia beetles are vectors for fungi causing canker disease in native trees and shrubs. Insects are attracted to drought stressed trees and attack them preferentially. In some, cases these insects are vectors of fungal pathogens and, in some cases, the pathogens are insect symbionts. The newly described foamy canker (caused by *Geosmithia pallida*) is associated with the oak bark beetle (*Pseudopityophthorus pubipenis*) and has been the cause of much disease in oaks in California over the last several drought years (Lynch et al. 2014). Thousand cankers disease caused by *Geosmithia morbida* is also spread by a beetle affiliate *Pityophthorus juglandi* and causes damage to walnuts throughout the Mediterranean climate areas of California. (Tisserat et al. 2011)

19.4.1 Symptoms and Diagnosis

Canker diseases are mostly undetectable in the early phases of their infection and development in trees. Most of them are diseases of the vascular cambium. Foliar symptoms do not begin to appear until the cambium is killed by girdling of the stem on which the canker occurs. Yellowing of foliage is soon followed by browning and then complete necrosis of all parts distal to the cankered twig, branch or stem. When insects are involved, evidence of frass, entry/exit holes, galleries under the bark or the presence of adults and larvae may be helpful in finding cankers.

Cankered stems often have a sunken margin or depression which may appear slightly discolored. When bark is removed from the cankered area often, brown tissues abut green or healthy tissue indicating a clear margin between cankered and healthy tissues (Fig. 19.2). Fruiting bodies usually appear in the necrotic tissue of the oldest part of the cankered area. Both pycnidia and perethecia may form if ascomycete fungi are involved. Some ascomycetes form their perethecia in an ascomata

Fig. 19.2 (**a**) Canker caused by *Geosmithia morbida* (Thousand Cankers Disease), (**b**) Fruiting bodies of *Annulohypoxylon thousarianum* (**c**) Xylem staining by *Botrysophaeria dothidea* in *Alnus rhombifolia*

or are buried in a charcoal like stroma which replaces host tissues. Other fungi like *Geosmithia* sporulate within the galleries made by their beetle symbiont.

Manion (1981) characterizes cankers as either pathogen or host dominant. Host dominant diseases do not rapidly kill affected branches and the tree while wounded may recover. Pathogen dominant canker or "diffuse" cankers rapidly kill host tissues and cause progressive disease throughout a tree. Cankers can be annual or perennial, with perennial cankers producing classic target shaped lesions.

Incipient infections by canker fungi give no overall symptoms to a tree when viewed at some distance. As canker fungi girdle limbs yellowing or flagging of branches becomes apparent. This may occur at any place in a tree. When one branch shows distinct symptoms it is likely that many others have also formed incipient cankers. Progressive crown thinning may lead to eventual death of entire trees.

19.4.2 Etiology of Canker Causing Diseases

Most canker fungi are in the Ascomycota and are members of the Botryosphaerales. *Botryosphaeria* is responsible for disease in a wide host range (Sinclair 1993) and is perhaps the most common canker causing pathogen in California. Several anamorphic fungi of *Botryosphaeria* (*Diplodia* spp.) cause a complex of decline and branch diseases in Coast Live Oak (Lynch et al. 2013). *Geosmithia* causes disease in both oak and walnut (Lynch et al. 2014; Tisserat et al. 2011). *Anullohypoxylon* forms globular fruiting bodies (ascomata: Fig. 19.2) that at first form conidia and later develop perithcia and acsi with ascospores.

19.5 Diseases in the Wood of Forest Trees

As a consequence of their age, trees accumulate wounds. Branch senescence, storm or fire damage, or damage from animals all cause wounds that act as infection courts for fungi. This group of fungi attack wood which is rich in stored carbohydrates and sugars. The fungi are able to depolymerize either cellulose only (leading to brown rots) or both lignin and cellulose causing white rots in wood. These organisms have two devastating effects on trees: the loss of stored carbohydrates and the loss of structural integrity of the wood in their branches or main stem. Death results when portions of the tree or the entire tree fail and are separated from roots. Decay may occur in various locations with butt rot being defined as any decay at the base of a living tree (McCracken 1977), sap rots occurring in the sapwood (living) and heart-rots in the heartwood (physiologically dead) portions of limbs and the main stem (Gilbertson 1969; Gleaser and Smith 2010). While there are thousands of fungi that decay "downed" wood or slash, many of these are saprophytes and do not occur in standing tree or as pathogens of the living parts of trees. We have restricted this section to fungi that have a pathogenic role in standing trees.

19.5.1 Symptoms and Diagnosis

Often the most notable symptoms of wood decay are the wounds that originally served as the infection court or the fungi themselves as they sporulate at the infection site or at the base of the tree. Fire scars, large branch wounds (where a major break has occurred) or other evidence of internal failure such as cracks, bulges and swellings all indicate possible wood decay. Since wood decay organisms deplete stored carbohydrate in wood, trees decline in vigor and deadwood increases in the upper canopy giving the overall tree an "unthrifty" appearance. Carbohydrate depletion of sapwood can be visualized with iodine stains (Fig. 19.3). Saprots may kill large branches or portions of the main stem causing death of significant portions of a tree.

19.5.2 Etiology of Wood Decay

While most fungi in this group are in the Basidiomycota, there are also members of the Ascomycota (*Anullohypoxylon*). Most decay causing fungi produce sporophores on living trees (McCracken 1977) at the site of an old injury or wound (Fig. 19.3). Ascomycetes usually form fruiting bodies only on killed tissues. Since most of these organisms do not cause diseases with a specific name we have omitted that category from Table 19.4.

19.6 Diseases of the Roots and Root Crown

Root and crown rot pathogens are some of the most destructive pathogens of trees (Table 19.5). *Armillaria* species cause disease in most angiosperm woody plants in both managed and natural forests (Kile et al. 1991). Kile and other also assert that Armillaria caused diseases are more severe in Mediterranean climates and Shaw and Kile (1991), further suggest that as Mediterranean climates warm, disease incidence will increase. While crown rot disease development from infection to death of the tree may require a period of years, if trees are predisposed, root and crown rots may cause rapid death. Predisposing events such as high water tables or water flows that pile debris and soil around the main stems of trees increase the likelihood of crown rot and early tree demise. Since these fungi attack wood in the upper roots and lower bole (the root collar or root crown) they predispose trees to catastrophic failure and can create hazards where native species are encroached upon by man-made facilities such as cabins, campgrounds or other recreational features in forest settings.

Armillaria root rot spreads from tree to tree by rhizomorphs or from root contact of a susceptible tree with resident *Armillaria* in a dead root or stump. Spread of the

Fig. 19.3 (**a**) *Ganoderma applanatum* (**b**) *Ganoderma orbiforme* (**c**) *Inonotus arizonicus* (**d**) *Hericium erinaceus* (**e**) *Laetiporus gillbertsonii* (**f**) *Phellinus gilvus* (**g**) *Abortiporus biennis* (**h**) *Phellinus ignarius* (**i**) *Ganoderma brownie* (**j**) Sapwood stained with iodine to show the starch reaction. Decay fungi are clearing a zone in the inner wood as they absorb starch from the wood

Table 19.4 Sporophore type, pathogen name and symptoms of wood decay organisms

Host	Sporophore description	Pathogen name	Symptoms; type and location of rot
Oak, Maple	Stalked basidiome with wavy margin variously colored pink, buff or white	*Abortiporus biennis* (Bull.) Singer 1944	Sap rot in the lower bole of trees
Oak, Sycamore	Shellacked mahogany colored perennial conks	*Ganoderma orbiforme* (Fr.) Ryvarden 2000	Tree declines, loss of vigor, Butt rot, white rot of heartwood, sapwood and bark
Oak, Bay Laurel, Madrone, Ash, Maple, Sycamore	Large shelf-like, woody, perennial conks, near ground level	*Ganoderma applanatum* (Pers.) Pat. 1887	Slow or rapid decline, crown thinning, and dieback or no symptoms. White rot of lower bole and major roots
Oak spp	Smaller (20 cm), perennial fruiting bodies	*Ganoderma brownii* (Murrill) Gibb. 1961	White rot of lower trunk and roots
Ash, Maple, Oak	Large, annual toothed fruiting bodies handing down from old wounds or pruning cuts	*Hericium erinaceus* (Bull.) Pers. 1797	Pocket rot, white rot
Oak, Poplar, Willow	Resupinate tube-like basidiocarp often lining the undersides of branches or under bark. Fruiting only on dead wood	*Inonotus andersonii* (Ellis, & Everh.) Nikol. 1955	Decline, poor growth, dieback, canopy dying from the top down. Causes a white rot of the heartwood and may decay strips of sapwood in living trees. Kills the vascular cambium causing noticeable cankers
Sycamore	Shelf-like annual conks	*Inonotus arizonicus* Gilb 1969	Heartrot in living sycamores
Oak spp., Poplar, Willow, Prunus	Annual hoof-shaped conks solitary. Fruiting only on dead wood	*Inonotus dryophilus* (Berk.) Murrill 1904	Decline, failure and mortality. Rot similar to *I. andersonii*
Oak spp. Prunus,	Large annual orange colored conks, rapidly fading to white often located on branch cuts or wounds	*Laetiporus gillbersonii* Burds. 2001	Often no external symptoms; Butt rot, brown cubical rot. Major cause of failure related mortalities
Oak spp. Sycamore	annual to perennial clusters or solitary shelf-like conks	*Phelinus gilvus* (Schwein.) Pat. 1900	Decline symptoms in stressed trees; Causes a white rot in declining branches, dead wood and sapwood of stressed trees

(continued)

Table 19.4 (continued)

Host	Sporophore description	Pathogen name	Symptoms; type and location of rot
Oak, Poplar	Hoof-like perennial conk with cracks and darkened above	*Phelinus igniarius* (*L.*) *Quel. 1886.*	White rot in the trunk or main stem
Oak spp.	Hoof-like, Perennial conks	*Fomitiporia robusta* (P. Karst.) Fiasson & Niemela 1984. (Syn. *Phellinus robusta*)	Tree decline, loss of vigor. White rot of trunk, large branches and large woody roots

Table 19.5 Sporophore type, pathogen name and symptoms of root decay organisms

Host	Pathogen	Basidiome	Symptoms
Oak, Sycamore, Maple, Alder, Poplar, Walnut and many others	*Armillaria mellea* (Vahl) P. kumm. 1871	Mushrooms, gregarious, honey to brown colored with an annulus	Decline, defoliation and death of uppermost branches and ultimately of the entire tree
Oak, Maple, Ash, Cherry, Willow, Elderberry, Poplar, California Bay Laurel	*Oxyporus latemarginatus* (Duriewu & Mont.) Donk 1966	1966 Resupinate white fading to cream or buff poroid fruiting bodies	Root rot and white rot in sapwood of the main stem
Oak spp. Tanoak	*Pseudoinonotus dryadeus* (Pers) T. Wagner & M. Fish 2001	Annual conks that persist and when fresh have droplets of liquid on them	White rot decay in the root crown and major roots. Symptoms of decline and crown thinning
Madrone	*Heterobasidion auraucariae* P.K Buchanan 1988	Conk forming on the lower stem of the tree	White rot of roots and the lower bole
Oak spp. Tanoak, Manzanita, Redbud	*Omphalotus illudens* (*Schwein.*) *Bresinsky & Besl* 1979	Annual orange mushrooms forming at the base of trees. Gills descend the stipe	White rot of the lower stem and roots. Sap rotter that is found on declining and death of trees. Pathogenicity not proven

other pathogens covered here is less studied and the infection process is uncertain in most cases. Incipient root rot can linger in trees without symptoms for many years. When predisposed by fire, flood, or other environmental stresses, trees can become symptomatic. Early symptoms including thinning of the uppermost canopy, yellowing of leaves, lack of shoot elongation, defoliation of the uppermost canopy followed by complete defoliation and death of the tree. Sometimes if trees are severely affected, they will die rapidly and brown leaves will remain on the tree. *Armillaria* commonly infests trees in riparian corridors causing death of trees such as Alder in an entire stream bed.

19.6.1 Symptoms and Diagnosis

Diagnosis of incipient root rot is often by recognition of fruiting bodies that may occur on the base of the tree or near the tree emerging from root infections. Mushrooms of *Armillaria* and *Omphalotus* may occur without foliage symptoms. As infections progress and larger roots or the main stem are involved foliage may be lost from the uppermost portion of infected trees. Severely predisposed trees may die rapidly with all foliage turning brown and remaining on the tree. Rapid death often accompanies the girdling of the main stem. Most of these pathogens remain as saprophytes in the dead wood of roots or stumps and will continue to produce basidiomes after trees have died. These organisms form white-rot decays in the sap wood of trees. Often severely infected or declining trees near forest edges may fail (windthrow) before they have died of disease.

Root symptoms are seldom observed because most roots are not examined. However, inspection of infected trees will often reveal punky, rotted or decayed tissues in the root flares. Depending on the progress of the disease, the bole of an infected tree may flatten on the side where a major root has been killed by these pathogens. As the fungi spread into the vascular cambium of the main stem, cambial growth is stopped and if the remaining portions the infected tree are healthy and grow, an eventual flat side will be formed that may be diagnostic of incipient root rot disease.

19.6.2 Etiology of Root Rots

These organisms are mostly in the Basidiomycetes with many Oomycetes also causing significant root rot of forest trees but most of these being introduced pathogens (See Chap. 20). While roughly nine species of *Armillaria* have now been described in North America (Shaw and Kile 1991). *A. mellea* is the predominant pathogen in Mediterranean climate forests. These Basidiomycete pathogens all form basidiomes (mushrooms) in fall or winter months and their formation is not predictable (Fig. 19.4). Infection may proceed for some time before fruiting bodies are formed.

19.7 Summary

While Mediterranean plants in California are subject to long dry summers followed by cool moist winter/spring rains, they are also susceptible to drought. Anthracnose diseases are dependent on rain for spores to splash and infect new growing tissues. Timing and frequency of rains and temperature all regulate the severity of these diseases. Mediterranean climates in California are subject to wildland fires on a regular basis. Fire ecology is required for reproduction of many native Chaparral

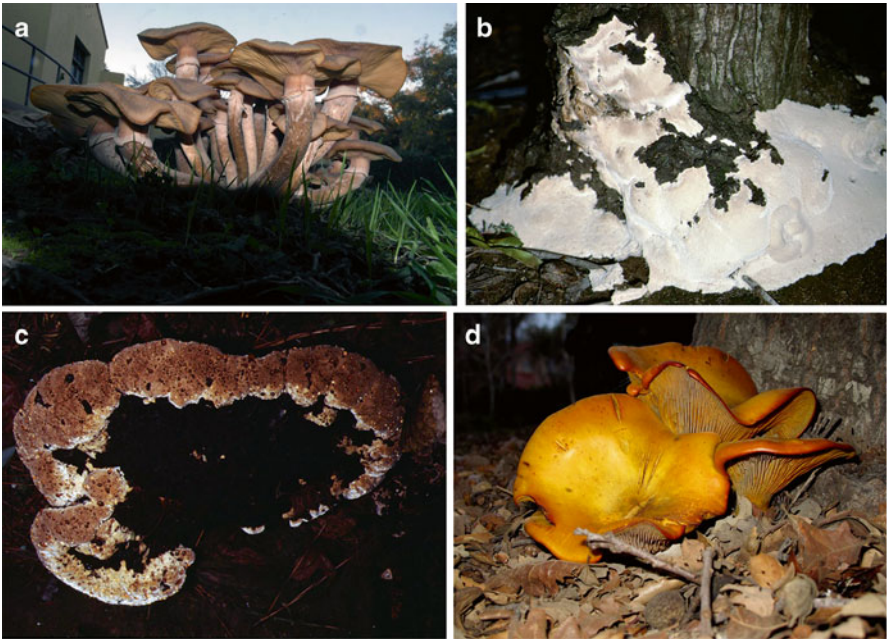

Fig. 19.4 (**a**) *Armillaria mellea* (**b**) *Oxyporus latemarginatus* (**c**) *Pseudoinonotus dryadeus* (**d**) *Omphalotus illudens*

species. In years when rains are slight, especially when drought continues of over several years, native plants become stressed and are predisposed to pathogenic attack. Crist and Schoeneweiss (1975) established a key principle that canker fungi cause more severe disease in drought stressed plants. This stress is certainly related to environmental conditions--the two greatest stress factors being drought and fire. Environmental stresses may also exacerbate root invading fungi. Severe droughts and fires which often follow drought are episodic and so are the epiphytotics that affect many forest trees in California.

Some remarks should be made about where plants grow. Native trees growing in their native range grow in a manner such that they can resist the pathogens they are genetically "acquainted" with. When the same natives are grown in a different location, they may grow worse and become susceptible to canker or other fungi or they may grow better but because they do not allocate resources for plant defense, rather to growth, they still may suffer increased disease attack (Herms and Mattson 1992). Since many trees and other woody angiosperms are older than the changes in climate that we are now experiencing in California, they may already be growing outside of their adaptive range and thus predisposed to increased attack by pathogens resident in their natural environments. Looking ahead, it seems there will be an increase in cankers, root rots and wood decay but that leaf affecting fungi may be somewhat decreased in their severity as warmer and drier conditions ensue.

References

Allen CD, Macalady AK, Chenchouni H et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manage 259:660–684

Berry FH (1985) Anthracnose diseases of Eastern Hardwoods, Forest insect & disease leaflet 133. U.S. Department of Agriculture Forest Service, Washington, DC

Bloomquist CL, Scheck HJ, Haynes J et al (2014) First published report of rust on white alder caused by *Melampsoridium hiratsukanum* in the United States. Plant Dis 98:155

Brooks FE, Ferrin DM (1994) Branch dieback of southern California chaparral vegetation caused by *Botryosphaeria dothidea*. Phytopathology 84:78–83

Crist ER, Schoeneweiss DF (1975) The influence of controlled stresses on susceptibility of European white birch stems to attack by *Botryosphaeria dothidea*. Phytopathology 65:369–373

Desprez-Loustau ML, Robin C, Reynaud G et al (2007) Simulating the effects of a climate-change scenario on the geographical range and activity of forest-pathogenic fungi. Can J Plant Pathol 29:101–120

Farr DF, Bills GF, Chamuris GP et al (1994) Fungi on plants and plant products in the United States. APS Press, St Paul, 1252 pp

Gilbertson RL (1969) A new species of *Inonotus* on southwestern sycamores. Southwest Nat 14:123–125

Gleaser JA, Smith K (2010) Decay fungi of oaks and associated hardwoods for western arborists. Western Arborist. Winter 2010:32–46

Hansen EM, Goheen EM (2000) *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in western North America. Annu Rev Phytopathol 38:515–539

Hepting GH (1971) Diseases of forest and shade trees of the United States, Agriculture handbook #386. USDA Forest Service, Washington, DC, 558 pp

Herms DA, Mattson WJ (1992) The dilemma of plants: to grow or defend. Q Rev Biol 67:283–335

Jepson WL (1993) In: Hickman JC (ed) The Jepson manual: higher plants of California. University of California Press, Berkeley

Kile GA, McDonald GI, Byler JW (1991) Ecology and disease in natural forests. In: Shaw CG III, Kile GA (eds) Armillaria root disease, Agricultural handbook No 691. US Department of Agriculture, Washington, DC, pp 102–121

Lynch SC, Eskalen A, Zambino PJ et al (2013a) Identification and pathogenicity of Botryosphaeriaceae species associated with Coast Live Oak (*Quercus agrifolia*) decline in southern California. Mycologia 105:125–140

Lynch SC, Zambino PJ, Scott TA et al (2013b) Occurrence, incidence and associations among fungal pathogens and *Agrilus auroguttatus* and their roles in *Quercus agrifolia* decline in California. For Pathol 44:62–74

Lynch SC, Wang DH, Mayorquin JS et al (2014) First report of *Geosmithia pallida* causing foamy bark canker, anew disease on Coast Live Oak (*Quercus agrifolia*), in association with *Pseduopityophthorus pubipenis*, in California. Plant Dis 98:1276

Manion PD (1981) Tree disease concepts. Prentice Hall, Englewood Cliffs, 399 pp

McCracken FI (1977) Butt rot of Southern Hardwoods, Forest insect and disease leaflet 43. U.S. Department of Agriculture, Washington, DC

Schoeneweiss DF (1975) Predisposition, stress, and plant disease. Annu Rev Phytopathol 13:193–211

Shaw CG III, Kile GA (1991) Armillaria root disease, Agricultural handbook 69. US Department of Agriculture, Forest Service, Washington, DC

Sinclair WA (1993) Diseases of trees and shrubs, 3rd edn. Cornell University Press, Ithaca, 575p

Sogonov MV, Castlebury LA, Rossman AY et al (2007) The type species of *Apiognomonia*, *A. veneta*, with its *Discula* anamorph is distinct from *A. errabunda*. Mycol Res 111:693–709

Sogonov MV, Castlebury LA, Rossman AY et al (2008) Leaf inhabiting genera of the *Gnomoniaceae*, *Diaothales*. Stud Mycol 66:1–77

Sturrock RN, Frankel SJ, Brown AV et al (2011) Climate change and forest diseases. Plant Pathol 60:113–149

Swiecki TJ, Bernhardt EA (2006) A field guide to insects and diseases of California oaks, Gen. Tech Rep. PSW-GTR-197. Pacific Southwest Research Station, Forest Service, USDA, Albany

Tisserat N, Cranshaw W, Putnam ML et al (2011) Thousand cankers disease is widespread in black walnut in the Western United States. Plant Health Prog. doi:10.1094/PHP-2011-0630-01-BR

Wolf FA (1938) Life histories of two leaf-inhabiting fungi on sycamore. Mycology 30:54–63

Worrall JJ, Marchetti SB, Egeland L et al (2010) Effects and etiology of sudden aspen decline in southwestern Colorado, USA. For Ecol Manage 260:638–648

Chapter 20
Diseases of Conifers in California

Philip G. Cannon, Pete Angwin, and Martin MacKenzie

> *Yo no estoy en peligro. Yo soy el peligro.*
>
> *(Walter Blanco, Metastasis)*

Abstract California has 52 native coniferous tree species and collectively, these populate approximately 15 % of all land in the state (6,170,500 ha), over a wide range of climatic conditions. It is not surprising that a number of pathogens have evolved to take advantage of this extensive resource. In this chapter, three groups of conifer pathogens are given special attention. Group 1 is the "heavy hitters". This group includes three genera of pathogens that have exacted a particularly heavy toll on conifers in California, including: (1) the *Arceuthobium* genus of dwarf mistletoes (15 species), (2) two species of *Heterobasidion*, which cause root rot problems for almost all of California's conifers, and (3) three varieties of the blackstain root disease fungus (*Leptographium wageneri*) which kill yellow pines, Pinyon pine and Douglas-fir. Group 2 includes 25 additional pathogens of conifers which are common in California but do not cause great levels of damage in this state. A few of these, however, have caused serious damage when they have found their way to other countries with Mediterranean climates, and therefore merit attention in this report. Finally, Group 3 includes five pathogens that have been introduced into California. *Phytophthora lateralis*, which causes Port-Orford-cedar root disease, is described in depth in this chapter. The remaining four (*Cronatium ribicola*, causal agent of white pine blister rust, *Fusarium subglutanans*, causal agent of pitch canker, *Phytophthora ramorum*, causal agent of sudden oak death, and *Bursaphelenchus xylophylus*, the

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pine wood nematode) cause so much damage elsewhere around the world that entire chapters of this book are dedicated to them and they are only briefly covered in this chapter. While *Cronartium ribicola, Phytophthora lateralis, Fusarium subglutanans* are highly damaging to California conifers, the other two pathogens are not (*P. ramorum* primarily damages California hardwoods, while damage by *B. xylophylus* to California pines is minor). A great deal of information already exists on the diseases of California conifers. However, the potential for export of these pathogens to other countries with Mediterranean climates and the extent of damage that could occur are seldom discussed. This report includes a discussion of this risk for each of 54 pathogens that are found in California. Six were determined to present a high risk of causing severe damage if exported to other suitable environments. These include*: Cytospora spp., Diplodia spp., Dothistroma pini, Cronartium ribicola, Phytophthora ramorum,* and *Fusarium subglutanans.* Four present a medium-high risk of causing severe damage if exported including *Heterobasidion irregulare, H. occidentale, Phomopsis lokoyae and Endocronartium occidentale.* Another 13 present a medium risk, while the remaining 13 present a low degree of risk. Ultimately, land managers who are charged with protecting the forests of these receiving countries will need to adapt this information to their own particular situations in order to prevent potentially dangerous pathogen introductions. Factors such as the extent and distribution of suitable conifer hosts, the characteristics of various existing avenues of introduction, and the effectiveness of existing quarantine regulations and infrastructure will need to be considered for each of the pathogens listed in this chapter.

20.1 Introduction

Over the past 80 years, the pathogens of California's conifers have been studied extensively, providing a wealth of literature that includes over 3000 reports and scientific papers. Distilling all of this information into a meaningful, but brief summary is a challenge. However, since a major objective of this book is to report on pathogens and insects that have the potential to cause forest protection problems in other countries, especially those with Mediterranean climates, the information that is presented can be more narrowly focused.

Not all forest pathogens cause the same amount of damage in California's conifers. In addition, some pathogens are native while others have been introduced. It is therefore convenient to divide these pathogens into three groups as follows:

1. The "heavy hitters"- native pathogens that cause huge amounts of damage in California's conifers;
2. The common but less damaging native pathogens that affect California's conifers and;
3. Important exotic pathogens of California. This group is further divided into ones that currently cause significant damage on California conifers and ones that don't.

The pathogens that are discussed in this chapter, and the group to which they belong, are shown in Table 20.1.

Table 20.1 Native and introduced pathogens of California conifers. Native pathogens that cause the most mortality and growth loss in California are listed as: Group 1, “the heavy hitters”. Common native pathogens that cause lesser amounts of damage and mortality are listed in Group 2. Exotic invasives that currently cause significant or slight damage to conifers in California or elsewhere are listed in Group 3

Group 1: “Heavy hitting” native pathogens of California conifers		
Disease	Causal organism	Primary hosts
Root rots		
Heterobasidion root disease	*Heterobasidion irregulare*	Pines, incense-cedar, Juniper
	Heterobasidion occidentale	True fir, hemlock, Giant Sequoia
Black stain root disease	*Leptographium wageneri*	Pines, Douglas-fir
Dwarf mistletoes		
Dwarf mistletoe	*Arceuthobium* spp. (15 species)	21 conifer species
Group 2. Common but less damaging native pathogens of California conifers		
Disease	Causal organism	Primary hosts
Root rots		
Armillaria root rot	*Armillaria mellea*	Oaks, other hardwoos and some conifers
Armillaria root rot	*Armillaria nabsnona*	Oaks, occasionally conifers near oaks
Armillaria root rot	*Armillaria gallica*	Hardwoods and some conifers
Armillaria root rot	NABS X	Red and white fir
Rusts		
Western Gall rust	*Endocronatium harknesii*	Many pine species
Pinyon rust	*Cronatium occidentale*	Pinyon pine with *Ribes* as the alternate host
Stalactiform rust	*Cronartium coleosporioides* (= *Peridermium stalactiforme*)	Lodgepole, Jeffrey, ponderosa and coulter pine
		Alt. hosts *Castilleja* and *Pedicularis*
Filamentosum rust	*Peridermium filamentosum*	Jeffrey and ponderosa pine alternate host is *Castilleja spp*.
Commandra blister rust	*Cronartium comandrae*	Lodgepole and ponderosa pine
		Commadra spp. is alternate host
Incense-cedar rust	*Gymnosporangium libocedri*	Incense-cedar and alternate hosts
		Amelanchier and *Cretageous*
Yellow witches broom	*Melampsorella caryophyllacearum*	White and red firs with alternate hosts of *Stellaria* and *Cerastium*

(continued)

Table 20.1 (continued)

Group 2. Common but less damaging native pathogens of California conifers		
Disease	Causal organism	Primary hosts
Wood decays		
Red ring rot	*Phellinus pini*	Douglas-fir, true fir, ponderosa, Jeffrey, and sugar pine, hemlock, spruce, western red cedar and incense-cedar
Rust red stringy rot	*Echinodontium tinctorium*	True fir, Douglas-fir, Englemann spruce
Dry pocket rot	*Oligoporous amarus*	Incense-cedar true fir
Schweinitzii root and butt rot	*Phaeolus schweinitzii*	Most conifers
Brown trunk rot	*Fomitopsis officinalis*	Ponderosa, Jeffrey and sugar pines, Douglas-fir, spruces, hemlocks and true fir
Brown cubical rot	*Laetoporus sulphureus*	Many true fir and hardwood species
Cytospora canker	*Cytospora abietis*	True fir, occasionally Douglas-fir
Atropellis canker	*Atropellis pinicola*, *Atropellis piniphila*	Sugar, western white ponderosa and lodgpole pine
Phomopsis canker	*Phomopsis lokoyae*	Douglas-fir, grand fir
Nectria canker	*Nectria fuckeliana*	True fir and spruce species
Botryosphaeria canker	*Botryosphaeria dothidea*	Redwood, giant sequoia, incense-cedar
Cypress canker	*Seiridium cardinale*	Monterey and other cypress species
		Leyland cypress, coast redwood
		Port-Orford-cedar
Diplodia blight	*Diplodia pinea* (= *Sphaeropsis sapinea*)	Most pines
Foliage diseases		
Elytroderma disease	*Elytrodema deformans*	Ponderosa, Jeffrey, Coulter, knobcone, lodgepole and pinyon pine
Sugar pine needle cast	*Lophodemella arcuata*	Sugar pine
Red band needle blight	*Dothostroma pini (= D. septosporia)* *Mycosphaerella pini (= Scirrhia pini)*	Ponderosa, western white, lodgepole, knobcone, bishop, Monterey pines

(continued)

Table 20.1 (continued)

Group 2. Common but less damaging native pathogens of California conifers		
Disease	Causal organism	Primary hosts
Douglas-fir needle cast	*Rhabdocline pseudotsugae*	Douglas fir
True fir needle cast	*Lirula abietnus-concoloris*	White, red, grand, noble, Pacific silver fir
True mistletoes		
Incense-cedar mistletoe	*Phoradendron libocedri*	Incense cedar
Juniper mistletoe	*Phoradendron juniperinum*	Juniper
Cypress-juniper mistletoe	*Phoradendron densum*	Cypress, juniper
Fir mistletoe	*Phoradendron pauciflorum*	White fir
Group 3. Exotic pathogens of California conifers		
Highly damaging to California conifers		
Disease	**Causal organism**	**Primary hosts**
White pine blister rust	*Cronartium ribicola*	7 species of "white" pines
Port-Orford-cedar root disease	*Phytophthora lateralis*	Port-Orford-cedar
Pitch canker	*Fusarium subglutanans*	Monterey and knobcone pine
Not highly damaging to California conifers		
Sudden oak death	*Phytophthora ramorum*	Douglas-fir and coast redwood shoots and foliage (oaks, tanoak)
Pine wood nematode	*Bursaphelenchus xylophilus*	Pinus spp.

This chapter provides detailed information on the biology and damage which the pathogens listed in Groups 1, 2 and 3 have caused on California conifers. Focus is also given to the most likely pathways through which these pathogens may be transmitted to countries where they are not yet present. However, before descriptions of the characteristics of individual pathogens are given, it is important to recognize that all plant diseases are greatly influenced not only by the pathogen, but by the characteristics of the host which is under attack and the environmental conditions in which the attack takes place. A brief summary of the native species of California conifers and the environments in which they are found is therefore needed in order to provide a complete understanding of each disease and its potential to spread to other lands.

One of the reasons that California has such a large number of pathogens is that it has a large number of coniferous trees growing in a large number of environments. There are 40,000,000 ha of land in California (Fig. 20.1); 13,000,000 of these hectares are classified as forest, and 4,920,000 ha of this forested area (38 %) is covered mainly by coniferous species. A full list of coniferous species growing in the state is shown in Table 20.2.

The wettest coniferous forests of California are the coast redwoods (*Sequoia sempervirens*) which are found in the central and northern coastal sections of the state. Where redwoods are most common, annual rainfall can vary from about 1000 to 2000 mm per year, while average monthly temperatures can vary from a high of 18 °C to a low of 10 °C. Along most of this coastal zone, redwood forest types gen-

Fig. 20.1 Distribution of forests in California (Blackard et al. 1997)

erally exist within 35 km of the coast, but occasionally extend as far as 70 km up coastal river valleys. These forest types are most common on slopes with northerly exposures. Redwoods are capable of tremendous growth and some stands of these coast redwood forests have the greatest basal areas and volumes per hectare of any terrestrial ecosystems. Individual trees can exceed 112 m in height and 4.5 m in diameter at breast height. Spruce trees (*Picea sitchensis*) are often also found in this forest type, especially where internal soil drainage is slow.

The Douglas-fir (*Pseudotsuga menziesii*) forest is the next wettest forest type and is generally found immediately inland and upwards in elevation from the redwood forests. In general, Douglas-fir is most common in the northern and central coastal

Table 20.2 Scientific and common names of all coniferous species native to California

Scientific name	Common name	Scientific name	Common name
Abies amabilis	Pacific Silver fir	*Pinus balfouriana*	Foxtail pine
Abies bracteata	Bristlecone fir	*Pinus contorta*	Lodgepole pine
Abies concolor	White fir	*Pinus coulteri*	Coulter pine
Abies grandis	Grand fir	*Pinus edulis*	Pinyon pine
Abies magnifica	Red fir	*Pinus flexilis*	Limber pine
Calocedrus decurrens	Incense-cedar	*Pinus jeffreyi*	Jeffrey pine
Chamaecyparis lawsoniana	Port Orford cedar	*Pinus lambertiana*	Sugar pine
Cupressus nevadensis	Piute cypress	*Pinus longaeva*	Bristlecone pine
Cupressus stephensonii	Cuyamaca cypress	*Pinus monophylla*	Singleleaf pine
Cupressus bakeri	Modoc cypress	*Pinus monticola*	W. White pine
Cupressus govenniana	Pigmy cypress	*Pinus muricata*	Bishop pine
Cupressus forbesii	Tecate cypress	*Pinus ponderosa*	Ponderosa pine
Cupressus macnabiana	MacNab cypress	*Pinus quadrifolia*	Parry Pinyon
Cupressus macrocarpa	Monterey cypress	*Pinus radiata*	Monterey pine
Cupressus nooketensis	Yellow cedar	*Pinus sabiniana*	Grey pine
Cupressus sargentii	Sargent cypress	*Pinus torreyana*	Torrey pine
Juniperus californica	California juniper	*Pseudostuga macrocarpa*	Bigcone Doug.-fir
Juniperus communis	Common juniper	*Pseudostuga menziesii*	Douglas-fir
Juniperus occidentalis	Western juniper	*Sequoia sempervirons*	Redwood
Juniperus osteosperma	Utah juniper	*Sequoiadendron gigantum*	Big tree
Picea breweriana	Weeping spruce	*Taxus brevifolia*	Pacific Yew
Picea englemannii	Engelmann spruce	*Thuja plicata*	West. redcedar
Picea sitchensis	Sitka spruce	*Torreya californica*	Calif. Nutmeg
Pinus abicaulis	Whitebark pine	*Tsuga heterophylla*	West. Hemlock
Pinus attenuata	Knobcone pine	*Tsuga mertensiana*	Mount. Hemlock

mountains but it is also common in the north-central part of the state and can also be found in the mountains of northeastern California. These forests typically receive 600–1200 mm/year of precipitation.

Monterey pine (*Pinus radiata*), one of California's most famous and widely planted species in many other countries with mild Mediterranean climates, naturally occupies only tiny parts of Santa Cruz, the Monterey Peninsula and San Luis Obispo county on the Central California coast. In total there are 4500 ha of naturally occurring *P. radiata* (Dilworth 2004).

The yellow pine forests include ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*) and Coulter pine (*P. coulteri*). They are generally found further inland and at elevations between 1000 and 2000 masl across northern California, 1200 and 2200 masl in the central Sierras and between 1400 and 2600 masl in the Southern Sierra. These hard pine forests have moderate basal areas and volumes on a per-hectare basis, but they are very widespread in distribution and extremely easy to cultivate in plantations or through natural regeneration. As a result, many of California's forest industries may be found operating in these forests. Total precipitation in these forests is in the 400–600 mm/year range, much of which occurs in the winter in the form of snow. Sugar pine (*Pinus lambertiana*), which often grows to a very large size, is common in this forest type as well.

White fir (*Abies concolor*) forests are quite common throughout the Sierra Nevadas in an elevation band just above the yellow pines, while the red fir (*A. magnifica*) forests prevail at elevations between 1700 and 2500 masl. Precipitation is typically a little heavier at these elevations and mostly comes in the form of winter snow. Other high-elevation five needle pines, including western white pine (*Pinus monticola*) and foxtail pine (*P. balfouriana*), grow scattered in these forests as well. Because several different conifer species may be present on any hectare, these forests are often referred to as mixed conifer forests.

Lodgepole pine (*Pinus contorta*) forests are found even higher in elevation than the red fir forests, between 2500 and 3000 masl. They are also common in frost flats that are found around lakes and in basins at 1500–2500 masl elevation bands. Lodgepole pine tolerates poor internal soil drainage better than most conifers. Although it is a resilient tree, it rarely grows to a large size (greater than 20 m in height or 35 cm in diameter).

Whitebark pine (*P. abicaulis*) is occasionally found at elevations just below timberline (3200 masl) throughout the Sierra Nevadas. Bristlecone pine (*P. longaeva*) survives at even slightly higher elevations and under drier conditions. Bristlecone pine is the earth's longest living tree species, with some individuals exceeding 4800 years of age.

Several other California conifers also deserve mention. Giant Sequoia (*Sequoia gigantea*), which is by far the world's largest tree on a volume basis and one of the earth's longest living tree species, is one of these. Although the species can grow in a wide range of environments when planted, it does not regenerate from seed as easily as many other conifers, and therefore occupies only a few small stands at roughly the same elevation as the firs in the central Sierras.

Grey pine (*P. sabaniana*), juniper (*Juniperus occidentalis*) and pinyon pine (*P. edulis*) primarily occupy areas of California that are in rain shadows and therefore receive limited amounts of rainfall, commonly less than 500 mm per annum. Grey pine occupies a huge area that surrounds California's central valley between the 200 and 900 masl elevation bands. Juniper is extremely common in lower elevation zones of northeastern California which transition into the desert of the Great Basin. By contrast, pinyon pine is most prevalent in drier mid-elevation areas in the mountains of central and southern California.

Although one-third of the state is forested, there are also several regions where no trees are found. Timberline is at 3200 masl, so no trees are above that. Also, the southern interior valleys, the central valley and the Great Basin east of the Sierra Nevada mountains are areas where strong rain shadows, allowing less than 200 mm of annual precipitation, prevent the natural establishment of conifers.

Additional information about the terrestrial vegetation of California may be found in Sawyer et al. (2009)

20.2 Background Information on Pathogens of California's Conifers

The following section contains information on the biology, epidemiology and impacts of each of the 53 pathogens that are listed in Table 20.1. The pathogens are presented in the following order: (1) Heavy Hitting Native Pathogens, (2) Common, But Less Damaging Native Pathogens, and (3) Non-Native Introduced Pathogens. More information is presented for the "heavy hitting" native pathogens than for the common but less damaging native pathogens. The amount of information presented for the non-native introduced pathogens varies since three of these pathogens are represented with whole chapters elsewhere in this book.

20.3 Group 1: Heavy Hitting Native Pathogens

Heavy-Hitting Native Pathogens include the dwarf mistletoes (*Arceuthobium spp.*), two species of *Heterobasidion* (causal agent of Heterobasidion root disease), and *Leptographium wageneri* (the causal agent of black stain root disease).

20.3.1 Arceuthobium spp. – *Dwarf Mistletoes*

Dwarf mistletoes are parasitic plants which have long been associated with conifers in the western hemisphere. They have leaves and flowers, so they are capable of photosynthesis and reproduction, but they cannot extract water or nutrients from the soil. To obtain these ingredients essential for plant life, their seeds germinate on the stems of conifers and they send haustoria (root-like structures), into the xylem tissue of their new conifer host. Once established, the mistletoe plant extracts water, minerals and nutrients from their host. Although dwarf mistletoes are capable of manufacturing limited amounts of photosynthates, most are extracted from their hosts as well. Branch swelling commonly takes place at the point of infection, and advanced dwarf mistletoe infections can cause a tree to branch profusely, forming witches brooms (Fig. 20.2). When trees are lightly infected, impacts on tree growth are generally insignificant. However, on heavily infected trees, growth can be reduced by as much as 30–60 %.

Fifteen species of dwarf mistletoe are common in California (Table 20.3). Nine of these attack several (2–5) species of conifers and five attack only a single conifer species. Dwarf mistletoes in California can be found wherever conifers are present (Fig. 20.1), though pathogen distribution and disease severity can vary considerably, depending on the history of the stand. In the western U.S., dwarf mistletoes cause the loss of billions of board feet of lumber each year, cause serious damage to trees in developed recreation areas and lead to increased fire risk as a result of the

Fig. 20.2 Western dwarf mistletoe (*Arceuthobium* campylopodum) on ponderosa pine

production of witches' brooms which significantly increase the occurrence of crown fires. However, on the flip side, at low to moderate levels of infestation, dwarf mistletoes have been shown to promote stand diversity and provide a supplemental source of food, as well as enhanced hiding, resting and nesting habitat to several species of birds and small mammals. On rare occasions, Californian dwarf mistletoes have been recorded growing on conifer species not native to California, e.g., the Grey pine dwarf mistletoe growing on Aleppo pine.

It takes about 4–5 years from the time that a conifer is first infected with a dwarf mistletoe seed until the seed develops into a mature plant and begins to produce fruits and seeds on its own. Once the seeds are ripe, they are explosively propelled by a hydrostatic mechanism that is triggered by progressive ripening then desiccation of the fruit pod (Hinds et al. 1963). Seeds that are shot from their fruits have been shown to be propelled at speeds of over 27 ms^{-1}. However, because they are light in weight, their initial velocity is quickly dampened, and while some may be propelled as far as 16 m, most land within 10 m of their starting point.

The liquid within the dwarf mistletoe fruit that propels the seed (viscin) is sticky, so if it comes in contact with any object before hitting the ground, it can easily stick to that object. In a successful transmission, the seed hits and sticks to an upright needle of a new conifer host. Rain dissolves the viscin, allowing the seed to slide down and become lodged in the needle fascicle. The seed then germinates, establishes a holdfast, where it penetrates into the stem of the new host.

Because dwarf mistletoe seeds can only be propelled a relatively short distance, most spread of the pathogen only takes place within a very limited distance. Dwarf

Table 20.3 Species of dwarf mistletoes in California (US Forest Service and California Department of Forestry and Fire Protection 2015)

Common name	Causal organism	Primary hosts
White fir dwarf mistletoe	*Arceuthobium abietinum f. sp. concoloris*	White fir, grand fir
Red fir dwarf mistletoe	*Arceuthobium abietinum f.sp. magnificae*	Red fir
Wiens' dwarf mistletoe	*Arceuthobium abietinum ssp. wiensii*	Red fir, brewer spruce, occ. white fir
Lodgepole pine dwarf mistletoe	*Arceuthobium americanum*	Lodgepole pine, occ. ponderosa pine
Sugar pine dwarf mistletoe	*Arceuthobium californicum*	Sugar pine
Western dwarf mistletoe	*Arceuthobium camplyopodum*	Ponderosa, Jeffrey, Coulter logegpole
Limber pine dwarf mistletoe	*Arceuthobium cyanocarpum*	Whitebark, limber, foxtail and western white pine
Pinyon pine dwarf mistletoe	*Arceuthobium divaricatum*	Pinyon pine
Douglas-fir dwarf mistletoe	*Arceuthobium douglasii*	Douglas-fir
Coastal dwarf mistletoe	*Arceuthobium littorum*	Monterey and Bishop pine
Western white pine dwarf mistletoe	*Arceuthobium monticola*	Western white and occ. sugar pine
Grey pine dwarf mistletoe	*Arceuthobium occidentale*	Grey, knobcone, Coulter ponderosa and Jeffrey
Knobcone pine dwarf mistletoe	*Arceuthobium siskiyouense*	Knobcone, Jeffrey, and rarely ponderosa and shore pine
Mountain hemlock dwarf mistletoe	*Arceuthobium tsugense spp. mertensianae*	Mountain hemlock
Western hemlock dwarf mistletoe	*Arceuthobium tsugense spp. tsugense*	Western hemlock

mistletoe seeds have been observed on the feathers and fir of birds and small mammals, but long-distance pathogen spread has only been indirectly indicated in a handful of instances where infected solitary trees have been found in isolated new areas. If long-distance spread of the pathogen occurs, it does so in only extremely rare instances.

While dwarf mistletoes can damage and kill susceptible host trees on their own, they also predispose trees to secondary attack by other insects and pathogens. Bark on mistletoe branch swellings of red fir is very susceptible to colonization by canker-causing species of *Cytospora*. Swellings of dwarf mistletoe-infected branches, especially in combination with *Cytospora*, can also serve as infection courts for wood decay fungi. In addition, dwarf mistletoes can easily stress their conifer hosts to the point in which they are extremely vulnerable to attack by bark beetles, engraver beetles and wood boring beetles. These impacts are particularly widespread and severe during periods of drought. Stress induced by dwarf mistletoes also can also make their hosts vulnerable to root rots. Again, the impacts are particularly severe during droughts.

Because the biology of dwarf mistletoes largely involves localized transmission from overstory to understory trees, fairly simple silviculture practices can be used to manage the disease. Even-aged management, clear-cutting and patch cutting are particularly effective in sanitizing stands and limiting spread, especially in heavily-infested stands. However, because these methods have, for a variety of reasons, been largely discontinued in California in favor of uneven-aged management, partial cutting or no cutting at all, most California forests now have multiple-storied stand structures that are optimal for perpetuation of the disease. With a few notable exceptions, sanitation thinning of lightly infested stands and favoring of non-host species are the only two silvicultural practices currently used to address this disease on a significant scale.

Nearly every coniferous tree species in the western hemisphere has at least one dwarf mistletoe that has evolved along with it and become widely dispersed throughout its host range. Even so, it is highly unlikely (close to nil) that dwarf mistletoe could be exported to other countries outside of North America. This is due to a number of factors. First, dwarf mistletoe cannot survive outside of an infected host, so the only means of long-distance transmission can be through the movement of an infected live host. Nursery stock is generally produced under even-aged conditions further than 16 m from infested natural stands. In addition, nursery stock, particularly for export, is relatively small, and is therefore less of a target for locally-dispersed seeds in the unlikely event that an infested stand is located adjacent to a nursery. There are no recorded cases of mistletoes from the Western Hemisphere being found outside of North America.

20.3.2 Heterobasidion spp. – *Heterobasidion Root Disease*

Heterobasidion spp. belong to the basidiomycete class of fungi, causes rot in the butt and root system of coniferous trees and commonly form a characteristic basidiocarp, which is also known as a fruiting body, sporophore or conk (Fig. 20.3).

Two species of Heterobasidion occur in California, *Heterobasidion irregulare* and *H. occidentale*. The first colonizes pines, incense-cedar, western juniper and manzanita, while the latter infects true fir, hemlock and giant sequoia. Although Douglas-fir is a listed host of *H. occidentale*, its occurrence on this host in California is extremely rare. Until 2010, *H. irregulare* and *H. occidentale* were known as the "P and S intersterility groups" of *H. annosum*, respectively. These two Heterobasidion species constitute two of the five known species of this genus, the other three species (*H. annosum, H. parviporum and H. abietinum*) are all native to Europe and Asia (Otrasina and Garbelotto 2010).

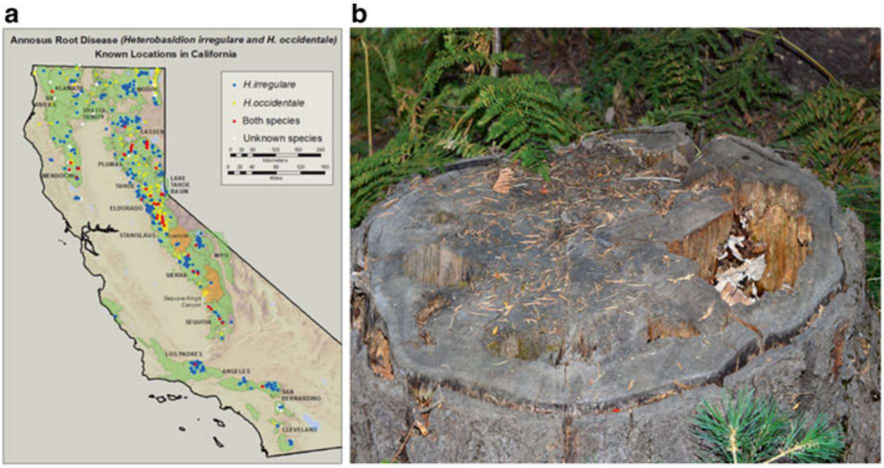

Fig. 20.3 (**a**) Reported distribution of *Heterobasidion occidentale* (*blue dots*) and *H. irregulare* (*red dots*) in California. (**b**) Typical Heterobasidion fructification (white fruiting body *right side* of photo) in a *white* fir stump

Each of these Heterobasidion species evolved in different geographic locations or as pathogens capable of attacking a certain set of coniferous species, but they all have the capacity to infect and colonize respective host species while they are alive and then, after causing the host to die, they can survive as saprotrophs for a period of years.

Studies conducted by Rishbeth (1950, 1951a, b) show that primary infection by Heterobasidion occurs by spores landing on exposed wood. Heterobasidion produces both sexual spores and conidia, but only the sexual spores appear to cause infections in nature (Redfern and Stenlid 1998). Resin, which is produced by many coniferous species, and especially the pines, can prevent successful colonization of trees, even when these trees have been wounded. For this reason, for most coniferous species, freshly cut stumps, are often the most common court of primary infection. After they are formed by cutting, stumps remain susceptible for a period that may range from a few days to a month (Redfern 1982).

When conditions are favorable, Heterobasidion can grow at 0.2–0.5 cm per day, Hunt et al. (1976). Secondary infection occurs when the fungus spreads to the roots of neighboring trees. Because of these characteristics of primary and secondary transmission, the most common method used in California to prevent the spread of the disease is to treat stumps of recently cut trees with boron-based fungicide, such as Sporax or Cellu-Treat. Application of these chemicals to stumps within 4 days of cutting is very effective in preventing the colonization of stumps by the pathogen.

Although both of these species coevolved with their hosts and have been present in California for many millennia, neither was a significant cause of mortality until after the Gold Rush of 1848. Since that time, millions of people poured into the state and needed wood for a variety of purposes. Land was also cleared for farming and other uses. In the process, hundreds of millions of trees were felled and their stumps were colonized by Heterobasidion. Subsequent spread to the roots of adjacent hosts resulted in an explosion of new infection centers of dead and dying trees. As a result, Heterobasidion is currently present in forested lands in almost all parts of the state. Even so, the pathogen is not found in every stump in every coniferous stand.

It was not until about 30 years ago that the chemical (borax)-based method was developed to prevent the spread of Heterobasidion to freshly cut stumps. An additional biological control agent (*Plebiopsis gigantea*) was also developed, but it is currently not registered by the Environmental Protection Agency for use in California.

Although dispersal of this fungus and the root rot that it causes is almost always by spores or via root to root spread, because it is able to survive saprophytically in dead wood for up to 50 years, it is also possible to transport the fungus in solid wood products. One instance where this occurred was in Italy after World War II, when a strain of Heterobasidion from the US was inadvertently introduced to that country during the rebuilding period. This case has been well documented in several publications, including one by Gonthier et al. 2004.

20.3.3 **Leptographium wagneri –** ***Black Stain Root Disease***

Black stain root disease, caused by the fungal pathogen, *Leptographium wageneri,* was first identified in California in 1939 by the entomologist, J. W. Bongberg. At the time, he was trying to figure out what was killing groups of ponderosa pine near the current Black's Mountain Experimental Forest near Mt. Lassen in northeastern California. During his investigation, he could not identify any insect-related cause of the mortality, but observed that many of the affected trees had a "peculiar dark brown staining fungus" associated with them (Fig. 20.4a) When stained roots were put under the microscope by California Forest pathologist W.W. Wagener, he saw masses of large, brownish hyphae filling up the water-conducting tracheid cells and some of the intercellular spaces. It was evident that the observed pine mortality was caused by blockage of the water-conducting tissues of infected trees, and that this fungus appeared to spread through roots to adjacent trees, resulting in the small groups of dead and dying trees. In the ensuing years, many more of these "black stain root disease" infection centers were identified in northeast California and other locations around the state. The fungus was described as a new species, *Verticicladiella wageneri*, by Kendrick in 1962, but was later renamed *Leptographium wageneri* by Wingfield in 1985. Rather than killing its hosts by decaying their roots, the pathogen acts as a vascular wilt pathogen (Harrington and Cobb 1986), similar to *Ophiostoma ulni*, the causal agent of Dutch Elm Disease. Like *O. ulmi, L. wageneri* was later found to also be spread by insect vectors, as well as by underground root to root contacts. It is currently considered to be one of the five most damaging root diseases in western forests (Hadfield et al. 1986).

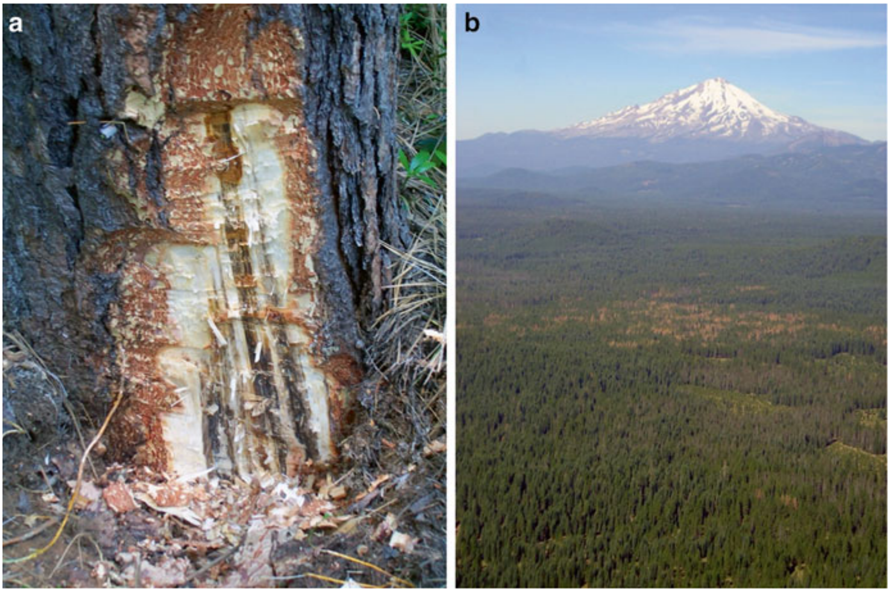

Fig. 20.4 (**a**) Black Stain Root Disease (BSRD) on ponderosa pine at McCloud Flats. The *black streaking* is caused by *Leptographium wageneri* which renders vascular tissue useless.(**b**) Hundreds of hectares of ponderosa pine killed (*the yellow trees*) by black stain and western pine bark beetle (*Dendroctonus* brevicomis) at the foot of Mount Shasta

In California, three different host specific varieties of *Leptographium wagneri* are recognized. *L. wageneri* var. *ponderosum* which infects ponderosa and Jeffrey pine, *Leptographium wageneri* var. *pseudotsugae*, which infects Douglas-fir, and *Leptographium wageneri* var. *wageneri*, which infects singleleaf pinyon pine (*Pinus monophylla*). A number of other coniferous hosts have been reported by Jacobs and Wingfield (2001).

Several species of root-feeding bark beetles and weevils, including *Hylastes macer*, *Hylurgops subcostulatus* and *H. porosus* and *Pissodes faciatis* and *Steremnius carinatus* are vectors of the disease in ponderosa and Jeffrey pine. The spore load per beetle can vary from 0 to 1×10^6 spores (Harrington and Cobb 1986; Ferguson 2009). Three insect vectors have been identified in Douglas-fir- *Hylastes nigrinus, Steremnius carinatus* (root feeding bark beetles), and *Pissodes fasciatus*. All of these vectors are especially drawn to their hosts when roots are wounded, which commonly occurs when stands are disturbed by human activity.

The distribution of black stain root disease is currently increasing in many pine stands of north-eastern California. A likely reason for this is that many of the forests where the disease is found are more densely populated, allowing the pathogen to more easily spread from tree to tree via root contacts. This fungus, when well established, can cause a wilt-like disease in the tree (Harrington and Cobb 1986).

Black stain root disease is widespread across much of the range of its hosts, but incidence and severity, and thus the importance to forest management, varies greatly. Wagener and Mielke (1961) reported that “the fungus does not appear to maintain its viability for long after the affected host or host part dies”, but noted it had been isolated one time from a pinyon pine dead for 10 years. Kearns and Jacobi (2005) found the pathogen could be isolated regularly from roots of pinyon dead that has been dead for 5 years, and occasionally from trees that have been dead for 8 years, and was once isolated from a tree that was estimated to be dead for 16 years. As such, it could be possible to export this fungus in exported logs and the chances of transferring this fungus to susceptible forests elsewhere could be increased if these logs were infested with any of the aforementioned insect vectors. Other related tree diseases, including Dutch elm disease, have been similarly transported across trans-continental distances.

20.4 Group 2: Common but Less Damaging Native Pathogens

Common but Less Damaging Native Pathogens include *Armillaria* spp. (causal agent of Armillaria (Shoestring) root disease), *Endocronartium harknessii* (causal agent of western gall rust), other California rust pathogens, wood decay fungi, canker-causing and foliar pathogens, and the true mistletoes.

20.4.1 Armillaria spp. – *Armillaria (Shoestring) Root Disease*

As seen in the previous section, California conifers are affected by two very serious fungal genera that affect roots (*Heterobasidion* and *Leptographium*), but it appears that California conifers dodged a bullet when it comes to *Armillaria* spp. In all of the other states of the western United States, as well as in the western provinces of Canada, very large sections of coniferous forest are commonly affected by *Armillaria ostoyae*, a particularly aggressive species of *Armillaria.* However, *Armillaria ostoyae* is not known to exist in California (Baumgartner and Rizzo 2001). Four other species of Armillaria have been reported in California, but the damage they cause is most common on hardwoods. Baumgartner and Rizzo (2001) examined 539 Armillaria samples from a wide variety of California forests and found the host-pathogen relationships shown in Table 20.4. It is not known why there so few problems with Armillaria attacking conifers in California, but it may have to do with the fact that in the state, most coniferous forests grow on soils derived from decomposed granite which are extremely well-drained. *Armillaria ostoyae* tends to be more damaging when soils are slowly drained (McDonald et al. 2005).

Although none of these species of Armillaria cause serious conifer damage in California, some could easily cause more damage in different environments or on different species. Some insightful work on the spread of the pathogen comes from

South Africa, where a few species of Armillaria are found, but only one is native. The *Armillaria mellea* found in Capetown was introduced by a sea captain named Jan Van Riebeeck on fruit trees that he planted to provide a source of Vitamin C for his sailors (to avoid scurvey), and/or in oaks (*Quercus rubar*) which were brought in to line a main avenue of the town (Wingfield et al. 2010; Coetzee et al. 2001). More recent spread of *A. mellea* in that country is thought to be by basidiospores or contaminated mulch.

20.4.2 Endocronartium harknessii –*Western Gall Rust*

Western gall rust has shown a capacity to attack 22 species of pine in California, including bishop pine, Monterey pine, shore pine, lodgepole pine and ponderosa pine. Like all rusts, this rust is an obligate parasite, meaning that it can only survive and reproduce when it is living on a living host plant. This particular rust is also autoecious, meaning that it does not require an alternate host to complete its life cycle. This makes it particularly capable of doing well in new environments. Galls formed by this rust can kill limbs and even entire trees. The principle means of infection occurs when spores land on fresh stem tissue of susceptible hosts and then germinate. The ambient air humidity must be close to 100 % for infection to occur. Susceptibility to this rust varies greatly, both between and within species (Adams 1997; Egan and Merrill 1997; Matheson et al. 2006).

Western gall rust causes branches to develop galls which are first pyriform (spindle-shaped) and later become globose (spherical) (Fig. 20.5). When infection takes place on a young seedling, there is a good chance that that all or part of the seedling will be girdled and die (Sinclair et al. 1987). If a gall develops on a larger

Table 20.4 Species of Armillaria in California and their conifer hosts (*y* yes, *n* no)

Conifer species/	Species of Armillaria			
Forest type	*A. mellea*	*A. gallica*	*A. nabsnona*	NABX
Grey pine	n	n	n	n
Douglas-fir	y	y	n	n
Jeffrey pine	n	n	n	n
Juniper	n	n	n	n
Ponderosa pine	n	n	n	n
Red fir	n	n	n	y
Redwood	y	y	y	n
Klamath mixed				
Conifer	n	y	n	n
Sierra mixed				
Conifer	n	y	n	n
Subalpine				
Conifer	n	n	n	n

seedling or young tree, that young tree will probably live, but its growth and form will be affected. If a gall develops on a branch, that branch may be girdled and die, but it might also survive and support a gall that is growing as well. Cases have been documented where galled limbs have survived for over 100 years.

About 1 year after infection, galls begin to exude small amounts of sap, then form bright yellow aecia (a fruiting structure) which make these galls especially visible. Formation of aecia, and the release of aeciospores, usually occurs in the late spring, as atmospheric humidity drops. At this time, terminal and lateral shoots are fully expanding, and are extremely succulent and susceptible to attack. For many weeks, visible signs of infection are subtle and can easily go unnoticed, but eventually swelling of host tissues begins in response to growth hormones that are produced by the fungus, which by this time is growing rapidly within the cells of the host. Galls occasionally develop so rapidly that the limb or branch it is growing on may be killed, resulting in the death of the fungus as well.

Two potential dispersal modes exist for this fungus. Dispersal may occur aerially by spores or the pathogen may be transported by humans in infected host material. Because of their rough, resistant exterior, western gall rust spores can survive for long periods of time without being killed by heat, desiccation or UV light. However, because the probability of a spore encountering a susceptible host decreases as a function of the square of the distance between the two, the likelihood of a new infection occurring from an airborne spore drops rapidly with distance.

As stated above, the other major potential dispersal mode of this fungus is by the human-caused movement of infected living hosts, particularly in the nursery trade.

Fig. 20.5 *Endocronartium harknessi*, Western Gall Rust on ponderosa pine

The probability for dispersal of the pathogen by this method, including movement across international boundaries, is definitely higher than by the aerial dispersal of spores. However, at present, there are no reports of western gall rust on conifers in Europe or elsewhere outside of North America, even though several North American species of pine that are highly susceptible to the disease are planted widely throughout Europe. This includes lodgepole pine (*Pinus contorta*), Monterey pine (*P. radiata*), and ponderosa pine (*P. ponderosa*). In addition, at least two European pines planted in the United States have shown susceptibility to this disease: Scots pine (*Pinus sylvestris*) and Aleppo pine (*P. halepensis*).

20.4.3 Other California Rust Pathogens

Six other native rust diseases are common in California and are listed in Table 20.1. However, because all of these require alternate hosts which are not commonly found outside of the United States, the potential of these to propagate themselves outside of this area is extremely limited. The only exception to this is the yellow witches' broom of fir, caused by the rust fungus *Melampsora caryophyllacearum.* Alternate hosts for this rust includes species of *Stellaria* (chickweed) and *Cerastium* (mouse-eared chickweed), which are both distributed widely.

20.4.4 Wood Decay Fungi

Table 20.1 lists six species of fungi that cause butt rot in living conifers. These are wood decay fungi that individually and collectively cause major amounts of damage to the conifers of California. Seldom is this rot the direct result of tree death, though trees with advanced internal decay are less stable in windstorms and under other forms of physical stress. Butt rot usually begins when wood exposed from recent wounds is colonized by the spores of one of these six fungi, which can then grow into the heartwood in the center of the tree. In contrast, growth of these fungi into sapwood is limited by the exudation of resin in this living portion of the tree. However, as the tree grows older, the sapwood gradually turns into transition wood and then heartwood, which no longer produces resin or restricts fungal growth in this way. While transition wood and heartwood cannot produce resin, they do produce some extractives which are also effective at deterring wood decay fungi. However, within 5–20 years after heartwood formation, most of these extractives are leached out and the wood that remains at the center of the tree no longer has the capability to retard fungal growth. By this means, spores which may have gained access to this heartwood via small broken branch stubs can now colonize the entire central columns of heartwood in the tree.

Wood decay fungi cause tremendous amounts of volume loss in standing timber in California (perhaps ten times as much as logging and twice that caused by wildfire), but there are several things about these wood decay fungi and current export practices that make their export to other countries unlikely. For one, whole logs are no longer exported from California; they are first converted into lumber which contains little or no decay. Production of fruiting bodies (conks) from the small amount of fungus in these wood products is unlikely. A second factor is that most wood products are kiln-dried or fumigated with fungicides such as methyl bromide prior to export.

20.4.5 Canker-Causing Pathogens

Any of the canker diseases listed in Group 2 of Table 20.1 could become problematic upon export if they come in contact with susceptible hosts in their new location, particularly if the hosts are under some form of physiological stress such as drought. By far the most likely way that any canker disease-causing pathogen might be exported to a new country is on living nursery material, as appears to have happened when the Sudden Oak Death pathogen, *Phytophthora ramorum*, was introduced to California in the mid-1990s.

Diplodia pinea (= Sphaeropsis sapinea) has demonstrated a great capacity to damage susceptible pine species overseas and is particularly likely to be carried in leader tissues that have been damaged by hail (Cannon 1990). The fungus infects at least 20 species of pine and has been reported in several overseas countries including Australia, New Zealand, Chile (Peterson 1997) and Ecuador (Cannon 1990). Since *Diplodia* is so widely distributed, one wonders if its further spread should be of concern. However, because California has a larger number of Diplodia varieties than almost anywhere else, limiting further spread is advisable (Legesse 2012).

Seiridium (cypress) Canker caused by *Seiridium cardinale,* was first identified in California's San Joaquin Valley in 1928. Today, it is found in Europe, Asia, New Zealand, Australia, South America and Africa on many trees in the cypress family (Cupressaceae), including Leyland cypress, Monterey cypress (*Cupressus macrocarpa*) and Italian cypress (*C. sempervirens*), as well as on Port-Orford-cedar (*Chamaecyparis lawsoniana*). Each of these species is highly susceptible and can be severely impacted by this disease (CABI 2013).

The high pathogenicity of *S. cardinale* on a wide range of hosts in the Cupressaceae family and Port-Orford-cedar, the relative stability of its virulence, the abundant production of asexual spores, its adaptability to various environments and the possibility of long-distance transport by vectors or through the trade of infected propagation material, have allowed this fungus to spread widely and to cause pandemics in several continents (Graniti 1998; Della Rocca et al. 2011). From 1980 to the present, this fungus has spread to many countries in the Mediterranean (CABI 2013).

Nectria Canker of Fir caused by *Nectria fuckeliana*, causes conspicuous cankers on the boles of the white fir in California and causes a similar problem on Monterey pine (*Pinus radiata*) in New Zealand. Cankered tissue is often attacked by the Sequoia pitch moth. Advanced cankers can make stems more vulnerable to wind breakage and can kill trees directly. The bright red fruiting bodies (perithecia) form in large numbers and make this disease relatively easy to identify. The disease is common in overstocked stands and could easily be transmitted long distances on infected nursery stock.

Atropellis Canker caused by *Atropillis pinicola* in sugar pine, western white pine, ponderosa pine and lodgepole pine, produces a long sunken resinous canker. A closely related fungus, *Atropellis piniphila*, causes the same symptoms on lodgepole pine. The fungus produces cup-shaped fruiting bodies (apothecia) 2–5 mm in diameter that resemble the fruiting bodies of several common stem rusts. However, Atropellis cankers are easily distinguished by the characteristic bluish-black wedge-shaped of stained sapwood under the dead bark. The disease rarely kills trees, but often causes deep depressions in the bole and reduces growth by as much as 50 %. The disease is most common in poorly drained meadows and lakeshores. It is one of the most feared forest diseases in Russia.

Phomopsis Canker of Douglas-fir caused by *Phomopsis (Diaporthe) lokoyae*, infects leaders and lateral branches of trees that have been stressed, particularly by drought. The disease causes a sunken canker, often with a yellow-red margin, that can lead to top and branch dieback. It is most common in seedlings and saplings. The fruiting bodies are small black pycnidia (0.5–1.5 mm in diameter), which produce rain-dispersed spores, and perithecia which produce wind-blown spores. This disease is endemic for most of the time but becomes epidemic during droughts. Overcrowding also favors disease development. Young seedlings and saplings are often killed by the disease, while older trees generally only suffer minor top dieback.

20.4.6 Foliar Pathogens

California's five native foliar diseases that could be problematic are Elytroderma needle blight *(Elytroderma deformans*)*,* Lophodermella needle cast (*Lophodemella* spp.), red band needle blight (*Dothistroma* spp.), Douglas-fir needle cast (*Rhabdocline* spp.) and true fir needle cast (*Lirula* spp.). These are all most likely to spread to other countries on infected nursery stock.

Elytroderma Needle Blight caused by *Elytroderma deformans*, is an extremely important foliage disease of ponderosa pine. When infected, long (10–15 mm), black, canoe-shaped fruiting bodies (hysterothecia) form on the underside of infected needles. These release windborne spores in late summer and autumn, which infect the current year's foliage. The fungus grows from the needle into the twig without initially killing either structure. The following spring, the needles die and new hysterothecia form on the dead needles. Infections in the woody twigs often remain for many years, reinfecting needles that produce spores that infect new needles of the host and other nearby pines. Growth of the fungus into the twigs causes characteristic brooming and deformation. The fungus is also capable of growing systemically into the bole of the tree (Hansen and Lewis 1997) and causing mild to heavy fluting all the way down to the ground. Cool temperatures and high humidity in the late summer and fall promotes infection by the windborne spores. Cool moist areas, including land around lakes, in stream bottoms and canyons, near meadows, and other similar locations are especially conducive to the development of the disease. As it weakens its hosts, *Elytroderma* predisposes trees to attack by root diseases and bark beetles. Trees with 30–60 % of infected crowns typically lose 52–65 % of normal diameter growth, while trees with more than 60 % of infected crowns lose 93–99 % of normal diameter growth.

Lophodermella Needle Cast caused by *Lophodermella cerina*, does not typically cause serious damage to the foliage of California's conifers. However, during wetter than average years, or in very foggy areas, the fungus can infect most of a tree's foliage, causing it to turn completely brown. Needles typically fall about a year after becoming infected, hence the name "needle cast". Commonly affected species include lodgepole pine, ponderosa pine and western white pine. When more than 40 % of the foliage is infected, tree growth rates drop. *Lophodermella* is an ascomycete fungus that produces light brown, oblong fruiting bodies (hysterothecia) on affected needles. During periods of high humidity, these fruiting structures engorge and burst open, liberating spores that can be splashed by rain to infect nearby foliage of the current year. California may experience more *Lophodemella*-related impacts in the future as atmospheric river events, which bring very heavy precipitation, are expected to last longer in northern California (although overall rainfall is expected to remain about the same). In other countries, Lophodermella needle cast could become a serious problem whenever California pines are grown in an environment wetter than their native environments in California because of more favorable conditions for sporulation and infection.

Red Band Needle Blight caused by *Dothistroma pini (= Dothistroma septospora)* and *Mycosphaerella pini (= Scirrhia pini)*, is most widely known for the devastating disease it causes to Monterey pine (*Pinus* radiata) when it's exposed to higher than usual levels of rainfall or fog. However, the pathogen is also known to attack ponderosa pine, western white pine, lodgepole pine, Bishop pine and knobcone pine in California, as well as over than 80 other pine species worldwide (Piou and Ioos 2010). The fungus infects needles of susceptible pines and often causes a red band (or multiple red bands) of necrotic tissue about half-way up the needle. This feature led to its common name, "red band needle disease". Needle tissue distal to the red bands dies off. During rainy weather, fruiting bodies (pycnidia) form and large numbers of spores may be disseminated by rain splash. As a result, disease epidemics are closely linked with periods of extended rainfall. Within months or years, infected needles fall off, leaving thin, sparse crowns. Reduction in tree growth starts when 25 % of the crown is infected by the pathogen, and shuts down when the infection level reaches 75 % (Bulman et al. 2008).

Rhabdocline Needle Cast caused by *Rhabdocline pseudotsugae* and *R. weirii*, are common on Douglas-fir in California. The impact of the disease is rarely notable in California, but when the disease was introduced to Europe and started to infect non-native plantations of Douglas-fir, impacts were much more serious. Resulting losses were attributed to the heavy spring rains that are much more common in Europe than in the native host range of Douglas-fir in western north America (Morgenstern et al. 2013).

***Phoradendron* spp.- True Mistletoes**

In addition to the dwarf mistletoes discussed above as "heavy-hitting native pathogens", four related true mistletoe species colonize California conifers. These are not nearly as damaging as the dwarf mistletoes. Although the true mistletoes are often referred to as "leafy mistletoes", in Juniper and Incense Cedar Mistletoe, the leaves are reduced to inconspicuous scales less than 3 mm long. Unlike the dwarf mistletoes, true mistletoes are spread over long distances by birds that ingest the seeds and deposit them on new susceptible hosts. Prominent true mistletoes on California conifers are as follows:

White Fir Mistletoe	*Phoradendron pauciflorum*
Juniper Mistletoe	*Phoradendron juniperinum*
Incense Cedar Mistletoe	*Phoradendron libocedri*
Cypress-Juniper Mistletoe	*Phoradendron densum*

True mistletoe species are very specific in their host preferences and mostly seen on mature trees. Because true mistletoes are very conspicuous on their hosts, the likelihood of shipping infected conifers is low.

20.5 Group 3: Non-native Introduced Pathogens

Five important exotic forest pathogens that cause significant damage to forests worldwide have also been introduced to California. These include *Cronartium ribicola* (causal agent of white pine blister rust), *Phytophthora lateralis* (causal agent of Port-Orford-cedar root disease), *Fusarium subglutinans* (causal agent of pitch canker), *Phytophthora ramorum* (causal agent of sudden oak death), and *Bursaphelenchus xylophilus* (the pine wood nematode). The first three cause heavy amounts of damage to conifers in the state, while last two do not (though sudden oak death is important because of the damage it causes on hardwoods).

20.5.1 Cronartium ribicola – *White Pine Blister Rust*

White pine blister rust was first found in California near the Oregon border in 1929. By 2002 it had steadily spread all the way down to the southernmost end of the Sierra Nevada mountains (Kliejunas and Adams 2003). Two factors account for the rapid spread of the disease in California. One is because of the abundance and diversity of susceptible five-needle (white) pine hosts, seven of which are native to the state. The other is because of the abundance and diversity of the rust's alternate hosts (*Ribes*, *Castilleja* and *Pedicularis* spp.), which are plentiful in all areas where the susceptible pine species are found. Another chapter in this book is dedicated to covering this disease in depth.

20.5.2 Phytophthora lateralis – *Port-Orford-cedar Root Disease*

Port-Orford-cedar root disease, caused by the non-native oomycete pathogen, *Phytophthora lateralis*, is by far the most serious tree-killing disease of Port-Orford-cedar within its limited range in northwestern California and southwestern Oregon. Approximately 8 % of the 300,000 acres of mapped U.S. Forest Service and Bureau of Land Management Port-Orford-cedar land is infested with *P. lateralis* and has dead and dying Port-Orford-cedar trees (USDA Forest Service and U.S. Bureau of Land Management 2004). Nursery stock, ornamentals and forest trees of all sizes are subject to attack. Pacific yew is an additional, less susceptible host, which only becomes infected in association with infected Port-Orford-cedar. While the origin *of P. lateralis* remains unknown, recent isolations of the pathogen from native old-growth forests of *Chamaecyparis obtusa* in Taiwan indicate that Taiwan is probably within the natural home range of the pathogen (Brasier et al. 2010; Webber et al. 2011).

P. lateralis colonizes the roots and lower boles of its hosts, causing the inner bark and cambium to discolor to a deep cinnamon brown, in contrast with the rich cream color of healthy inner bark. Growth of the pathogen in the roots of infected trees cuts off the flow of water and nutrients, resulting in mortality. As these tissues are killed, foliage throughout the crown discolors in a progression from green to pale green, yellow, red, then brown. Large trees die within 2–4 years after infection; seedlings within a few weeks. However, the pathogen can survive in dead roots and root fragments for 4–7 years after the host tree has died.

P. lateralis is spread via water and soil. Spread occurs in several ways: (1) over long distances via resting spores (chlamydospores) transported in infested plant material or soil; (2) locally via waterborne spores (zoospores) moving in ditches, streams or overland flow; or (3) via mycelia growing across root contacts and grafts between infected and uninfected Port-Orford-cedar. Recent observations indicate that under certain climatic conditions, the pathogen may also be able to spread aerially via deciduous sporangia (Robin et al. 2010). Long-distance movement of the pathogen by humans typically occurs by the transport of chlamydospore-infested organic matter in soil on vehicles, equipment, boots, or by the transport of infected Port-Orford-cedar nursery stock. The pathogen is also spread by the movement of infested mud on the feet of cattle and game animals such as elk.

Port-Orford-cedar root disease was first reported on ornamental host seedlings near Seattle, Washington in 1923 (Zobel et al. 1985). The pathogen continued to spread in ornamental landscape plantings, ultimately destroying the multi-million dollar ornamental cedar industry. The pathogen was identified and named in 1942, from infected landscape hosts in the Willamette Valley of Oregon (Tucker and Milbrath 1942). The disease continued to spread south, and was finally observed in the natural range of Port-Orford-cedar near Coos Bay, Oregon in 1952 (Roth et al. 1957). The pathogen appeared to have come from *P. lateralis*-infested soil from an infested nursery that was used for planting rhododendrons or other non-host plants. By the 1960s, *P. lateralis* was introduced into several small areas in the Smith River watershed, the northernmost major watershed in California. However, rapid spread of the disease from these isolated sites near Crescent City did not occur until the 1980s (USDA Forest Service and USDI Bureau of Land Management 2003). The pathogen is now widespread throughout the northern half of the range of Port-Orford-cedar in southwestern Oregon and the northernmost portion of California, and has been identified in small numbers of isolated locations in all major watersheds in the southern half of the range.

The ability of *Phytophthora lateralis* to easily move over long distances through the commercial movement of infested soil and ornamental nursery stock, together with the widespread use of Port-Orford-cedar as an ornamental tree species made the accidental spread of Port-Orford-cedar root disease to other areas of the world somewhat inevitable. From 1996 to the present, the pathogen has been identified in landscape plantings in France, the Netherlands, Scotland, England and northern Ireland (Hansen et al. 1999; Meffert 2007; Robin et al. 2010; Green et al. 2013). *P. lateralis* is currently classified on the European Plant Protection Organization A2 List (EPPO 2009) of pests recommended for regulation as a quarantine pest.

20.5.3 Fusarium subglutinans – *Pitch Canker*

Pitch Canker, caused by *Fusarium subglutinans*, is a disease thought to have come from Florida or Mexico. Since its arrival in California, it has caused a great deal of damage, especially to the Monterey pine (*Pinus radiata*) and Bishop Pine (*P. muricata*) seedlings and trees within a few miles of the Pacific coastline. It does not often kill trees that it infects, but usually causes leader dieback and unnatural forking of branches in the crown. As a result, infected trees lose all commercial value as lumber. Because of the huge risk posed by the export of this pathogen to other locations where Monterey pine is grown, an entire chapter of this book is dedicated to reviewing this fungus and the disease it causes.

20.5.4 Phytophthora ramorum – *Sudden Oak Death*

As the name of this disease suggests, the trees that are most affected by this disease are oaks. However, the tree species that is most heavily affected in California and Oregon is not a true oak but an oak relative, the tanoak, *Lithocarpus densifolia*. It has been estimated that about four million tanoak trees have been killed by this pathogen in California since the Sudden Oak Death epidemic began about 20 years ago. While some natural genetic resistance to this pathogen has been found in tanoak studied under laboratory conditions, this has not been sufficient to slow the advance of the disease in natural conditions. Four of California's true oak species, coast live oak (*Quercus agrifolia*), black oak (*Q. kellogii*), canyon live oak (*Q. chysolepis*), and Shreve's oak (*Quercus parvula var. shrevei*), are also susceptible, but to a lesser degree than tanoak. And fortunately, at least one of these, *Quercus agrifolia*, does exhibit a wide range in resistance to the pathogen (Conrad et al. 2012). All of the other 24 species of oaks that are native to California are immune to the disease. Information on Sudden Oak Death is available on the California Oak Mortality Task Force website (www.suddenoakdeath.org) and in the chapter of this book titled "Sudden Oak Death".

Although most of work that has been done on *Phytophthora ramorum* in California has been performed on susceptible oak species, it has also been conclusively demonstrated that *P. ramorum* also infects the twigs and foliage of several coniferous species. These include Douglas-fir, coast redwood, Pacific yew, and white, red and grand fir (APHIS 2013). Although these conifers only exhibit minor twig and foliage discoloration or dieback, it is conceivable that they could pass the pathogen on to the more susceptible oak species. Phytosanitary and regulatory measures to ensure that susceptible conifer seedlings or young trees (including Christmas trees) are neither infected or transported are therefore appropriate.

20.5.5 Bursaphelenchus xylophilus – *Pine Wood Nematode*

The pine wood nematode can cause a dramatic disease because it usually kills infected trees within a few weeks to a few months. Because of the devastation that the nematode has caused elsewhere in the world, an entire chapter of this book is dedicated to describing its impacts and control. There are no records of the nematode causing conifer problems in California, but in one study by Holderman (1980) of lumber that had been cut for export, some *Bursephalenchus* nematodes were found. However, hundreds of follow up attempts to isolate the nematode in samples of green Douglas-fir and redwood were all negative (Dwinell 1993).

The life cycle of this nematode is unusual. Spread from tree to tree occurs via the pine sawyer beetle (*Monochamus* spp.). When the beetles feed on the branches of healthy trees, the nematodes emerge from the beetles and enter the new host trees through feeding wounds. The adult sawyers are attracted to and lay their eggs in recently dead or dying trees. After the eggs hatch, the developing beetle larvae feed for several weeks in the cambium, then bore into the sapwood where they can encounter new nematodes to vector. While large differences exist between pine species with respect to their susceptibility to this nematode (Furuno et al. 1993), high levels of damage inflicted on conifers in Asia after the nematode was introduced from Louisiana demonstrate the destructive potential of this pathogen (Mamiya 1983.

20.6 The Risk of Exporting Conifer Diseases from California to Other Countries

In order to determine the possibility that a conifer pathogen from California might be exported to another country with a Mediterranean (or other) climate, a Pest Risk for Export scoring system was developed for this purpose. At its heart, this system is the reverse of the Pesk Risk Assessment process developed by Orr et al. 1993. Its main objective is to consider and integrate all significant components that might affect the risk and consequences of a pathogen being exported to and establishing itself in another country. The seven elements of the system are as follows:

(A) *Likelihood of Introduction*

Element 1	The pest (pathogen) is associated with conifer host-commodity in California.
Element 2	Entry potential – Probability of the plant pest surviving in transit and entering undetected into another country with a Mediterranean climate.
Element 3	Colonization potential – Probability that the plant pest will successfully colonize conifers once it has entered the new country.
Element 4	Spread potential – Probability of the plant pest spreading beyond the initially colonized area.

(B) *Consequences of Introduction*

Element 5	Economic damage potential – Economic impacts if the pest becomes established.
Element 6	Environmental damage potential – Environmental impacts if the pest becomes established.
Element 7	Social and political considerations – Social and economic impacts if the pest becomes established.

In general Elements 1–4 are combined to give a “Likelihood of Introduction” score; elements 5–7 are combined to give a “Consequences of Introduction” score and these two scores are then combined to give the “Threat Posed by the Pathogen”. Space does not permit a full explanation of this scoring system, but an example using *Heterobasidion* spp. as the pathogen of interest demonstrates how this system works.

20.6.1 Risk of Exporting **Heterobasidion** *spp.*

(A) *Likelihood of Introduction*

Element 1 Pest with host-commodity at origin potential: *High risk*

Both *Heterobasidion occidentale and H. irregulare* can colonize roots, sapwood and heartwood of affected plants, and have a good chance of being present in lumber when logs are harvested from infected trees. This fungus could also survive in infected seedlings or small trees, but not in wood chips or mulch.

Element 2 Entry potential: *High*

The pathogen is capable of surviving saprotrophically in wood and can remain viable during transport. It would be difficult to detect visibly, especially if it's transported as mycelium within the wood of infected butt logs or lumber processed from these logs. Fruiting bodies are relatively conspicuous when present, but are often rare or absent. They are almost never seen on lumber. The pathogen could likewise also survive and be difficult to detect in infected seedlings or small trees, unless they show symptoms or die in transit.

Element 3 Colonization potential: *High*

Three routes could be used for *Heterobasidion* to become established in the new area. The highest probability event would be for the pathogen in infected logs or lumber to come into contact with the root systems of susceptible trees within a reasonably short time frame (within 5 years, perhaps) after arriving in the new country. The odds of this occurring are not high, but it has happened. A documented case of this was when *Heterobasidion irregulare* was introduced into Italy during World War II when infected wood, that had been used for latrines, was left in the forests of that country (Gonthier et al. 2007).

Another pathway would be for the roots of infected imported seedlings or small trees to encounter a root or roots of a susceptible host after the imported stock is planted. Again, this would be a fairly low probability event.

Over shorter distances, the pathogen could fruit and the wind-dispersed basidiospores could land on susceptible host tissue. Studies have shown that 99.5 % of all spores travel less than 100 m (Garbelotto and Gonthier 2013). The likelihood of a host becoming infected by spores deposited in this manner depend heavily on the host species and conditions at the infection site (the degree and kind of wounding or the presence and size of freshly-cut stumps, the temperature and moisture conditions at the infection site, etc.).

Element 4 Spread potential: *High risk*

Once infected, fruiting bodies that are produced on diseased trees are capable of producing numerous spores that are capable of infecting new hosts. Wind dispersal of spores is the common means of spread for most basidiomycete decay fungi over intermediate distances 10–200 m. This has been demonstrated for *Heterobasidion occidentale* and *H. irregulare* as well. On the other hand, tree-to-tree spread via root contacts and grafting is slower and more local. Under favorable conditions, expansion of root disease centers has been estimated to occur at a rate of up to 33 cm per year.

(B) *Consequences of Introduction*

Element 5 Economic damage potential: *Low to High. Heterobasidion irregulare or H. occidentale* has very great potential for causing damage if there are natural stands or mature plantations of susceptible coniferous species in the country that that is being invaded.

Element 6 Environmental damage potential: *Low to Moderate*. This element can be addressed in much the same way as it was for the previous one. If there are extensive stands of mature, susceptible coniferous forests, then the potential for significant environmental damage may be high. However, *Heterobasidion* spp. moves fairly slowly, so the potential impacts are likely to be low to moderate.

Element 7 Social and political considerations: Medium to *High.* Damage from *Heterobasidion irregulare or H. occidentale* death or decline of coniferous resources in the new country could have significant social repercussions if the coniferous resources in that country were extensive and important.

(C) *Overall Pest risk potential of California's Heterobasidion species:*

High (Likelihood of introduction = *High*; Consequences of introduction = *Medium*)

Note: Pesk Risk Analyses have been run for every other disease considered in this chapter using this same approach and the net result of these analyses is presented in Table 20.5.

20.7 Final Considerations

Ultimately, the persons charged with safekeeping the forests of the receiving countries (the phytosanitary regulatory committee of each country) will need to reassess the threat risks to ensure that dangerous transfers to the receiving country do not take place. Much of this reassessment will be dependent on the experts in the receiving country asking and getting answers to questions like the following: is there a forest present in that country that holds large numbers of trees that are susceptible to one or more of the diseases covered in this chapter?; what are the chances of intercepting these diseases with that country's existing inspection system?; and, is this pathogen already present in a country and if so, to what degree? Ultimately, the success of efforts to prevent the movement of potentially harmful forest pathogens will depend on cooperation between plant disease specialists and officials in both the exporting and importing countries.

Table 20.5 Risk of exporting California's coniferous pathogens to other countries with Mediterranean climates

	Element number								
Pathogen	E1	E2	E3	E4	E5	E6	E7	Consequence of disease	Threat posed by pathogen
Root rots									
Armillaria mellea	M	H	M+	M	M	M	M	M	M
Armillaria nabsnona	M	H	M+	M	M	M	M	M	M
Armillaria gallica	M	H	M+	M	M	M	M	M	M
Heterobasidion irregulare	H	H	M+	M	M	M	M-H	M	M-H
Heterobasidion occidentale	H	H	M+	M	M	M	M-H	M	M-H
Leptographium wageneri	H	H	M+	M	H	M	M	M	M
Rusts									
Pinyon rust	H	M	L	M	M	M	M	M	L
Stalactiform rust	H	M	L	M	M	M	M	M	L
Filimentosum rust	H	M	L	M	M	M	M	M	L
Commandra rust	H	M	L	M	M	M	M	M	L
Incense cedar rust	H	M	L	M	M	M	M	M	L
Yellow witches broom	M	M	L	M	M	M	M	M	L
Western Gall rust	H	M	H	M	M	M	M	M	M-H
Wood decays									
Red ring	M	M	L	L	M	L	L	L	L
Red stringy	M	M	L	L	M	L	L	L	L
Dry pocket	M	M	L	L	M	L	L	L	L
Schweinitzii	M	M	L	L	M	L	L	L	L
Brown trunk	M	M	L	L	M	L	L	L	L
Brown cubical	M	M	L	L	M	L	L	L	L
Canker diseases									
Cytospora	H	H	H	H	H	M	M	H	H
Atropellis	H	H	M	H	M	M	L	M	M
Phomopsis	H	H	M	H	M	M	H	M-H	M-H
Nectria	H	H	H	H	M	M	M	M	M
Botryosphaeria	H	H	H	H	M	M	M	M	M
Cypress	H	H	H	H	M	M	M	M	M
Diploidea	H	H	H	H	H	M	M	H	H
Foliage diseases									
Elytroderma	H	H	M	M	M	L	M	M	M
Lophodermium	M	M	M	M	M	L	M	L-M	M
Red band	H	M	H	H	H	H	H	H	H

(continued)

Table 20.5 (continued)

Pathogen	Element number								
	E1	E2	E3	E4	E5	E6	E7	Consequence of disease	Threat posed by pathogen
Douglas fir needle cast	M	M	M	M	M	M	M	M	M
True fir needlecast	M	M	M	M	M	L	M	L-M	M
Mistletoes									
Evaluation of all 14 species of dwarf mistletoes	M	L	L	M	M	M-	M	M	L
Introduced diseases									
White pine blister rust	H	H	M	H	H	H	H	H	H
Sudden oak death	M	M	H	H	M	M	H	M	H
Pitch canker	M	M	H	H	H	H	H	H	H
Port Orford cedar root rot	M	M	M	M	M	M	M	M	M
Pine-wood nematode	M	H	H	H	H	H	H	H	M

It is often technically difficult to determine if pathogens are present on live or dead plant material being imported into a country and studies have shown that many pathogenic (and saprophytic) fungi have been easily overlooked during inspections of imported materials (Berube and Nicolas 2014). However, new technologies are continually being developed to improve inspection procedures and results (Berube and Nicolas 2014).

This chapter highlights most of the major forest pathogens currently in California that are likely to cause major to minor damage if they were to reach other countries where they do not yet exist. Information on the life cycles of each of these pathogens, along with descriptions of their signs and symptoms point out the kinds and amount of damage that these pathogens might cause, based on the damage that they cause in California. Other excellent references on these pathogens include Wood et al. 2003; Sharpf 1993; Sinclair et al. 1987; Hansen and Lewis 1997 and USDA Forest Service and California Department of Forestry and Fire Protection 2015.

References

Adams D (1997) Western gall rust, vol 22, Tree notes. California Department of Forestry and Fire Protection, Sacramento

APHIS (2013) APHIS list of regulated hosts and plants proven or associated with *Phytophthora ramorum*. http://www.aphis.usda.gov/plant_health/plant_pest_info/pram/downloads/pdf_files/usdaprlist.pdf

Baumgartner K, Rizzo DM (2001) Distribution of Armillaria species in California. Mycologia 93(5):821–830

Berube JA, Nicolas JG (2014) Alien fungal species on asymptomatic live woody plant material imported into Canada. Can J For Pathol 37:67–81

Blackard JA, Finco MV, Helmer EH et al (1997) Mapping US forest biomass using nationwide forest inventory data and moderate resolution information. Remote Sens Envion 112:1658–1677

Brasier CM, Vettraino AM, Chang TT et al (2010) *Phytophthora lateralis* discovered in an old growth *Chamaecyparis* forest in Taiwan. Plant Pathol 59:595–603

Bulman L, Ganley R, Dick M (2008) Needle diseases of radiata pine in New Zealand. http://www.nzfoa.org.nz/images/stories/pdfs/content/needlecast/needle-cast_research_review_final.pdf

CABI (2013) Seridium cardinal http://www.cabi.org/isc/datasheet/49497

Cannon PG (1990) Patologia forestal en El Ecuador. Proteccion Forestal DINAF/MAG-USAID. 209 pp

Coetzee MPA, Wingfield BD, Harrington TC, Steimel J, Coutinho T, Wingfield MJ (2001) The root rot fungus *Armellaria mellea* introduced into South Africa by early Dutch settlers. Mol Ecol 10(2):387–396

Conrad AO, McPherson BA, Wood SR et al (2012) Metabolite profiling to predict coast live oak resistance to *Phytophthora ramorum*, poster presented at the American Phytopathological Society, North Central Division annual meeting, 13–15 June 2012

Della Rocca G, Eyre CA, Danti R et al (2011) Sequence and SSR analyses of the fungal pathogen *Seiridium cardinale* indicate California is the most likely source of the Cypress canker epidemic for the Mediterranean region. Phytopathology. doi:10.1094/PHYTO-05-11-0144

Dilworth DJ (2004) Status of monterey pine (*Pinus radiata*) ecosystems and the first monterey pine forest ecosystem conservation plan. http://www.1hope.org/NativeMontereyPineStatus.pdf

Dwinell LD (1993) Incidence of pine wood nematode in green coniferous sawn wood in Oregon and California, Research note SE-367. USDA Forest Service, Southeastern Forest Experiment Station, Asheville

Egan AF, Merrill W (1997) Susceptibility of ponderosa pine to *Endocronartium* harknessii and other causes of mortality in Pennsylvania. Plant Dis 81:1173–1176

Ferguson BA (2009) Blackstain root disease ecology and management. Chapter 11.7 Forest insect and disease management guide for the northern and central Rocky Mountains. USDA Forest Service, Montana Department of Natural Resources, and Idaho Department of Lands, 12 pp

Furuno T, Nakai I, Uenaka K et al (1993) The pine wilt upon the exotic pine species introduced in Kamigamo and Shirahama experiment station of Kyoto University-various resistances among genus Pinus to pinewood nematode, Bursaphelenchus xylophilus. Rep Kyoto Univer For 25:20–34

Garbelotto M, Gonthier P (2013) Biology, epidemiology, and control of Heterobasidion, worldwide. Annu Rev Pyhtopathol 51:39–59

Gonthier P, Warner R, Nicolotti G et al (2004) Pathogen introduction as a collateral effect of military activity. Mycol Res 108:468–470

Gonthier P, Nicolotti G, Linzer R et al (2007) Invasion of European pine stands by a North American forest pathogen and its hybridization with a native interfertile taxon. Mol Ecol 16:1389–1400

Graniti A (1998) Cypress canker: a pandemic in progress. Annu Rev Phytopathol 36:91–114. doi:10.1146/annurev.phyto.36.1.91.PMID15012494

Green S, Brasier CM, Schlenzig A et al (2013) The destructive invasive pathogen *Phytophthora lateralis* found on *Chamaecyparis lawsoniana* across the UK. For Pathol 43:19–28

Hadfield JS, Goheen DJ, Filip GM, Schmitt CL, Harvey RD (1986) Root diseases in Oregon and Washington conifers, Report No RG-FPM-250-86. USDA Forest Service, Pacific Northwest Region, Portland

Hansen E, Lewis KJ (1997) Compendium of conifer diseases. APS Press, St. Paul

Hansen EM, Goheen DJ, Hessburd PF et al (1988) Biology and management of black stain root disease in Douglas fir. In: Harrington TC, Cobb FW (eds) Leptographium root disease in conifers. American Phytopathological Society, St Paul, pp 63–80

Hansen EM, Streito C, Delatour C (1999) First confirmation of *Phytophthora lateralis* in Europe. Plant Dis 83:587

Harrington TC, Cobb FW (1986) Varieties of *Verticicladiella wageneri*. Mycologia 78:562–567

Hinds TE, Hawksworth FG, McGinnies WJ (1963) Seed discharge in *Aceuthobium*: a photographic study. Science 140:1236–1238

Holderman QL (1980) The pinewood nematode (*Bursephelenchus lignicolus* Mamiya and Kiiohara, 1972) and the associated pine wilt disease of Japan. Prepared for the Department of Food and Agriculture Commission of California, Sacramento, 45 pp

Hunt RS, Cobb FW, Parmeter JR (1976) *Fomes annosus* stump colonization and fungus development in the California mixed conifer type. Can J For Res 6:159–165

Jacobs K, Wingfield M (2001) Leptographium species. American Phytopathological Society, St. Paul, 207 pp

Kearns HSJ, Jacobi WR (2005) Impacts of a blackstain root disease in recently formed mortality centers in the pinyon-juniper woodlands of southwestern Colorado. Can J For Res 35:461–471

Kliejunas J, Adams D (2003) White pine blister rust in California. Tree notes 27. California Department Foresty Fire Protect. http://ceres.ca.gov/foreststeward/pdf/treenote27.pdf

Legesse WB (2012) Understanding the global populations of Diplodia pinea and its life cycle in plantation pine. PhD thesis, The Faculty of Natural and Agricultural Sciences, Department of Genetics, University of Pretoria, 153 pp

Mamiya Y (1983) Pathology of the pine wilt disease caused by *Bursaphelenchus xylophilus*. Ann Rev Phytopathol 21:201–220

Matheson AC, Devey ME, Gordon TR et al (2006) The genetics of response to inoculation by pine pitch canker (*Fusarium circinatum* Nirenberg and O'Donnell) infection by seedlings of radiata pine (*Pinus radiata* D. Don). Aust For 69:101–106

McDonald GI, Rice TM, Hall DE et al (2005) Root disease analyzer –*Armillaria* Response Tool (*A*RT). USDA Forest Service, Rocky Mountain Research Station, Moscow

Meffert JP (2007) First record of *Phytophthora lateralis* in the Netherlands. http://www.minlnv.nl/cdlpub/servlet/CDLServlet?p_file_id=19844

Morgenstern K, Doring M, Krabel D (2013) Rhabdocline needle cast-investigations on various Douglas-fir tissue types. Eur J Plant Pathol 137:495–504

Orr RL, Cohen SD, Griffin RL (1993) Generic non-indigenous pest risk assessment process (for estimating pest risk associated with the introduction of non-indigenous organisms). U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Beltsville, 40 pp

Otrasina WJ, Garbelotto M (2010) *Heterobasidion occidentale* sp. nov. and *Heterobasidion irregular* nom. nov.: a disposition of North American Heterobasidion biological species. Fung Biol 114:16–25

Peterson GW (1997) Diplodia blight of hard pines. Forest insect and disease leaflet 161. Forest Service, US Govt. Printing Office 0-327-833

Piou D, Ioos R (2010) First report of *Dothistroma pini*, a recent agent of the Dothistroma needle blight, on *Pinus radiata* in France. Phytopathology 100:105

Redfern DB (1982) Infection of *Picea sitchensis* and *Pinus contorta* stumps by basidiospores of *Heterobasidion annosum*. Eur J For Pathol 1982, 12:11–25

Redfern DB, Stenlid J (1998) Spore dispersal and infection. In: Woodward S, Stenlid J, Karjalainen R, Huttermann A (eds) Heterobasidion annosum: biology, ecology, impact and control. CAB International, New York, pp 105–124

Rishbeth J (1950) Observations on the biology of *Fomes annosus*, with particular reference to East Anglian pine plantations. I. The outbreaks of disease and ecological state of the fungus. Ann Bot 14:365–383

Rishbeth J (1951a) Observations on the biology of *Fomes annosus* with particular reference to East Anglian pine plantations. II. Spore production, stump infection, and saprophytic activity in stumps. Ann Bot 15:1–21

Rishbeth J (1951b) Observations on the biology of *Fomes annosus* with particular reference to East Anglian pine plantations. III. Natural and experimental infection of pines and some factors affecting severity of the disease. Ann Bot 15:221–246

Robin C, Piou D, Feau N et al (2010) Root and aerial infections of *Chamaecyparis lawsoniana* by *Phytophthora lateralis*: a new threat for European countries. For Pathol 41:417–424

Roth LF, Trione EJ, Ruhmann WH (1957) *Phytophthora* induced root rot of native Port-Orford-cedar. J For 55:294–298

Sawyer JO, Keeler-Wolf T, Evens JM (2009) A manual of California vegetation. California Native Plant Society Press, Sacramento

Sharpf RF (ed) (1993) Diseases of pacific coast conifers, vol 521, USDA Forest Service Agriculture handbook. U.S. Dept. of Agriculture, Forest Service, Washington, DC, 197 pp

Shigo A (1979) Tree disease, and expanded concept. Information bulletin No. 419. USDA Forest Service, Washington, DC, 68 pp

Sinclair WA, Lyon HH, Johnson WT (1987) Diseases of trees and shrubs. Comstock Publishing Association, Ithaca

Tucker CM, Milbraith JA (1942) Root rot of Chamaecyparis caused by a species of Phytophthora. Mycologia 34:94–101

USDA Forest Service and California Dept of Forestry and Fire Protection (2015) California insect and disease training manual. Forest Health Protection USDA Forest Service Region 5, 260 pp

USDA Forest Service and USDI Bureau of Land Management (2003) A range-wide assessment of Port-Orford-cedar (*Chamaecyparis lawsoniana*) on Federal lands. Oregon/Washington State Office, Portland, 182p

USDA Forest Service and USDI Bureau of Land Management (2004) Final supplemental environmental impact statement: management of Port-Orford-cedar in Southwest Oregon. USDA Forest Service and USDI Bureau of Land Management, Portland, 485p

Wagener WW, Mielke JL (1961) A staining-fungus root disease of ponderosa, Jeffrey and pinyon pines. Plant Dis Rep 45:831–835

Webber JF, Vettraino AM, Chang TT et al (2011) Isolation of *Phytophthora lateralis* from *Chamaecyparis* foliage in Taiwan. For Pathol 42:136–143

Wingfield MJ, Coetzee MPA, Crous PW et al (2010) Fungal phoenix rising from the ashes? IMA Fungus 1:149–153

Wood DL, Koerber TW, Scharpf RW et al (2003) Pests of native California conifers. University of California Press, Berkeley

Zobel DB, Roth LF, Hawk GM (1985) Ecology, pathology, and management of Port-Orford-cedar (*Chamaecyparis lawsoniana)*, vol 184, General technical report PNW. USDA Forest Service, Portland

Chapter 21
Invasive Bark and Ambrosia Beetles in California Mediterranean Forest Ecosystems

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Abstract This chapter discusses the native ranges, histories of introduction, recent research efforts, and the potential impacts of some of 22 species of invasive scolytids in California's Mediterranean forest ecosystems. The diversity of native and ornamental tree species, the varied climatic zones, and the widespread importation of nursery stock and packaged cargo have made California a fertile location for the introduction and establishment of bark and ambrosia beetles. Eight of the twenty two taxa are ambrosia beetles; four are spermophagous (e.g., *Coccotrypes* and *Dactylotrypes* sp.); six are hardwood bark beetles (*Hypothenemus eruditus*, *Scolytus* sp., *Phloeotribus liminaris*, and *Pityophthorus juglandis*); and four are coniferophagous bark beetles (*Hylurgus ligniperda*, *Ips calligraphus*, *Orthotomicus erosus*, and *Phloeosinus armatus*). Five of the species have probable native ranges elsewhere in North America (indigenous exotic species), whereas nearly all of the remaining species have likely origins in Eurasia with at least four of those with clear roots in true Mediterranean ecosystems. Several appear to be from Africa. Many of the species were first detected in heavily urbanized southern California. Detailed overviews are provided for an ensemble of species that have had or could potentially have the most impact on California forest or orchard resources (*H. ligniperda*, *O. erosus*, *P. juglandis*, *Scolytus multistriatus, S. rugulosus*, *S. schevyrewi*, and *Xyleborinus saxeseni*). Another potentially damaging species, the polyphagous shot hole borer, *Euwallacea* nr. *fornicatus*, is treated elsewhere (Chap. 26). The introductions of these taxa range from species that may have invaded over 100–150 years ago (e.g., *Hypothenemus eruditus*, *S. rugulosus*, or *X. saxeseni*) to 10–15 years ago (10 of the 22 species have been detected since 2000). *Dactylotrypes longicollis* (a spermophage); *Euwallacea*

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nr. *fornicatus*; and *Hylurgus ligniperda* represent new generic records for California. Trends and conditions that favor future invasions by other members of this group of insects and a California watch list are presented.

21.1 Introduction

Since the earliest entomological surveys of forests in California (Hopkins 1899) until the latter stages of the twentieth century, the occurrence and impact of invasive species of bark and ambrosia beetles (Coleoptera: Scolytidae, *sensu* Wood 2007; Bright 2014) on trees and shrubs have been almost negligible. The rich endemic fauna in the State (Bright and Stark 1973; Seybold et al. 2008b) seemed to occupy nearly every available *niche* associated with the diverse collection of trees and shrubs in California's many native forest, savanna, and rangeland ecosystems (Bakker 1984). This diversity of native scolytids is no doubt linked to the size of California, its wide climatic and topographic variation, and the attendant diversity of woody plants available as hosts (Hickman 1996). Approximately one-third of California is forested (33,238,000 acres) (USDA Forest Service 2015), and its large metropolitan areas are adorned with major urban forests and parks (e.g., Balboa, Golden Gate, and Griffith Parks) (Anonymous 2015a). Lanner (1999) lists 59 species of native conifers in California, more than any other U.S. state. Griffin and Critchfield (1972) mapped distributions of 86 native forest and woodland tree species and noted that 21 species of trees grow only in the State. In addition, California's urban forests are wildly diverse and replete with a multitude of non-native tree species. Muller et al. (1974) recorded 600 species of indigenous and introduced trees in 86 families in the city of Santa Barbara alone. Thus, the scolytid biodiversity in California is predicated on both diverse native woody plants and an enormous number of exotic woody plants that occur as ornamental plantings or escapees throughout the vast state.

Throughout much of the development of forest entomological investigation in California, the coniferous forests of the Sierra Nevada, Southern Cascade, Transverse, and Coastal Mountain Ranges; the riparian and rangeland hardwood forests; and the urban and periurban collections of adventive trees have been largely unchallenged by invasive insect species in the phloem- and wood-boring guilds (Mattson et al. 1988). In their comprehensive forest entomological monograph, Furniss and Carolin (1977) listed only two bark beetles, the European elm bark beetle, *Scolytus multistriatus* (Marsham), and the shothole borer, *S. rugulosus* (Müller), and one ambrosia beetle, the European shothole borer, *Xyleborus dispar* (F.), as introductions from other continents to the western USA. They treated another ambrosia beetle, the fruit-tree pinhole borer or lesser shot hole borer, *Xyleborinus saxeseni* (Ratzeburg), as a "transcontinental" species, though it is now more widely considered to be a long-naturalized invasive species (Bright and Stark 1973; Rabaglia et al. 2006). All four of these taxa occur in California. In retrospect, an ensemble of other invasive bark beetles, the walnut twig beetle, *Pityophthorus* *juglandis* Blackman (an indigenous exotic, Dodds et al. 2010), the extremely minute bark beetle, *Hypothenemus eruditus* Westwood, the spermophage, *Coccotrypes dactyliperda* (F.), and another invasive ambrosia beetle, *Xyleborus californicus* Wood [now *Cyclorhipidion bodoanum* (Reitter)] (Hobson and Bright 1994) had all been long present in California at the time that this publication was released, but were overlooked by the authors as invasive species. None of these latter species was considered economically significant, so as a group they did not draw the attention of these forest entomologists or their colleagues. Taxonomists, however, were aware that other invasive bark and ambrosia beetles had become established in the western USA prior to the end of the twentieth century (Chamberlin 1939; Wood 1977). For example, Chamberlin (1939) listed six species as introduced Scolytidae in North America [*C. dactyliperda*, *Coccotrypes pygmaeus* (Eichhoff) [= *carpophagus* (Hornung), *Hylastinus obscurus* (Marsham) (on clover, not trees or shrubs), *S. multistriatus*, *S. rugulosus*, and *Xyleborus germanus* Blandford]. Wood (1977) listed 39 introduced species in the USA, but many of these were interception records and not established populations. He noted that many of these invasive species reproduced by means of "facultative arrhenotokic parthenogenesis" whereby one female establishes an entire breeding population. This strategy presumably facilitates their capacity to quickly colonize and invade new habitats.

Since the publication of the monograph by Furniss and Carolin, increasing numbers of invasive bark beetles and woodborers (ambrosia beetles, roundheaded borers, flatheaded borers, and false powderpost beetles) have been detected and have established populations in urban and wildland forests of the West, including California (Lee et al. 2007; Seybold and Downing 2009) (Table 21.1). New invasive bark and ambrosia beetles that have established populations or increased their distributions in California with the potential to significantly impact forest and landscape trees include the redhaired pine bark beetle, *Hylurgus ligniperda* (F.), the Mediterranean pine engraver, *Orthotomicus* (*Ips*) *erosus* (Wollaston), the banded elm bark beetle, *Scolytus schevyrewi* Semenov, the polyphagous shot hole borer, *Euwallacea* nr. *fornicatus* (Eichhoff), and *P. juglandis*. The latter was established in (if not native to) California prior to this recent period, with collection records as early as 1959 from Los Angeles County (Bright 1981; Seybold et al. 2013b; Rugman-Jones et al. 2015). However, surveys over the past 7 years have revealed that this pest of walnut, if not associated indigenously with the native California riparian walnut trees, *Juglans californica* S. Wats. and *J. hindsii* (Jeps.) Rehder, has spread to remote regions of the state and invaded the orchard agroecosystems of English (= Persian) walnut, *J. regia* L., in the Central Valley (Beede and Hasey 1997; Flint et al. 2010; Rugman-Jones et al. 2015). The system of production orchards, which are essentially adventive forests of *J. regia* often surrounded by windbreaks of *J. hindsii*, have been moved with changing land use practices from the greater Los Angeles Basin to the Central Valley in the same time frame that the awareness of the extent of the distribution of *P. juglandis* has changed.

Urban landscapes facilitate the introduction and establishment of invasive species of subcortical insects. They serve as portals where the species can consolidate and build their populations prior to dispersal into wildland forests. Southern California, which is

Table 21.1 Selected major species of invasive bark and woodboring beetles established in the western USA as of 2015[a]

Species	Family	State where initially detected
Heterobostrychus brunneus (Murray)	Bostrichidae	California
Sinoxylon ceratoniae (L.)	Bostrichidae	California
Agrilus anxius Gory	Buprestidae	California/Nevada
Agrilus auroguttatus Schaeffer	Buprestidae	California
Agrilus prionurus Chevrolat	Buprestidae	Texas
Arhopalus syriacus (Reitter)	Cerambycidae	California
Nathrius brevipennis (Mulsant)	Cerambycidae	California
Phoracantha recurva Newman	Cerambycidae	California
Phoracantha semipunctata (F.)	Cerambycidae	California
Dendroctonus mexicanus Hopkins	Scolytidae	Arizona
Euwallacea nr. *fornicatus* (Eichhoff)	Scolytidae	California
Hylurgus ligniperda (F.)	Scolytidae	California
Orthotomicus erosus (Wollaston)	Scolytidae	California
Phloeosinus armatus Reitter	Scolytidae	California
Pityophthorus juglandis Blackman	Scolytidae	Colorado/Utah
Scolytus schevyrewi Semenov	Scolytidae	Colorado/Utah
Trypodendron domesticum (L.)	Scolytidae	Washington
Xyleborinus alni (Niisima)	Scolytidae	Washington
Xyleborus similis Ferrari	Scolytidae	Texas
Xylosandrus crassiusculus (Motschulsky)	Scolytidae	Oregon

[a] Updated from Seybold and Downing (2009). We consider Texas to be part of the continental western USA; these introductions were documented in Haack (2006), except for *P. semipunctata*, which was reported in Scriven et al. (1986); *N. brevipennis* (Linsley 1963; Linsley and Chemsak 1997); *D. mexicanus* (Moser et al. 2005); *H. ligniperda* (Liu et al. 2007); *A. anxius* (Duckles and Švihra 1995; Carlos et al. 2002); *A. auroguttatus* (Coleman and Seybold 2008, Chap. 22); *T. domesticum* (R. Rabaglia, USDA Forest Service, Washington, DC, personal correspondence); and *X. crassiusculus* (LaBonte et al. 2005)

particularly replete with nonindigenous trees and high volumes of imported cargo, appears to have served as an entry point for many of the state's invasive species in this feeding guild. Among the non-native trees are an ensemble of species of Mediterranean pines, such as Aleppo pine, *Pinus halepensis* Mill., Canary Island pine, *Pinus canariensis* Smith, Italian stone pine, *Pinus pinea* L., and Turkish red pine, *Pinus brutia* Tenore, whose attendant subcortical insect fauna in California has not been characterized previously. These trees have been planted widely along city streets, in parks and golf courses, as landscaping in industrial parks, and along highways (particularly at highway on ramps and off ramps) (Fig. 21.1). Both *H. ligniperda* and *O. erosus,* and the roundheaded borer, *Arhopalus syriacus* (Reitter) (Cerambycidae) (Table 21.1), are examples of invasive forest pests that have achieved a toehold in urban or peri-urban environments of California by colonizing these adventive Mediterranean hosts. From there the beetles appeared to have shifted onto native pines as they have moved into California's wildland forests in the U.S. National Forest system.

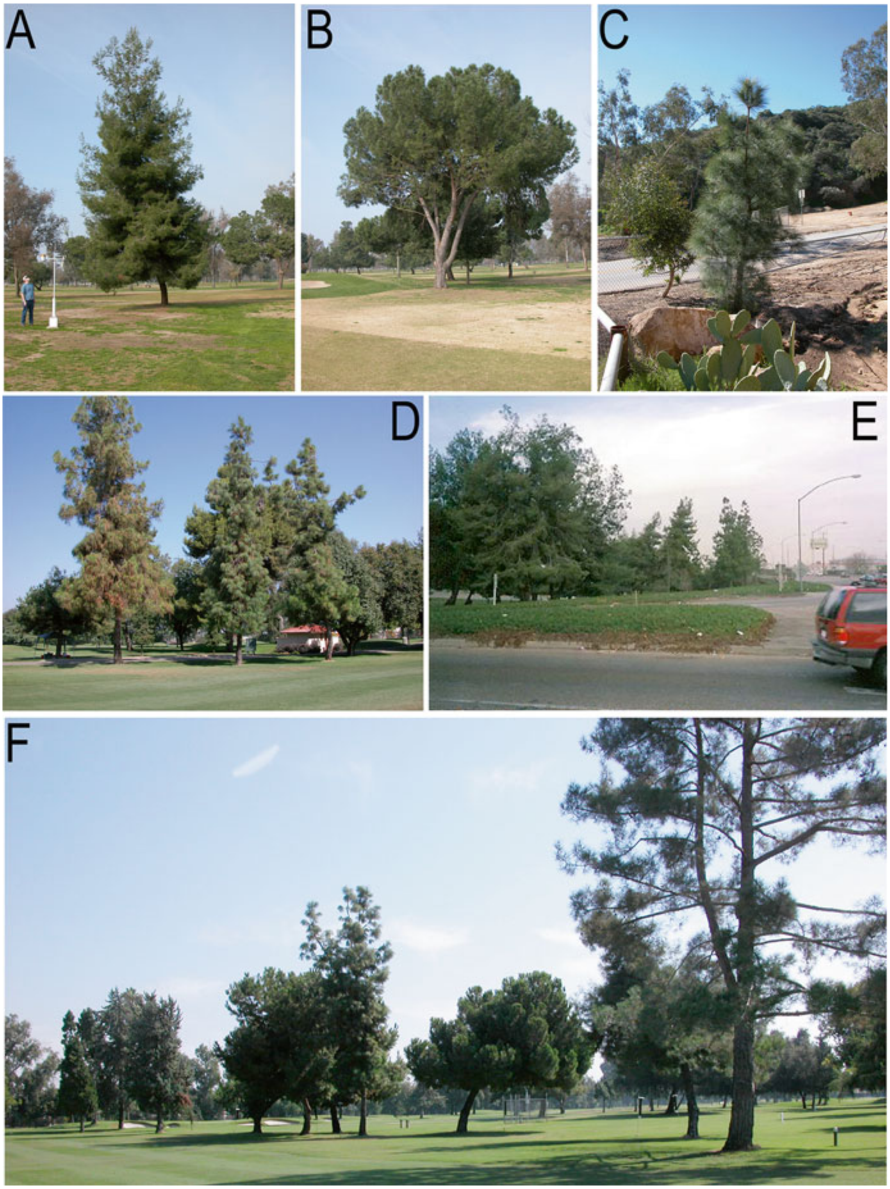


Fig. 21.1 Frequently planted Mediterranean pines in the California urban forest are hosts of invasive species of bark beetles. These hosts include: (**a**) Aleppo pine, *Pinus halepensis* Mill. and (**b**) Italian stone pine, *Pinus pinea* L., both on Valley Oaks Golf Course, Visalia, Tulare Co.; (**c**) Canary Island pine, *Pinus canariensis* Smith at Burbank green waste processing facility, Los Angeles Co.; (**d**) same on grounds of Visalia Country Club, Visalia, Tulare Co.; (**e**) a "stand" of *P. canariensis* and *P. halepensis* on the Highway 58 offramp at Union Avenue, Bakersfield, Kern Co.; and (**f**) a "stand" of *P. halepensis*, *P. canariensis*, and Turkish red pine, *Pinus brutia* Tenore (foreground), on grounds of Visalia Country Club, Visalia, Tulare Co. (SJS, photos)

From 2002 to 2009, one of us (RLP) led an annual detection survey for bark beetles and woodborers in California implemented by personnel from the California Department of Food and Agriculture (CDFA), Pest Detection and Emergency Projects Branch. The primary objective of the survey was to detect exotic species in seven families of xylophagous or phloeophagous Coleoptera and Hymenoptera with an emphasis on the bark and ambrosia beetles. A benefit of the survey is that it also provided baseline data on California's native bark beetle and woodborer fauna, particularly in urban forests. Depending on year, the survey covered 53 (2002) to 101 (2005) locations across 14 (2002) to 40 (2004) counties. Within the state (2002–2005), 35 % of the sites were located in southern California (south of the Tehachapi Mountain range), 28 % of the sites were in the Central Valley, and 37 % of the sites were in northern California (north of the Tehachapi range) outside of the Central Valley. Each year the statewide general survey involved placement of 127 (2002) to 302 (2005) 12-unit Lindgren funnel traps (Lindgren 1983) baited with (1) ethanol, (2) ethanol and α-pinene, or (3) a formulation of the aggregation pheromone of the Eurasian spruce engraver, *Ips typographus* L. The release devices were ethanol [plastic pouch, 275 mg/day (at 20 °C) = ultra high release (UHR)], (−)-α-pinene [plastic pouch, 2 g/day (at 20 °C), UHR], and the *I. typographus* lure (= "exotic *Ips* lure") comprised of racemic ipsdienol (PVC bubble cap, 110 µg/day), 83 %-(−)-*cis*-verbenol (PVC bubble cap, 300–600 µg/day), and 2-methyl-3-buten-2-ol (plastic pouch, 17–19 mg/day) (all at 20 °C). Between 2002 and 2006, the semiochemicals were products of Pherotech Inc., Delta, British Columbia, Canada (now The Scotts MiracleGro Company); in 2007 and thereafter, the products were purchased from Synergy Semiochemical, Burnaby, British Columbia, Canada. The trap cups contained about 100–150 ml of a mixture of water and propylene glycol (50:50 by volume, Sierra Antifreeze, Old World Enterprises, Northbrook, Illinois) to immobilize the insects. Surveys after 2009 (see below) utilized a more diluted form of propylene glycol, with an emphasis on non-ethanol bearing products (Seybold et al. 2013a).

In some cases, delimitation surveys were carried out to characterize the extent of the distribution of specific taxa by placing one or two additional traps at locations in counties adjacent to previous detection sites. Each year, the traps in the general survey (approx. three per location) were deployed in the field in April or May and insects were collected bi-weekly until October or November in locations selected to maximize detection of immigrant scolytids and other woodborers. These locations included urban and peri-urban parks or industrial landscapes with large densities of introduced woody plants (Fig. 21.2a, b); landfills and green waste facilities (Fig. 21.2c, d); wood recyclers/pallet companies (Fig. 21.2e); mills handling logs/rough-cut lumber from foreign sources; ports; and distribution centers or destinations for foreign commodities such as tools, tiles, and marble, which are often associated with wood packing material (Fig. 21.2f). This material was hypothesized to serve as the "Trojan horse" for many species of invasive subcortical insects (USDA 2000). At some survey sites, ground inspections of moribund, dead, or decadent trees and shrubs or woodpiles were conducted; biological attributes of the invasive species were recorded; and infested materials were returned to the laboratory for further rearing and screening to establish subcortical insect community

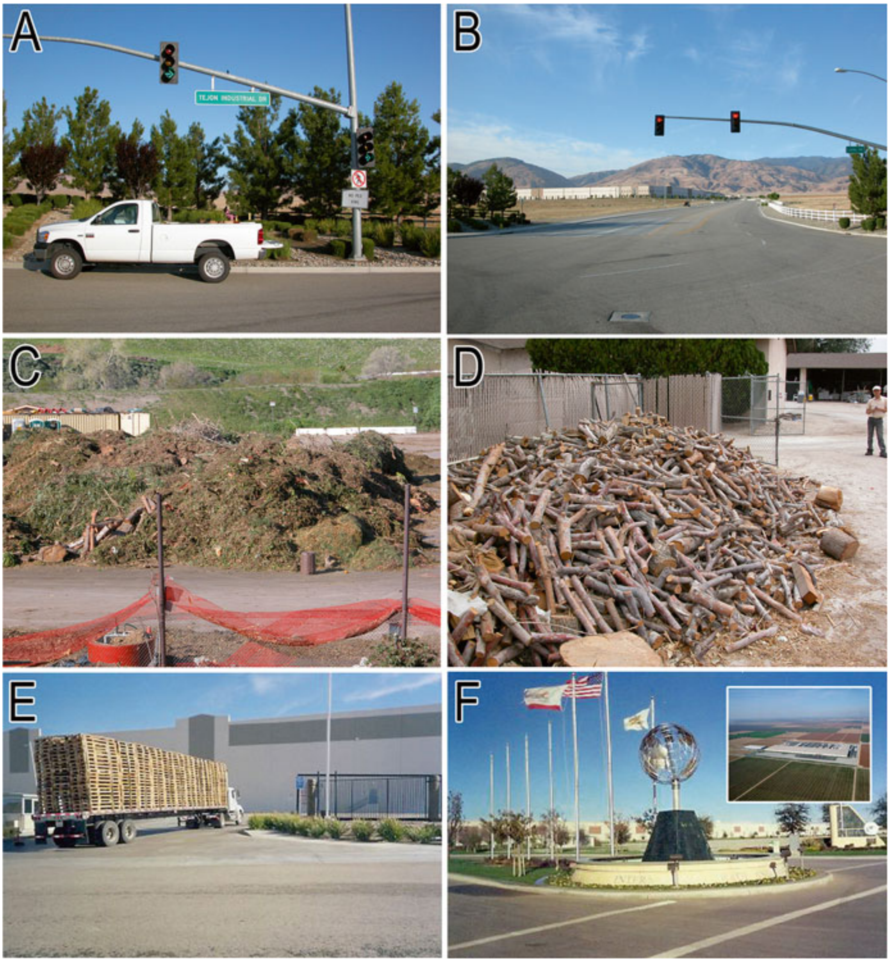


Fig. 21.2 Survey sites for invasive Scolytidae in California included (**a**, **b**) Industrial parks landscaped with adventive tree species (Tejon Industrial Park, Grapevine, California, Kern Co.); (**c**, **d**) Greenwaste processing or storage sites (Burbank and Victorville, California); (**e**) Pallet recycling facilities (Tejon Industrial Park, Grapevine, California); and (**f**) Large scale distribution centers (International Trade and Transportation Center, Seventh Standard Road, Shafter, California, Kern Co., *Inset*, aerial view of the same) (SJS photos)

relationships (Browne 1972). Specimens were curated and pre-identified by the authors; final identifications were confirmed by authorities associated with major North American collections.

Between December 2004 and October 2009, frequent ground surveys of additional sites were conducted by the authors and their colleagues to delimit the distributions and investigate the life histories of several economically important species, and long trapping transects were installed that targeted *O. erosus* (2008–2009) and *H. ligniperda* (2009–2010). These transects led from urban or agricultural areas where these taxa had been detected into U.S. National Forest locations (Seybold 2008; Seybold et al. 2008a). Behavioral studies of the invasive elm bark beetles, *S. multistriatus* and *S. schevyrewi*, were conducted in the greater Sacramento area (northern Central Valley) and in Reno and Carson City, Nevada (western Great Basin) (Lee et al. 2009, 2010, 2011). Surveying continued after 2009 when the principal author began a statewide program of detection and demonstration of the efficacy of the pheromone of *P. juglandis*. This involved monitoring traps in Central Valley orchards and in U.S. National Forest sites (Seybold and Munson 2010; Seybold et al. 2013a, 2015). Some invasive scolytids were also collected or reared as bycatch in various research projects involving the flight behavior and population genetics of *P. juglandis* and other species (Seybold et al. 2012b; Chen and Seybold 2014; Coleman et al. 2014a; Hishinuma et al. 2015; Rugman-Jones et al. 2015). Major California insect collections (Table 21.2, footnotes) were also examined for additional records of interception or establishment prior to 2002. All of these data were integrated into distribution maps for the major invasive species.

Table 21.2 Invasive Scolytidae known to occur in California[a]

Subfamily, tribe, species (common name)	Probable native range[b]	Year first collected in CA	Reference
Hylesininae			
1. Tomicini: *Hylurgus ligniperda* (F.) (Redhaired pine bark beetle)	Europe, Mediterranean	2003	Current study; Liu et al. 2007
2. Phloeotribini: *Phloeotribus liminaris* (Harris) (Peach bark beetle)	Eastern North America	2002	Current study
3. Phloeosini: *Phloeosinus armatus* Reitter (Oriental cypress bark beetle)	Mediterranean, Middle East	1989[c]	Current study; Mendel (1984); Wood (1992); Garrison (1993)
Scolytinae			
4. Dryocoetini: *Coccotrypes advena* Blandford	Asia	2006	Current study
5. Dryocoetini: *Coccotrypes carpophagus* (Hornung)	Africa	2001[d]	Current study; LaBonte and Takahashi (2012)
6. Dryocoetini: *Coccotrypes dactyliperda* (Fabricius)	Africa	1930[e]	Bright and Stark (1973); Wood (1982); Holzman et al. (2009)
7. Dryocoetini: *Dactylotrypes longicollis* (Wollaston)	Canary, Madeira Islands	2009	Current study; Whitehead et al. (2000); Penrose (2010); LaBonte and Takahashi (2012)
8. Scolytini: *Scolytus multistriatus* (Marsham) (European elm bark beetle)	Europe	1951	Armitage (1951); Bright and Stark (1973)
9. Scolytini: *Scolytus rugulosus* (Muller) (Shothole borer)	Europe	1910, 1913[f]	Essig (1915, 1926); Smith (1932, 1945); Bright and Stark (1973); Wood (1982)
10. Scolytini: *Scolytus schevyrewi* Semenov (Banded elm bark beetle)	Asia	2002	Current study; Negrón et al. (2005)

(continued)

Table 21.2 (continued)

Subfamily, tribe, species (common name)	Probable native range[b]	Year first collected in CA	Reference
11. Ipini: *Orthotomicus* (*Ips*) *erosus* (Wollaston) (Mediterranean pine engraver)	Mediterranean, Middle East, Asia	2004	Current study
12. Ipini: *Ips calligraphus* (Germar) (Sixspined ips)	Southeastern USA	1914[g], 1929	Herbert (1916); Wood and Stark (1968); Connor and Wilkinson (1983); Lanier et al. (1991)
13. Xyleborini: *Xylosandrus germanus* (Blandford)	Asia	2003[h]	Current study
14. Xyleborini: *Xyleborus dispar* (Fabricius) (European shothole borer)	Europe	1926	Essig (1926); Bright and Stark (1973); Hobson and Bright (1994)
15. Xyleborini: *Xyleborus californicus* Wood=*Cyclorhipidion bodoanum* (Reitter)	Asia	1944	Wood (1982); Hobson and Bright (1994)
16. Xyleborini: *Xyleborus pfeili* (Ratzeburg)	Eurasia	2003[h]	Current study
17. Xyleborini: *Xyleborus xylographus* (Say)	Eastern North America	1948	Wood (1982); Hobson and Bright (1994)
18. Xyleborini: *Xyleborinus saxeseni* (Ratzeburg) (Fruit-tree pinhole borer/Lesser shothole borer)	Europe	1904[i]	Wood (1982)
19. Xyleborini: *Euwallacea* nr. *fornicatus* (Eichhoff) (Polyphagous shothole borer)	Asia	2003	Current study
20. Cryphalini: *Hypothenemus eruditus* Westwood	Tropical America	1936[j]	Bright and Stark (1973); Wood (1982)
Corthylinae			
21. Pityophthorini: *Pityophthorus juglandis* Blackman (Walnut twig beetle)	SW USA and Mexico	1959	Bright and Stark (1973); Wood (1977); Bright (1981)
22. Corthylini: *Monarthrum mali* (Fitch)	Eastern North America	unknown	Wood (1982)

CSCA California State Collection of Arthropods, Sacramento, CA
EMEC University of California, Essig Museum of Entomology, Berkeley, CA
LACM Los Angeles County Museum of Natural History, Los Angeles, CA
SBNM Santa Barbara Museum of Natural History, Santa Barbara, CA
SDMC San Diego Natural History Museum, San Diego, CA
SJSC San Jose State University, San Jose, CA, J. Gordon Edwards Museum of Entomology
UCDC University of California, The Bohart Museum of Entomology, Davis, CA
UCRC University of California Riverside, Riverside, CA
USNM-US National Museum, Washington, DC

Other collections that we surveyed that do not have codens include California State University Chico, California State University Fresno, California State University Stanislaus, California State

(continued)

Table 21.2 (continued)

University San Francisco, Oakland City Museum, and San Bernardino County Museum. The USDA Forest Service Pacific Southwest Research Station Collection (USDA Forest Service Hopkins U.S. System Index 1929–1955) was also surveyed

[a] Museum survey by the authors included 17 collections. Museum acronyms (Based on Evenhuis, N. L. Abbreviations for Insect and Spider Collections of the World, http://hbs.bishopmuseum.org/codens/codens-inst.html, accessed July 8, 2015

[b] Probable native ranges based on Wood (1977, 1982) and Wood and Bright (1992)

[c] *Phloeosinus armatus* has been known at least since 1989 from southern California (Los Angeles, Los Angeles Co.) where Garrison (1993) reported a specimen collected from firewood. He also noted an additional collection from 1990 in dying branches of Italian cypress, *Cupressus sempervirens* L., in a nursery (Irwindale, Los Angeles Co.). Correspondence among agricultural entomologists from Orange and Los Angeles Cos., CDFA personnel, and SL Wood (Brigham Young University) revealed that this beetle was collected in the early 1990's in Orange Co. and was also found infesting ornamental cypress trees planted in three widely scattered residential areas in southern Los Angeles Co. Wood (1992) briefly reported the establishment in Los Angeles Co. In March 1992, a series of specimens was collected in Redlands (San Bernardino Co.) in a *C. sempervirens* tree. We collected the species in *Cupressus* spp. stem wood from a cut tree in a green waste yard in the Southern Central Valley (S. of Visalia, Tulare Co.), which represents an extension of the state range

[d] As a consequence of this survey, *C. advena* was collected on October 6, 2006 at Whittier Narrows Recreational Area in Los Angeles Co.; C. *carpophagus* was collected in Los Angeles (2004), Orange (2004), Riverside (2006) and San Bernardino (2013) Cos.; and *C. dactyliperda* was collected in Fresno (2004), Riverside (2006), and Tulare (2006) Cos., which represents a range extension in the state for the latter species

[e] San Diego, California, Balboa Park, July 1, 1930, caught at light trap (*CAS*, 1 specimen; *EMEC*, 1 specimen)

[f] Ontario, San Bernardino Co., California, August 1913, breeding in apricot limbs (*CAS*, 2 specimens; *EMEC*, 2 specimens)

[g] F.B. Herbert noted that he observed *I. calligraphus* in 1914–1915 at a site 1.6 km NW of Placerville (El Dorado Co.)

[h] As a consequence of this survey, *X. germanus* was collected on May 30, 2003 at the El Dorado Nature Center in Los Angeles Co., whereas *X. pfeili* was first collected on May 16, 2003 at 3195 Athens Road in Lincoln, Placer Co

[i] Pacific Grove, Monterey Co., November 1904 (*UCRC*), 1 specimen

[j] Los Angeles, March 1936 (*CSCA*), 1 specimen

In this chapter we present an overview of exotic Scolytidae in California with a focus on new species that have been discovered during this survey and subsequent ground reconnaissance. We will explore some of these more significant invasive species from the perspectives of their biology in the new habitat, the case histories of their introductions and establishments, recent research efforts, and potential or realized interactions of the invaders with the native bark and ambrosia beetle fauna in California.

21.2 Invasive Ambrosia Beetles in California

There are records of eight species of ambrosia beetles that have been introduced into California (Table 21.2). Most of these are in the tribe Xyleborini; the exception is *Monarthrum mali* (Fitch), which is in the Corthylini and is an invader from eastern North America (Wood 1982; Wood and Bright 1992). These insects are woodborers that feed as adults and larvae on fungi that grow in their galleries (Solomon

1995; Ranger et al. 2015). They do not construct brood galleries or feed to any great extent in the phloem of trees or shrubs (Solomon 1995). "Host" is a relatively loose term for this group because the trees or shrubs serve primarily as a moistened scaffold or structure in which the fungal food source grows. Thus, any biochemical or physical (e.g., moisture) characteristics of the woody plant are likely to be more indirectly relevant to the feeding and reproductive activity of these species than they are to the phloem feeders (see below).

Of the Xyleborines, fruit-tree pinhole borer or lesser shot hole borer, *Xyleborinus saxeseni* (Ratzeburg), is an interesting case as an invasive species in California (Fig. 21.3, Seybold et al. 2013a). Known as *Xyleborus xylographus* (Say) in the older literature (Essig 1915, 1926; Chamberlin 1939; Bright and Stark 1973), this ambrosia beetle appears to be ubiquitous in North America (Rabaglia et al. 2006) and with a particularly broad distribution in California (Fig. 21.4). It has not only a widespread and transcontinental distribution in North America, but has been collected on five other continents (Wood and Bright 1992). Rabaglia et al. (2006) speculate that it is ultimately a native of Asia, but likely came to North America *via* Europe. It is highly responsive to ethanol used as a semiochemical lure in many generic flight trapping baits across North America and has been a frequently encountered "nuisance" species in many trapping survey programs for bark beetles and woodborers, including ours. It has also been trapped relatively frequently in response to white and black lights (museum survey, *EMEC*). It colonizes both hardwoods and conifers by boring into the xylem and has an enormous host range. Commenting on this host range, Bright and Stark (1973) reported: "possibly no species is exempt from invasion." The breadth of the host range of *X. saxeseni* is illustrated by an April

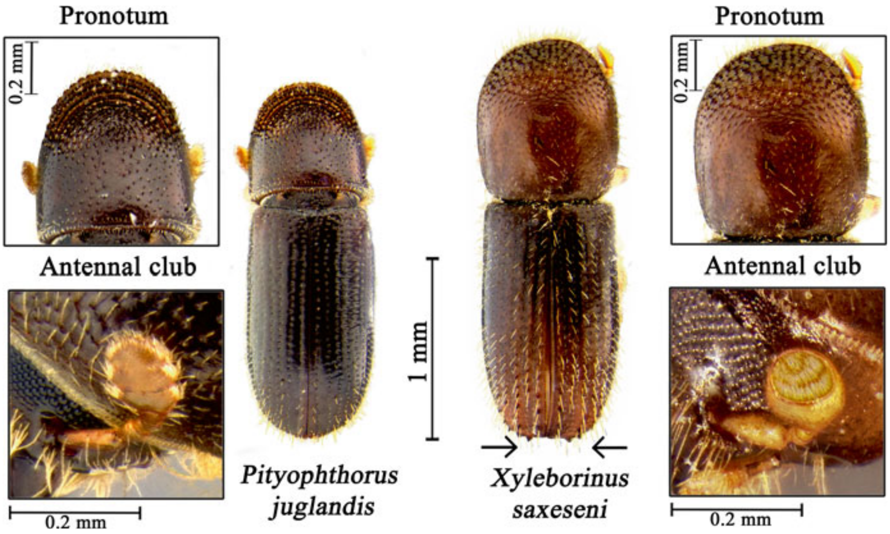
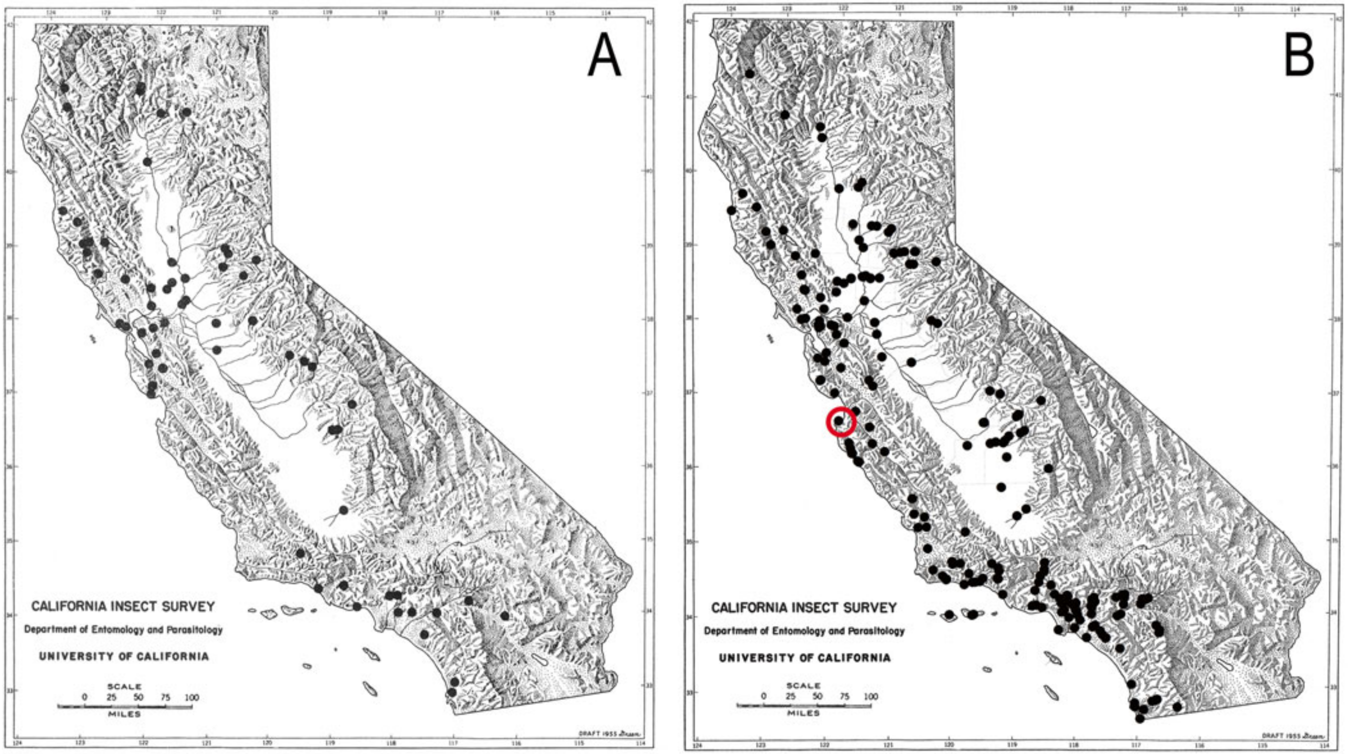


Fig. 21.3 Comparison of dorsal profiles, close up of pronota, and antennal clubs of female walnut twig beetle, *Pityophthorus juglandis* Blackman, and female fruit-tree pinhole borer, *Xyleborinus saxeseni* (Ratzeburg). *Arrows* indicate spines in the elytral declivity and lower right is the truncated antennal club of *X. saxeseni* (Figure by S.M. Hishinuma, UC Davis, from Seybold et al. 2013a)



Map 56. California distribution of *Xyleborus saxeseni* (Ratzeburg).

Fig. 21.4 Distribution of the fruit-tree pinhole borer, *Xyleborinus saxeseni* (Ratzeburg), in California. (**a**) California Insect Survey map from Bright and Stark (1973); (**b**) Map from recent literature review, field surveys, and museum survey by the authors (1904-present). *Red circle* indicates the oldest dated collection record in the museum survey (XI-1904, Pacific Grove, Monterey Co., *UCRC*, Table 21.3)

2014 collection on the campus of the University of California Santa Barbara, where it was found boring into the stem of a declining queen or cocos palm, *Syagrus romanzoffiana* (Cham.) Glassman (B. Cabrera, County of Santa Barbara, personal correspondence). Its ubiquity and abundance make it somewhat reminiscent of invasive and now cosmopolitan species of the bird world like house sparrows, *Passer domesticus* L. (Aves: Passeriformes: Passeridae) or common starlings, *Sturnus vulgaris* L. (Aves: Passeriformes: Sturnidae). Male *X. saxeseni* are flightless (apterous) and relatively rare in the population. The males are generally only trapped when the traps are placed on the stem of trees so that they can crawl to the trapping surface.

Although *X. saxeseni* is generally accepted to have invaded North America, it was unusually widespread at a relatively early point in the history of insect collections in western North America (Table 21.3). This suggests that either it was native or it was introduced early during European colonization and then spread rapidly and completely to many forest ecosystems. There are specimens in several California insect collections dating to the period of 1904–1918, which was an era when even the native bark and ambrosia beetle fauna were collected and recorded for the first time in the State (Hopkins 1899). Also, Essig (1915) noted that it was already "widely distributed throughout this State and the Pacific slope" in the early part of the twentieth century (San Diego Co. to Monterey Co. in our museum survey, Table 21.3). It was also collected from the 1920s to the 1950s from relatively remote locations and in native tree species such as the Six Rivers National Forest near Weitchpec (misspelled in the record as Weitchipac)/ Orrick in Humboldt County in tanoak, *Notholithocarpus densiflorus* (Hook. & Arn.) Rehd.; in the south central Sierra Nevada in Merced County in white fir, *Abies concolor* (Gordon) Lindley ex Hildebrand; and from several out-of-the-way locations in British Columbia (Agassiz, Mission, and Steelhead) in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (then known as *Ps. taxifolia*), and hemlock [likely *Tsuga heterophylla* (Raf.) Sarg] (Table 21.3). The breadth of the distribution of *X. saxeseni* in the early 1900s and the degree to which it occurred in remote wildland forests of California and British Columbia raises some doubt about its status as an invader of western North America. Like the striped ambrosia beetle, *Trypodendron lineatum* (Olivier) (Scolytidae) and the ribbed pine borer, *Rhagium inquisitor* (L.) (Cerambycidae), it is possible that *X. saxeseni* was a Holarctic native forest insect to North America. Chamberlin (1939) noted that its distribution included both the eastern and western USA, and that "it may be an introduced species or it may be that our species is native yet identical with the European species of the same name."

Xyleborinus saxeseni and another invasive ambrosia beetle, *C. bodoanum* (Wood 1982; Hobson and Bright 1994; Wood and Bright 1992; Bright 2014) were recently trapped landing on *N. densiflorus* in an ecological study in redwood-tanoak and mixed evergreen forests in the remote Big Sur region of the Santa Lucia Mountains in the California Coastal Range (Beh et al. 2014). Both *X. saxeseni* and *C. bodoanum* were also detected landing on coast live oak, *Quercus agrifolia* Née, in another research study of sudden oak death conducted north of the San Francisco Bay area (McPherson et al. 2008), and females of both also land on and bore into declining walnut trees in the Central Valley (SJS pers. observation). In most instances where they have been encountered together, *X. saxeseni* is

Table 21.3 Historic collection records of fruit-tree pinhole borer, *Xyleborinus saxeseni* (Ratzeburg) in California and other western North American localities[a]

Date	County	Location	Collection method	Specimens
XI-1904	Monterey	Pacific Grove	*ex: Pinus radiata*	1, *UCRC*[b,c]
II-1910/V-1912	Fresno	Camp Greeley	No data	2, *CAS*[d]
IV-29-1915	Ventura	Ventura	*ex:* apricot	1, *EMEC* 1, *CAS*
V-1915	Los Angeles	Whittier	No data	1, *UCRC*[e]
V-14-1915	San Diego	San Diego	No data	1, *EMEC* 1, *CAS*[f]
IX-25-1918	Santa Clara	Mayfield	*ex:* Monterey cypress	1, *USDA-PSW*[g]
VIII-21-1929	Merced	Yosemite, Happy Oaks (= Happy Isles)	*ex*: white fir, *Abies concolor*[h]	2, *CAS*
VI-29-1930	Yuba	Unknown	*ex:* pear stump	1, *LACM*[i]
VI-14-1939	Mendocino	Ryan Creek	No data	1, *CAS*
VIII-24-1953	Humboldt	Weitchipac/Orrick	*ex:* tanoak	6, *USDA-PSW*[j] 15, *CAS*[j]
No date; Accessioned *LACM* 1964	Santa Clara	Harkins Collection, Stanford University Collection	No data	2, *LACM*
No date; Accessioned *LACM* 1964	San Diego	Harkins Collection, Stanford University Collection	No data	1, *LACM*
V-1928	B.C. (Canada)	Agassiz	No data	*CAS*
I-28-1931	B.C.	UBC	*ex:* green Hemlock	*CAS*
VI-1932	B.C.	Mission	*ex: Tsuga heterophylla*	*CAS*
VII-2-1933	B.C.	Steelhead	*ex: Pseudotsuga taxifolia*	*CAS*

[a] From a museum survey by the authors
[b] Museum acronyms as in Table 21.2
[c] *UCRC* ENT 158376
[d] R. Hopping, coll
[e] *UCRC* ENT 157508
[f] H.A. Weinland, coll
[g] Mayfield (=South Palo Alto) in Santa Clara Co. (*ex*: stem and large limbs of recently burned 8″ Monterey cypress, Hopkins No. 15802, *USDA FS PSW* Collection, HUSSI (1929–1955)
[h] H.E. Burke, coll
[i] Yuba Co. (*ex*: reared from pear stump, CA Dept Ag No. 30222, *LACM* Collection)
[j] Six Rivers National Forest near Weitchipac/Orrick in Humboldt Co. in the main stem of a 26 in. diameter tan oak, *Notholithocarpus densiflorus*, Hopkins No. 33920, *USDA FS PSW* Collection, HUSSI (1929–1955). Note that Weitchpec was misspelled as Weitchipac on the label (*CAS* Collection, Hopkins No. 33920A)

abundant and *C. bodoanum* is relatively rare. *Cyclorhipidion bodoanum* (as *Xyleborus californicus*) had been known previous to our survey work from specimens collected in El Dorado (1986), Santa Clara (1944), and Yolo (1949) Cos. (Wood 1982; Hobson and Bright 1994); in this survey we collected it from Butte, Merced, Monterey, Napa, Placer, Sacramento, Shasta, Solano, and Stanislaus Cos., which extends the distribution to the northern limits of the Central Valley of California. We also found a series of specimens in the museum survey (*EMEC*) collected in 1975 from the central Sierra Nevada community of Arnold (Calaveras Co.). In 2012, it was collected for the first time in southern California (Cleveland National Forest, Riverside County) and then in 2014 in San Diego County (Fig. 21.5). The capacity of species such as these to reach remote corners of the state is a testament to their dispersal capacity and their extreme flexibility to find and utilize reproductive sites in host trees.

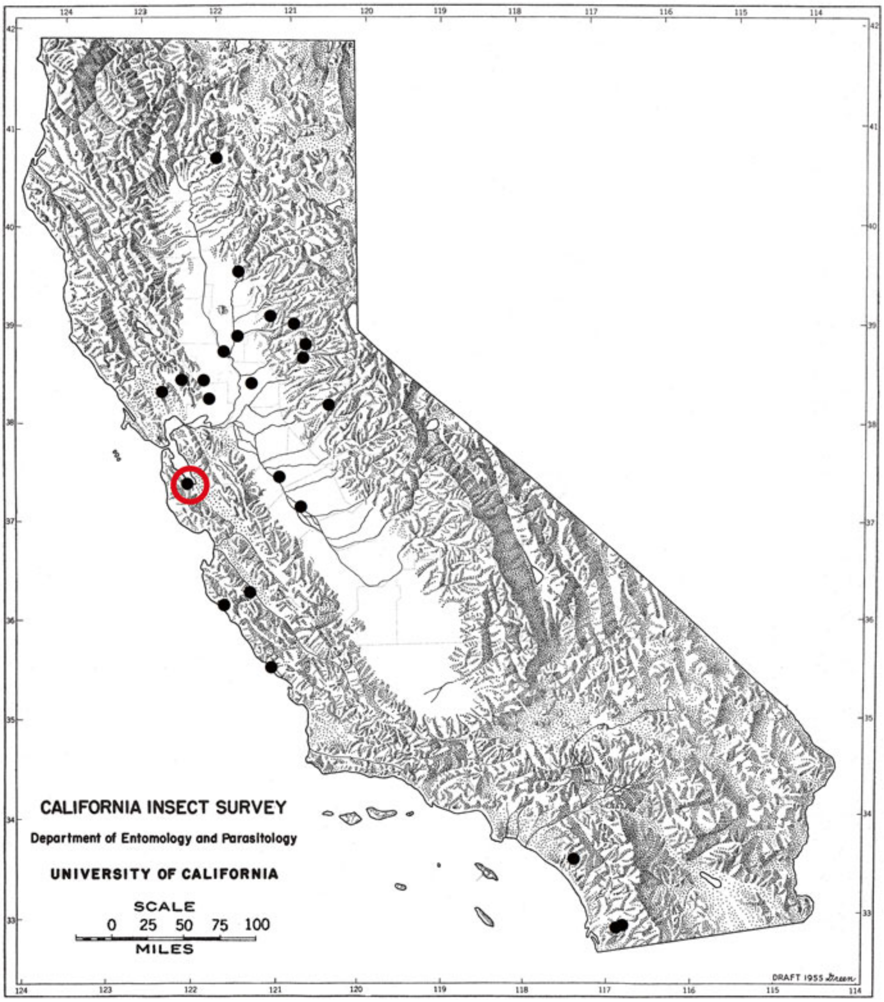


Fig. 21.5 Distribution of the ambrosia beetle, *Cyclorhipidion bodoanum* (Reitter) (formerly *Xyleborus californicus* Wood), in California from recent literature review, field surveys, and museum survey by the authors (1944-present). *Red circle* indicates the oldest dated collection record (III-15-25-1944, Santa Clara Co., *SBMNH*, Wood 1982)

The European shothole borer, *Xyleborus dispar* (Fabricius) was noted by Essig (1926) as an ambrosia beetle pest of a wide variety of trees in Western North America. Its damage to smaller branches and the branch tips bore a resemblance to pear blight, hence it had the common name "pear blight beetle." Essig (1926) noted that it was known from California, Oregon, Washington, and British Columbia, and Linsley and MacLeod (1942) recorded an instance of attacks by *X. dispar* on branches of nectarine trees in Siskiyou County (Northern California), which was the only record listed in Bright and Stark (1973). We have reared it from dying black walnut, *J. nigra* or *J. hindsii x nigra* branches that were removed and brought to the laboratory from Humboldt County (2013), and from frost-damaged small diameter *J. regia* trees from Lake County (2012). In the museum survey (*EMEC*), a male specimen of *X. dispar* was recorded as "taken from walnut" in Corvallis, Oregon (Benton Co.). Despite extensive trapping near walnut trees or rearing from walnut branches and stems, we have not made any additional collections of *X. dispar* related to this host elsewhere in California. Thus, it appears that *X. dispar* is relatively rare with a generally northern distribution in California. Essig (1926) listed a wide range of hosts that included alder, ash, beech, birch, cedar, chestnut, elm, hemlock, maple, oak, pine, poplar, sycamore, tulip tree, and willow as forest trees among many other species normally found in orchards. Presumably, many of these were eastern U.S. records. Jurc et al. (2009) consider *X. dispar* to be polyphagous and reported it colonizing branches from several species of native oaks in Slovenia. Dreistadt et al. (2004) noted that *Xyleborus crassiasculus* (Motschulsky) may be a threat to invade California from neighboring Oregon. The historically northern distribution of *X. dispar* in California suggests that it may have invaded from Oregon as well.

The most dramatic recent addition to the collection of invasive ambrosia beetles in California is the polyphagous shot hole borer (Coleman et al. 2013; Eskalen et al. 2013; Chen et al. 2016, see Chap. 26). This insect is considered to be close phylogenetically to the tea shot hole borer, *Euwallacea fornicatus* (Eichhoff), which has been established for some time in North and Central America and the Pacific Islands with introduced populations in Florida, Hawaii, and Panama (Rabaglia et al. 2006). The tea shot hole borer appears to be native to Asia, but also occurs in Australia and Africa (the Reunion Islands). The polyphagous shot hole borer, which has not yet been assigned a scientific name, was first collected in California on 30 May 2003 near the Port of Long Beach in Whittier Narrows Recreational Area (Los Angeles County) by RLP. It has since expanded its distribution in southern California to include Orange, Riverside, San Bernardino, and San Diego Counties where it mass attacks box elder, sycamore, avocado, and a plethora of other hardwood trees, primarily in riparian areas. It has been a pest of the urban forest and various botanical collections, but is expanding its range into riparian forests in the U.S. National Forest system of southern California and into avocado orchards in San Diego County. The San Diego County population, first detected in 2013, may represent a closely related species or sub-species, which has been referred to provisionally as the Kuroshio shot hole borer. Like *X. saxeseni*, the males of the polyphagous shot hole borer are wingless, relatively sessile, and present at a low proportion relative to the females in the population. Thus, the females are driving the natural dispersal of the introduced population, though like most bark beetles and wood borers, expansion of the invasive population is expected to be highly accelerated by the movement of barked and potentially (in this case) unbarked raw wood products (Haack et al. 2010; Borchert et al. 2011; Jacobi et al. 2012; Jones et al. 2013).

Other new invasive ambrosia beetles in California (Table 21.2) include *Xyleborus pfeili* (Ratzeburg), which was known previously as an invader in Maryland (Vandenberg et al. 2000) and *Xylosandrus germanu*s (Blandford), which is a palaearctic species known from many eastern U.S. states as far west as Michigan and Illinois, and from Ontario and Quebec in Canada (Bright 1968, 2014; Wood 1982; Weber and McPherson 1983; Wood and Bright 1992; Bright and Skidmore 1997, 2002; Douglas et al. 2013). These two species were also recently collected in Oregon (Mudge et al. 2001; LaBonte et al. 2005), and *X. germanus* has been collected in British Columbia in Canada (Bright and Skidmore 2002). *Xyleborus pfeili* was first collected in 2003 near a wood recycling center near Lincoln (Placer Co.) (Table 21.2) and additional collections were made in Placer and eastern Sacramento Cos. *Xylosandrus germanu*s was only collected at El Dorado Regional Park (Los Angeles Co.), but is considered to be established there because it was collected both in 2003 and 2007 (Table 21.2). One other species of immigrant *Xyleborus* that has been previously recorded in California is *X. xylographus* Say (not to be confused with the old references to *X. saxeseni*). *Xyleborus xylographus* was known previously in California only from specimens collected (1948) in the Sierra Nevada in El Dorado Co. (Wood 1982; Hobson and Bright 1994), but in this survey we collected it from Marin, Orange, Shasta, Solano, Sonoma, Sutter, and Trinity Cos., which extends the distribution to the northern Central Valley, to coastal California, and to southern California.

21.3 Invasive Spermophagous and Miscellaneous Bark Beetles in California

To date, four scolytid species that feed on seeds of palms and other plants have been introduced into California (Table 21.2). The host range of this guild is rather unusual as it includes fresh and dry seeds of many plants (Wood and Bright 1992), as well as petioles of leaves (Bright and Skidmore 2002); logs of conifers (Bright 2014); and buttons made of "vegetable ivory" (Wood 1977) (Appendix 21.I). The earliest introduction of a member of this feeding group to California appears to have been with *Coccotrypes dactyliperda* (F.), for which the oldest record in our survey was 1930 in San Diego Co. (Fig. 21.6a). Chamberlin (1939) considered this species to have been established in Hawaii, but only introduced, not established, in the continental USA. He noted that Van Dyke had collected it from the Canary Island date palm, *Phoenix canariensis* Chabaud, in Los Angeles. Holzman et al. (2009) confirmed the general timing of the introduction by stating that it first occurred in

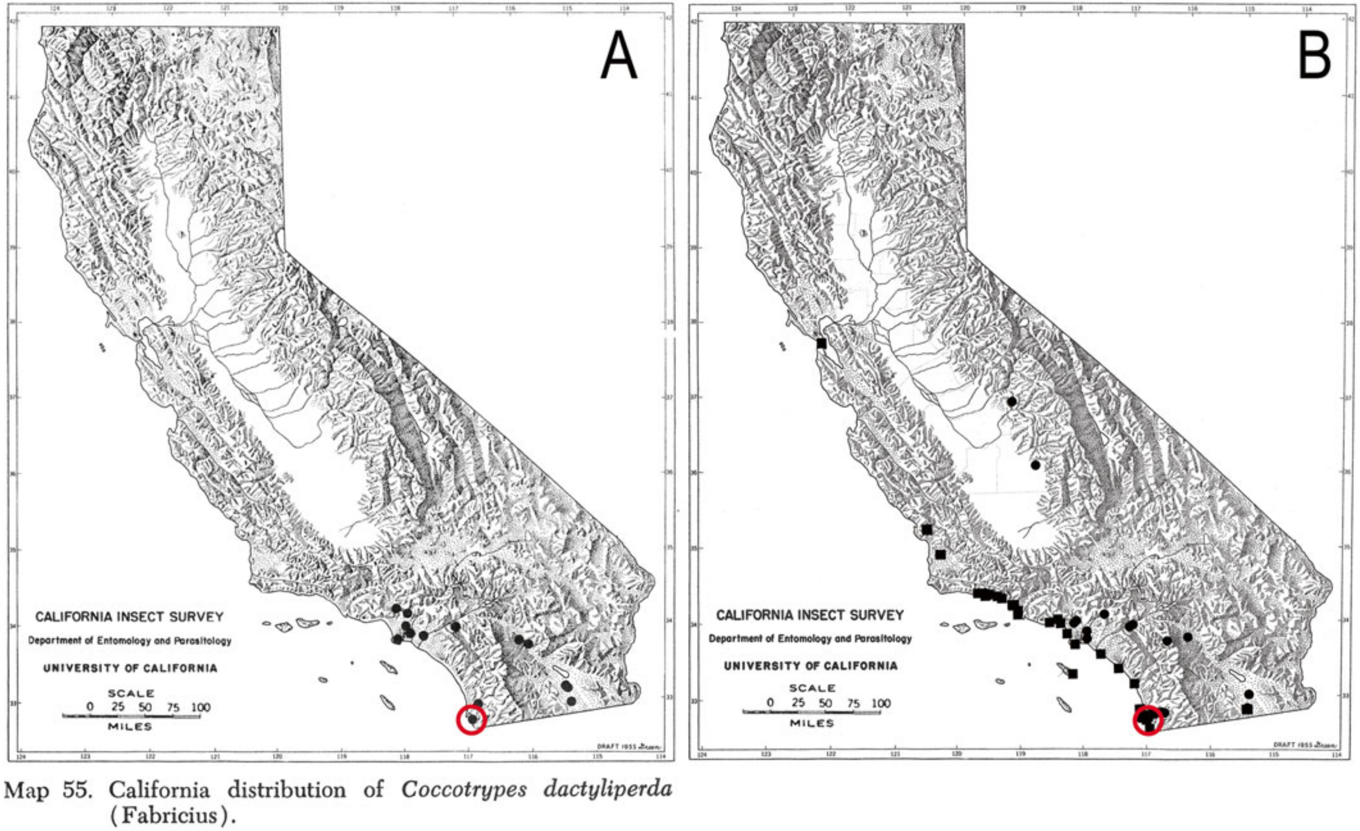


Fig. 21.6 Distribution of the spermophage, *Coccotrypes dactyliperda* (F.), in California from field survey data and museum records. (**a**) California Insect Survey map from Bright and Stark (1973); (**b**) Map from field and museum survey by the authors (1930-present) with squared entries from Holzman et al. (2009). *Red circles* indicate the oldest dated collection record (VII-1-1930, Balboa Park, San Diego, San Diego Co., *CAS* and *EMEC*)

California about 80 years ago. Our survey yielded records of *C. dactyliperda* from Fresno (2004), Riverside (2006), and Tulare (2006) Cos., which represent a range extension in the state (Fig. 21.6b). Holzman et al. (2009) also report a northern extension of the range along the Central Coast. Its distribution in the USA also includes Arizona, Florida, and Texas (Wood and Bright 1992). Two other more recently introduced species in this genus are *C. advena* Blandford and *C. carpophagus* (Hornung), both of which were first detected in the trapping survey or a related Early Detection Rapid Response survey executed by CDFA (Table 21.2). *Coccotrypes advena* was first collected in a survey trap on 6 October 2006 in Whittier Narrows Recreational Area near South El Monte in Los Angeles County (identified by D.E. Bright) and known only from this site based on collections in 2006 and 2007. It is likely from Southeast Asia (Indonesia) (Wood 1977), but also occurs in Australia, the Pacific Islands (including Hawaii, Bright and Skidmore 1997), the Caribbean (including Puerto Rico, Bright 2014), and South and Central America. It was first reported from North America (Florida) by Wood (1982) and again by Atkinson and Peck (1994), though the latter authors implied that it might not actually be established in south Florida. This species has a rather large host range (Wood and Bright 1992), and presumably colonizes the seeds of most of these hosts (Appendix 21.I). Another spermophage, *Dactylotrypes longicollis* (Wollaston), feeds on seeds of the date palm, *Phoenix dactylifera* L., and of *P. canariensis* (Whitehead et al. 2000; LaBonte and Takahashi 2012). So far it is only known in North America by several collection records in southern California (Orange and Los Angeles Cos.) (Penrose 2010; LaBonte and Takahashi 2012). These types of beetles constitute a threat to the California date industry, which has its origins in the Mediterranean.

Another unusual invasive species of scolytid in California is *Hypothenemus eruditus*. The collection history of this species is typical of a California invasive in that the earliest records (1936) were in urban southern California, and subsequent collections have been from urban, or disturbed habitats and agroecosystems. Bright and Stark (1973) suggest that the California distribution of *H. eruditus* is along the southern Pacific Coast, but we have found it to be widespread in the Central Valley as well (Fig. 21.7). Wood (1982) notes that it has bred in everything from the cover of a book (hence the name "*eruditus*"), to fungal fruiting bodies, and fruiting stalks of grass. The galleries may also be in the central axis (pith) of twigs and leaf stalks, or they may engrave the xylem surface in the more typical phloeophagous habit. The host range is enormous (Wood and Bright 1992; Bright and Skidmore 1997, 2002; Wood 2007; Bright 2014), and the intraspecific genetic diversity may also be quite high as Wood (2007) noted 72 synonyms. Wood (2007) also reported that *H. eruditus* may be the most widely distributed and abundant species of scolytid in the world. The structure of the female-constructed galleries and the larval mines has been described as "irregular" (Wood 2007). Although *H. eruditus* is not thought to be an ambrosia beetle, like many of the ambrosia beetles mentioned above, the males are flightless and they mate with their female siblings (Wood 2007). We reared this species from 5 to 7.5 cm and larger diameter branches of *J. regia*, *J. californica*, and *Pterocarya* spp. collected from Los Angeles and Solano Counties

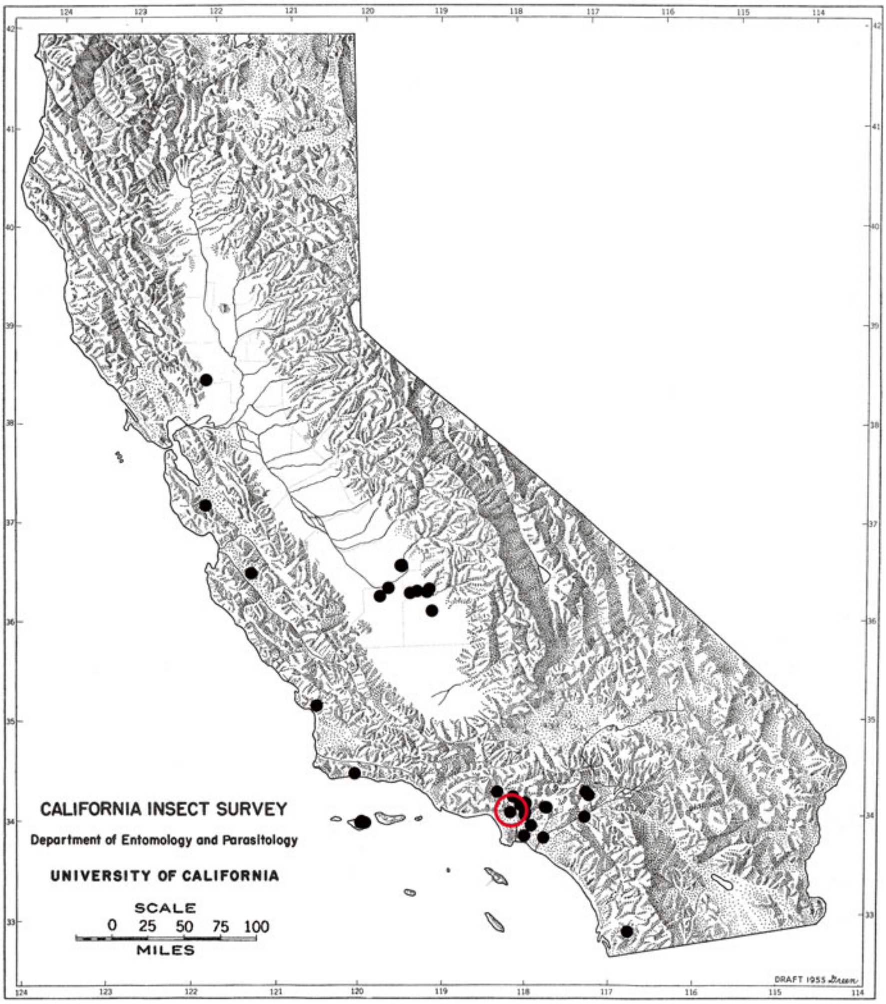


Fig. 21.7 Distribution of the minute bark beetle, *Hypothenemus eruditus* Westwood, in California from field and museum survey by the authors (1936-present). *Red circle* indicates the oldest dated collection record (III-1936, Los Angeles, Los Angeles Co., *CSCA*)

(Hishinuma et al. 2015). We have also reared it on several occasions from crown gall (*Agrobacterium tumefaciens*)-infected paradox walnut rootstocks (burls) collected in Kings County. It (and *X. saxeseni*) was also captured in funnel traps placed in three *J. regia* orchards as part of a *P. juglandis* seasonality study in Fresno and Tulare Counties when antifreeze laden with ethanol was inadvertently used in the trap cups instead of the recommended propylene glycol-based product (Seybold et al. 2013a). Because of its extremely small size (females, 1.0–1.3 mm; males, 0.7–0.8 mm in length, Mifsud and Knížek 2009), this species and its congeners are typically ignored in various research and survey efforts involving forest insects. Wood (2007) also attributed (in part) the large number of synonyms to the small size of *H. eruditus* and the inability of taxonomists to see the characters necessary to make an accurate species determination.

21.4 Invasive Phloem–Feeding Bark Beetles of Economic Importance in California

21.4.1 Scolytus

There are three species of introduced *Scolytus* in California. One is a pest of rosaceous fruit and nut trees [*Scolytus rugulosus* (Müller)], and two are pests of elms [*Scolytus multistriatus* (Marsham) and *Scolytus schevyrewi* Semenov]. As a threesome, they represent interesting comparative histories of establishment. Furthermore, the more recent invasion of North America by *S. schevyrewi* has created a case of competitive displacement whereby population densities of *S. multistriatus* appear to be on the decline as *S. schevyrewi* usurps the habitat (Lee et al. 2009).

21.4.1.1 Shothole Borer, *Scolytus rugulosus* (Müller)

North American populations of the shothole borer, *Scolytus rugulosus*, are thought to have been derived from Europe (Furniss and Carolin 1977), though Wood (1982) notes the strong potential for distinct geographic races from Europe and Asia, and it appears that no one has tried to evaluate the populations in North America for this diversity with modern molecular methods. Michalski (1973) also remarks on the morphological diversity of the specimens that he examined, with special emphasis on Central Asian populations. Wood and Bright (1992) list 13 subspecies or synonyms for *S. rugulosus*, also a reflection of this diversity of the species. In addition to southern Canada and every state of the USA, *S. rugulosus* has been collected in Chihuahua and Durango, Mexico, as well as in Argentina, Brazil, Chile, Peru, and Uruguay in South America (introduced) (Wood 1982, 2007; Wood and Bright 1992; Bright and Skidmore 1997). No major changes in status of the distribution or host range were reported in Bright and Skidmore (2002) or Bright (2014).

Scolytus rugulosus is a Palaearctic species that colonizes fruit trees and appears to have arrived in California long before the development of industrial-style agriculture; its origins in North America are unclear (Essig 1915, 1926; Bright and Stark 1973). Bright and Stark (1973) suggest that it was first collected or introduced into the USA in 1878, whereas Smith (1932) states that "It is believed to have been accidently introduced into the United States some time prior to 1877." From specimens in the Canadian National Collection, the first record in Canada is from 1917 in Prince Edward County, Ontario (Douglas et al. 2013). Wood (1977) suggests an even earlier introduction for *S. rugulosus* into the USA (colonial period). However, although five native bark and ambrosia beetles were present, *S. rugulosus* was not among the 42 species of Coleoptera recovered in the archaeoentomological study of refuse pits from seventeenth century colonial Boston (1635–1662) (Bain 1998).

Its entry into California most certainly came much later than colonial times. Smith (1932) noted that "The first authentic record of the occurrence of this pest in California is found in the files of E.O. Essig, who discovered it in Ventura County in 1910." However, Essig (1915) wrote that, "So far this species is recorded as limited in California to the deciduous fruit section adjacent to Ontario, San Bernardino County." Specimens in the *CAS* and *EMEC* from this era (1913) support this assertion (Table 21.2). It was also collected in 1915 in Chino (San Bernardino Co.) and El Modena (Orange Co.), and in 1916 in Pasadena (Los Angeles Co.) (museum survey, *EMEC*). Thus, if *S. rugulosus* were introduced into Ventura County it appears to have quickly established populations further south in the state, and particularly, in San Bernardino County (see red circles in Fig. 21.8). Smith (1932) also reported that it moved rapidly through the state such that by 1932 it was known to occur in the majority of counties in California (Fig. 21.8) and was responsible for injury to fruit trees in the Santa Clara, San Joaquin, and Sacramento Valleys, as well as in parts of southern California. It is somewhat amazing that during a period of rather limited transportation, *S. rugulosus* had the capacity to disperse and hitchhike its way throughout nearly the entire state of California in less than 20 years (1915–1932). It is also possible that Essig's discovery in Ventura Co. in 1910 raised awareness about *S. rugulosus* amongst growers and the limited pest detection community at the time such that already resident populations of the pest in other regions of the state were more quickly identified and documented. Nonetheless, this appears to be another case of an invader whose founder populations colonized southern California.

The ubiquity and abundance of *S. rugulosus* in California is underscored by its long and consistent collection record throughout the state (Fig. 21.8b, c); it is particularly abundant in the Central Valley for obvious reasons and with the major growth of the almond industry in recent years. For example, in 2011–2012, the senior author collected extremely large numbers of specimens on purple and green sticky panel traps targeting detection of the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer, at an almond and oak firewood processing site in Bakersfield (Kern County). From time-to-time *S. rugulosus* has been trapped dispersing through walnut orchards, likely when moving from one almond or fruit orchard to another. In cherry orchards in the state of Washington, Doerr et al. (2008) describe the dispersal of *S. rugulosus* from debris piles of fruit tree cuttings some 50 m distant to the edges of the orchard where they attacked healthy trees.

The beetle utilizes the phloem of branches or small diameter stems as host material. Feeding by adults and larvae at the phloem/xylem interface can lead to girdling, which can cause branch or tree death. When forming brood galleries, females colonize first and construct a short (1–4 cm) uniramous and generally longitudinal egg gallery without a nuptial chamber (Michalski 1973; Wood 1982). The females generally initiate the entrance hole on a lenticel where the soft spongy tissue may allow for easier access and leverage for tunneling through the outer bark (Smith 1932, 1945). Colonization attempts on healthy host trees may lead to a resin exudate (gumming) from entrance holes, which can kill the adults (Smith 1945; UC-IPM 2015). In stressed hosts, gumming may not occur in response to colonization attempts. One male joins the female, and the male removes the frass from the gallery. This gallery is etched relatively deeply onto the surface of the xylem and pupal

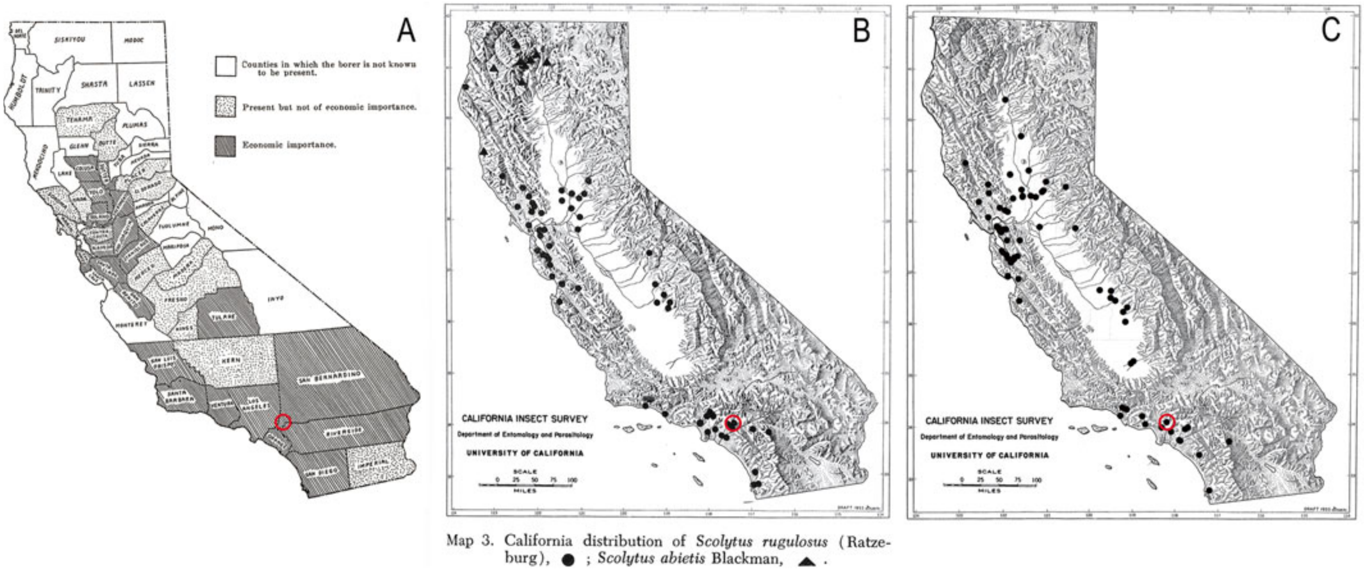


Fig. 21.8 Distribution of the shothole borer, *Scolytus rugulosus* (Müller), in California from the literature and from field survey data and museum records. (**a**) Distribution map from Smith (1932); (**b**) California Insect Survey map from Bright and Stark (1973); (**c**) Map from field and museum survey by the authors (1913-present). *Red circles* indicate the oldest dated collection record (VIII-1913, Ontario, San Bernardino Co., *CAS* and *EMEC*, Essig 1915, 1926; Smith 1932, 1945). The discovery of *S. rugulosus* in Ventura Co. by E.O. Essig in 1910 (Smith 1932) was not substantiated by any corresponding specimens in any of the collections in our museum survey

cells are frequently created deep in the wood (1–2 cm below the surface) (Michalski 1973; Furniss and Carolin 1977; Wood 1982). The gallery system has been described as "centipede-like" (UC-IPM 2015), but the galleries often overlap as a consequence of the aggregating adults, so they lose their distinction. Adults may also kill small twigs by feeding at the base of the bud; these wounds also exude considerable resin or gum (Smith 1945; Furniss and Carolin 1977). In California, Smith (1945) suggested that there are 3–4 generations in the warmest parts of the range, whereas Dreistadt et al. (2004) report 2+ generations per year with adults active primarily from April to June and the larvae as the primary overwintering stage.

The host range is rather broad, and the beetle seems quite capable of exploiting declining branches or stems of many fruit trees (*Malus, Prunus, Pyrus*, etc., and allied species (Appendix 21.I). Dreistadt et al. (2004) list the following pre-disposing factors: root diseases, insufficient irrigation, infestations of other insect pests, whereas Doerr et al. (2008) emphasize that a lack of orchard sanitation may be the key factor leading to colonization of residual healthy trees (in this case, cherry trees). Another stress factor related to the success of *S. rugulosus* is sun scald on newly planted trees or on pruning wounds created in the summer (UC IPM 2015).

It appears that *S. rugulosus* colonizes and kills healthy limbs and trunks when population densities are high, so management steps to reduce density are critical (Dreistadt et al. 2004). These steps include: (1) pruning off heavily infested limbs; (2) removing heavily infested trees from orchards; (3) practicing good orchard sanitation, which involves burning or removing infested or unifested prunings before the growing season starts (UC-IPM 2015). It is important not to leave branches, stems or stumps anywhere near where healthy trees are growing. There are no chemical ecological tools for managing *S. rugulosus*, but a female-produced aggregation pheromone component (4-methyl-3-hexanol) has been isolated from the closely related *S. amygdali* Guerin-Meneville (Ben-Yehuda et al. 2002). This semiochemical may have utility in detecting both *S. rugulosus* and *S. amygdali*. Both of these species were evaluated for their damage to fruit trees in the Mediterranean region (Israel) and the levels of damage to stone (64 % of sampled areas) and pome (18 % of sampled areas) were influenced by "grove" management, resistance to infestation by a local buprestid species; climatic conditions; and the conditions (health) of trees neighboring the orchard under survey (Mendel et al. 1997). Thus, the behavior and management of this pest in the Mediterranean *sensu stricto* appears to be similar to the situation in California.

21.4.1.2 European Elm Bark Beetle, *Scolytus multistriatus* (Marsham)

The European elm bark beetle, *Scolytus multistriatus*, was first detected in North America in 1909 in Massachusetts (Chapman 1910). In contrast to the uncertainty surrounding the introduction of *S. rugulosus*, the entrance of *S. multistriatus* into California was documented by Armitage (1951) when it was collected on the campus of San Jose State University (Santa Clara County) from an ornamental slippery elm, *Ulmus fulvus* (= *U. rubra* Muhl.), tree in what appeared to be a well-established population (Fig. 21.9a, red circle). It was soon thereafter (1955) collected in southern California (Glendale, Los Angeles Co., museum survey, *EMEC*) from Siberian elm,

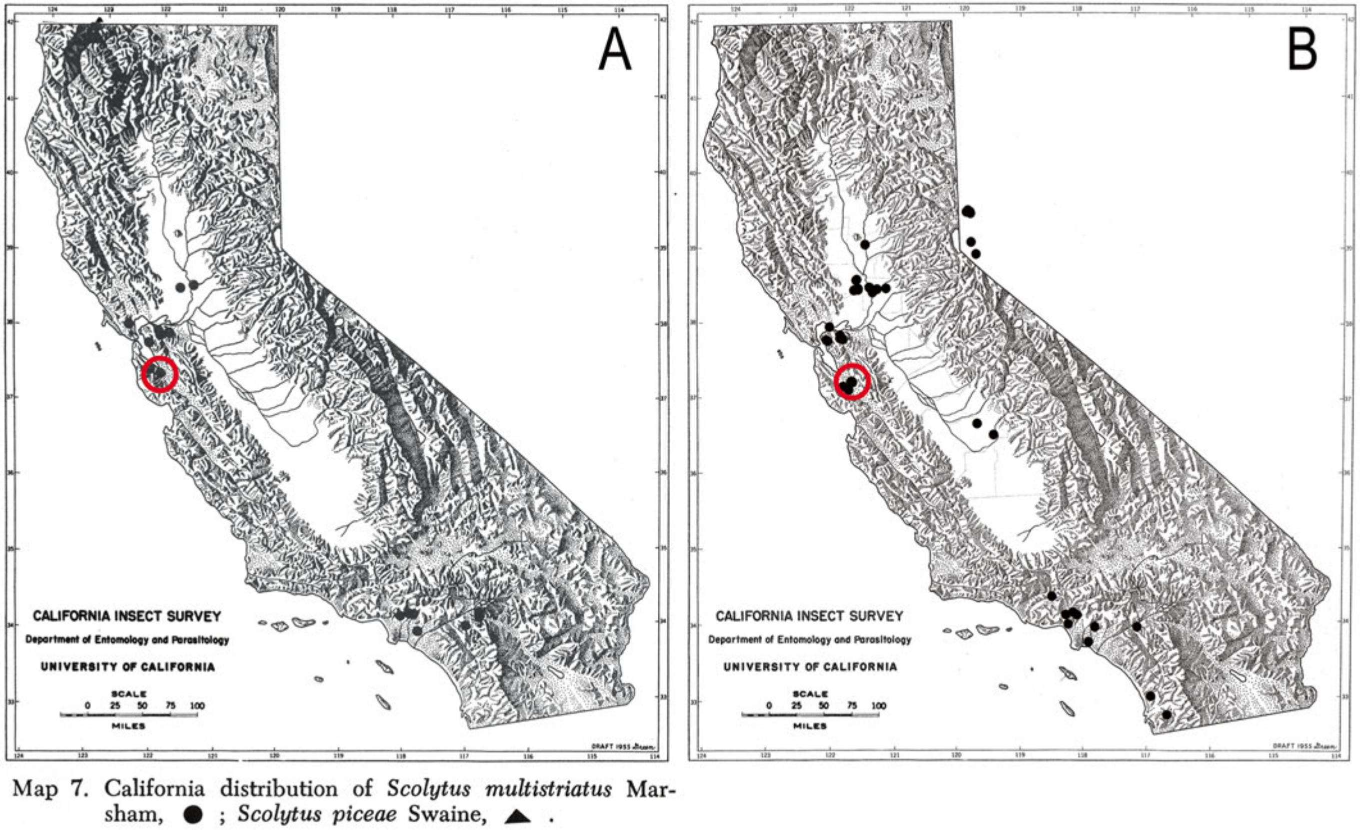


Fig. 21.9 Distribution of the European elm bark beetle, *Scolytus multistriatus* (Marsham), in California from the literature and from field survey data and museum records. (**a**) California Insect Survey map from Bright and Stark (1973); (**b**) Map from field and museum survey by the authors (1951-present). Note Nevada collection records from Carson City, Gardnerville, and Reno. *Red circles* indicate the oldest dated collection record (III-1-1951, San Jose, Santa Clara Co., *CSCA* and *EMEC*, Armitage 1951)

U. pumila L. Although *S. multistriatus* could have made a "long march" across the continent from its original introduction point in the East (Chapman 1910), it appears to have arrived in California as its first destination west of the Mississippi River (Armitage 1951). The remaining portions of the continent were invaded later punctuated by announcements of its "progress" from regulatory and detection entomologists and plant pathologists (Parker et al. 1947; Davidson and Newell 1957; Davidson et al. 1964; Barger and Hock 1971; Claflin and Dooling 1973; Ives and Petty 1976; Buth and Ellis 1981). This likely was a consequence of flight dispersal and elm firewood transport. By 1970, *S. multistriatus* was found in most of the contiguous United States except for Montana, Arizona, and Florida (Barger and Hock 1971), but it has since been collected in Montana in 1973 (Claflin and Dooling 1973), in Arizona in 1976 (B. Celaya, personal communication in Lee et al. 2009), and in Florida in 1997 (T. H. Atkinson, personal communication in Lee et al. 2009).

Since the 1930s, *S. multistriatus* has been known to be a principal vector of the pathogen that causes Dutch elm disease (DED) (Readio 1935), a disease that resulted in 50–75 % mortality of pre-1930s American elm, *Ulmus americana* L., populations in the northern and eastern USA (Bloomfield 1979). The causative agents of DED are the fungi *Ophiostoma himal-ulmi* Brasier & M.D. Mehrota, *Ophiostoma novo-ulmi* Brasier, and *Ophiostoma ulmi* (Buisman) Nannf. (Harrington et al. 2001), and the vector-pathogen interactions have been well studied in Europe (Webber 1990, 2000, 2004; Webber and Brasier 1984). In California, *S. multistriatus* is considered to be widely distributed, but the fungal pathogen is only thought to occur in the San Francisco Bay Area and the greater Sacramento area (Dreistadt et al. 2004). Our survey did not target *S. multistriatus* by using its aggregation pheromone, so the distribution reported here should be considered an underestimate of the true range of the species in California (Fig. 21.9b). This species was largely detected in the survey in urban areas where *U. americana*, and English elm, *U. minor* Mill., are grown as street trees. Surprisingly, it was also trapped in some of the agricultural sites in the Central Valley, perhaps dispersing through orchards between rural residences with planted elm trees.

The chemical ecology of *S. multistriatus* was reviewed in Negrón et al. (2005) (see next section), but there is one unusual host interaction of *S. multistriatus* in California that bears emphasis. A widely planted elm in the Central Valley and in southern California is Chinese elm, *U. parvifolia* Jacq. In flight assays in the Sacramento area, Lee et al. (2010) reported that the response of *S. multistriatus* toward uninfested *U. parvifolia* was low and not different from unbaited traps. This low preference for *U. parvifolia* was consistent with work reported by Švihra and Koehler (1981) where *S. multistriatus* showed a greater flight response to bolts of *U. pumila*, than to *U. parvifolia*. Although *S. multistriatus* has been reported to infest *U. parvifolia* (Brown 1965), many females provided with this host in the laboratory died before ovipositing and survival of progeny was low (Švihra and Volney 1983; Švihra 1998). Dreistadt et al. (2004) also note that the galleries of *S. multistriatus* are "more meandering" on *U. parvifolia* as well, thus this host may tolerate invasion by this beetle. Sanitation of cut elm wood is considered a sound management practice for *S. multistriatus* as long as the wood can be tarped for at least 7 months (Švihra 1987).

21.4.1.3 Banded Elm Bark Beetle, *Scolytus schevyrewi* Semenov

The banded elm bark beetle, *Scolytus schevyrewi*, native to Asia, was detected in the USA in 2003 (Negrón et al. 2005; Lee et al. 2006). In Asia, *S. schevyrewi* occurs in the northern Chinese provinces of Beijing, Hebei, Heilongjiang, Henan, Ningxia, Shaanxi, and Xinjiang, as well as in Korea, Mongolia, Russia, Kazakhstan, Uzbekistan, Kyrgyzstan, Turkmenistan, and Tajikistan (Michalski 1973; Krivolutskaya 1983; Wang 1992; Wood and Bright 1992; Bright and Skidmore 1997, 2002; Liu and Haack 2003). A seven-state survey revealed that *S. schevyrewi* was much more abundant than *S. multistriatus*, in areas of Colorado and Wyoming (Lee et al. 2009). This pattern of competitive displacement is likely to unfold both to the west and east of these Rocky Mountain states, and based on bycatches in various methylbutenol-baited survey traps for the walnut twig beetle, this displacement appears to be underway in California and Minnesota (SJS, personal observation). The key mechanistic components that facilitate the displacement appear to be the competitive advantage of *S. schevyrewi* larvae under the bark, and the more rapid response of *S. schevyrewi* to uninfested elm hosts established through flight studies (Lee and Seybold 2010; Lee et al. 2010, 2011).

Corresponding with the advent of the Age of the Internet, the entomological community became rapidly aware of *S. schevyrewi* as a North American invader in April 2003 when it was detected in a USDA Forest Service-USDA APHIS Plant Protection and Quarantine survey trapping program (Early Detection Rapid Response Pilot Project-EDRR) around pallet recycling sites near Aurora, Colorado and Ogden, Utah (Negrón et al. 2005; Lee et al. 2006, 2007, 2009; LaBonte 2010). However, the nearly simultaneous discovery of *S. schevyrewi* across the western USA in 2003–2004 indicated that the insect was not a recent introduction, but had been present in North America for many years. Indeed, a survey of museum collections and detection records revealed that *S. schevyrewi* had been collected in 1994, 1998, and 2000 in Colorado, New Mexico, and Oklahoma, respectively (Negrón et al. 2005). The specimens had likely been either amongst the unidentified material or misidentified and co-mingled with *S. multistriatus* in these collections. Of relevance to California, were specimens of *S. schevyrewi* collected in 2002 from southern California (Los Angeles Co., City of Industry, 1 July 2002, T. Galindo, collector; Table 21.2, Fig. 21.10) from funnel traps baited with ethanol and α-pinene. This species is now known from 28 U.S. states, as well as five Canadian Provinces (Alberta, British Columbia, Manitoba, Ontario, and Saskatchewan) (CFIA 2007; Lee et al. 2009; Humble et al. 2010; Bousquet et al. 2013; Douglas et al. 2013). It is present in at least 13 California counties ranging from San Diego in the south to Lassen in the north (Fig. 21.10). Surprisingly, it had not yet appeared to have invaded the northern Central Valley during the period of our survey.

The nearly decade long period from when specimens were accessioned into museum collections and the discovery of *S. schevyrewi* in North America was due in part to the morphological similarity of the species with *S. multistriatus* (Negrón et al. 2005). Although *S. schevyrewi* generally resembles *S. multistriatus*, the

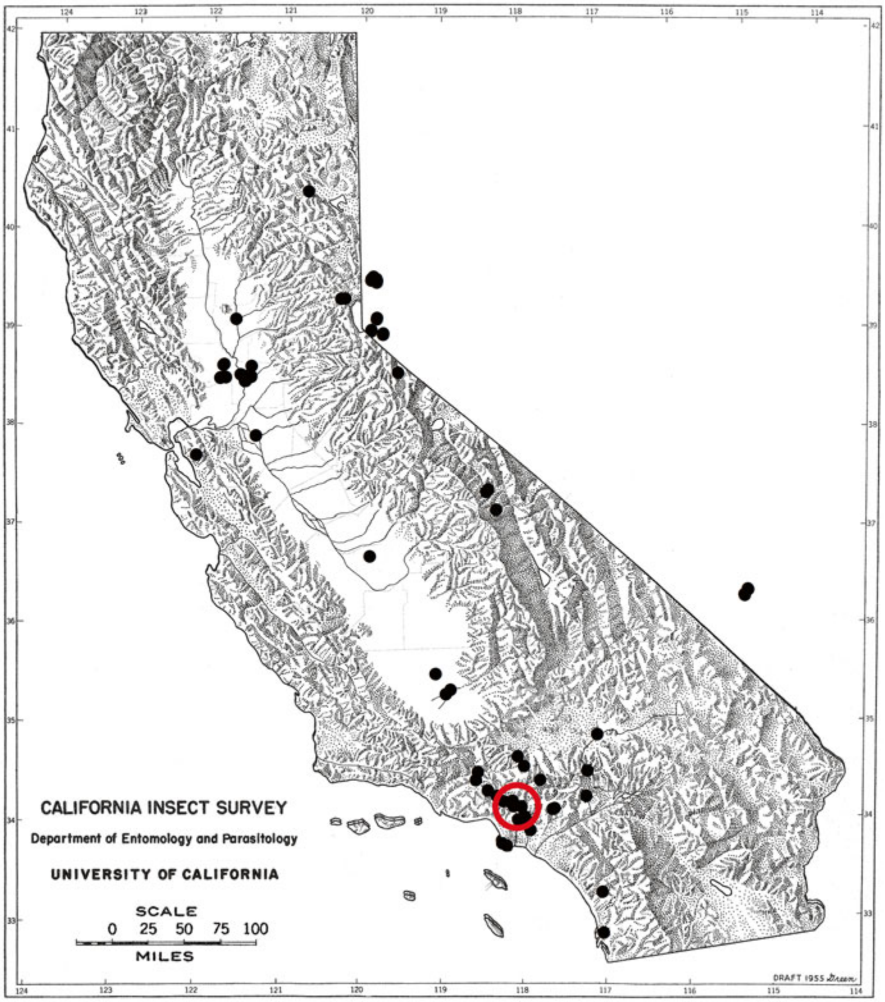


Fig. 21.10 Distribution of the banded elm bark beetle, *Scolytus schevyrewi* Semenov, in California from field and museum survey by the authors (2002-present). Note Nevada collection records from Carson City, Genoa, Las Vegas, and Reno. *Red circle* indicates the oldest dated collection record (VII-1-2002, City of Industry, Los Angeles Co., *CSCA*)

former often has a light-to-dark band across its wing covers (elytra), whereas the latter has tooth-like structures along the margin of some of the ventrites. The two species can be distinguished by size, ventral spine placement, presence/absence of elytral band, and the posteriolateral "teeth" (Lee et al. 2006, 2007; LaBonte 2010). There are also differences in the morphology of the single spine on the second ventrite and its alignment with the anterior margin of the ventrite (Lee et al. 2006). Johnson et al. (2008) provided a molecular technique for separating *S. schevyrewi* and *S. multistriatus* adults and larvae. Information on the basic biology of *S. schevyrewi* in its native range is sparse. The native host range was reviewed by Negrón et al. (2005); additional details of aspects of its host associations in North America are presented in Appendix 21.I). It appears to have a strong preference for *Ulmus pumila* in the western USA, and when cut logs (bolts) of this host were allowed to be colonized by wild populations in the field, *S. schevyrewi* did not differ in emergence density from 10- versus 24-cm-diameter bolts (Lee et al. 2011). In contrast, in research with *S. multistriatus* in northern California, Hajek and Dahlsten (1985a) reported that *Ulmus procera* Salisb. branch diameter demonstrated a strong positive relationship with the density of *S. multistriatus* eggs, attacks, gallery lengths, and emerged adults. In Colorado, *S. schevyrewi* often landed on elm bolts between 12:00 p.m. and 4 p.m.; and near large elm trees, they were captured more frequently on sticky traps at 1.8 and 3.7 m aboveground than higher along the main stem (Lee et al. 2011).

Banded elm bark beetle females construct single vertical egg galleries in the phloem that are about 4–6 cm long and lack a nuptial chamber. Males move about the bark surface searching for entrance holes and mate with multiple females at these entrances. Between 20 and 120 eggs are laid and females guard the egg gallery until death. Larvae develop through four or five instars and migrate to the outer bark to pupate. There are two to three generations in the USA. Larvae, pupae, and adults overwinter, and the adults start emerging in early spring. In Colorado/Nevada, *S. schevyrewi* initiated flight in April/March and ceased in October/September, whereas *S. multistriatus* initiated flight in April/May and ceased in October/September (Lee et al. 2011).

Populations of *S. schevyrewi* have damaged drought-stressed elms in the arid Rocky Mountain and Intermountain regions where *U. pumila* is a primary shade tree. For example, in 2004, 333 infested *U. pumila* trees were removed from Newcastle, Wyoming (Lee et al. 2007). As it displaces *S. multistriatus*, *S. schevyrewi* could threaten American elm populations across the USA. Beetles emerging from diseased American elm logs carried spores of *Ophiostoma novo-ulmi*, the causative agent of Dutch elm disease (Jacobi et al. 2007). Later studies showed that the pathogen could also be transmitted to healthy elms (Jacobi et al. 2013). Before mating, *S. schevyrewi* feeds in twig crotches; this behavior may facilitate transmission of the pathogen by the beetles to living trees.

In the 1970s, studies of the chemical ecology of *S. multistriatus* revealed aggregation behavior based on both female-produced pheromone components and host co-attractants (summarized in Negrón et al. 2005). The role of behavioral chemicals in the aggregation behavior of *S. schevyrewi* is poorly understood. In funnel trap flight assays of semiochemicals in Colorado or Nevada, Lee et al. (2011) demonstrated that *S. schevyrewi* had moderate responses, 3 to 10-fold greater than unbaited control traps, to Multilure (a commercial lure for *S. multistriatus*), 2-methyl-3-buten-2-ol (MB) combined with multistriatin, and MB combined with a plant extract that is included in a commercial formulation of Multilure. In contrast, *S. multistriatus* had a 226 to 259-fold greater response to Multilure than to the control. Both *Scolytus* species showed electroantennographic (EAG) responses to MB, racemic multistriatin, and (+)- and (−)-α-pinene (a host *Ulmus* monoterpene), with the greatest sensitivity to multistriatin. *Scolytus schevyrewi* was more responsive to (−)-α-pinene than was *S. multistriatus* (Lee et al. 2011).

The co-colonization of *Ulmus* by the two *Scolytus* spp. was characterized through tests of long-range flight responses to infested or uninfested small cut logs of *Ulmus americana, U. parvifolia,* and *U. pumila* (Lee et al. 2010). Trials were conducted in Colorado and Wyoming to test the flight response of *S. schevyrewi*; in California to test the response of *S. multistriatus*; and in Nevada to test the responses of both species simultaneously. Studies with *S. schevyrewi* showed that males and females aggregated toward *Ulmus* spp. host volatiles but provided no evidence of a putative aggregation pheromone during the 0–48 or 48–96-h period of infestation. In contrast, *S. multistriatus* was attracted to *U. pumila* over unbaited controls, more to *U. pumila* infested with conspecific females than without, and more during the 48–96- versus 0–48-h period of infestation. This confirmed that male and female *S. multistriatus* aggregated toward host volatiles and that females produced an aggregation pheromone. In a cross-attraction study, *S. schevyrewi* displayed neither flight preference nor interruption to *U. pumila* infested with conspecifcs, heterospecifics, or a mix of both species. Response of *S. multistriatus* was too low to draw conclusions. Although *S. multistriatus* aggregates moderately to host volatiles and strongly to female-derived pheromones emitted after a few days, *S. multistriatus* may have a relative disadvantage by selecting elm hosts more slowly than *S. schevyrewi*, which aggregates very strongly to host volatiles and does not appear to be deterred by the presence of its heterospecific. As noted above, the differential long-range host location strategy may be one factor in a chain of behavioral events that leads to advantageous host colonization and development by *S. schevyrewi*.

Lee and Seybold (2010) examined the sequence of behavioral interactions between the species on and below the bark surface. At the first step in the sequence, host acceptance behavior (i.e., time to tunnel into the host) was monitored among female *S. schevyrewi* and *S. multistriatus*. There was no substantial difference in host acceptance behavior when females were offered small cut logs (bolts) of *U. pumila* infested with con- or heterospecific females. At the second step, mating and oviposition usually follow after a female has excavated a gallery. Mean oviposition per parental female in 1 week was not significantly different among treatments: *S. schevyrewi* at medium density of 2.86 parental females per dm^2, at high density of 5.71 per dm^2; *S. multistriatus* at medium density, at high density; and mixed species (i.e., *S. schevyrewi* and *S. multistriatus* combined, with each at medium density). At the third step, progeny production and progeny size were monitored among the same density treatments, but the number of parental beetles and size of bolts were doubled. Differences in progeny production would reflect larval competition, since the number of eggs initially laid was not different. Both *S. schevyrewi* and *S. multistriatus* were sensitive to intraspecific competition because size of progeny was smaller in high than medium density treatments, but total progeny production was similar at both densities. *Scolytus schevyrewi* was a stronger interspecific competitor than *S. multistriatus*. Smaller *S. multistriatus* progeny, and fourfold more *S. schevyrewi* progeny were produced when both species developed on the same host. Thus, these proximal behavioral events contribute toward the mechanism for competitive displacement in the context of the host colonization behavior of these two elm *Scolytus*.

21.4.2 Walnut Twig Beetle, Pityophthorus juglandis *Blackman*

The walnut twig beetle is a very small (1.5–2.0 mm or about 1/16 in long), reddish brown bark beetle that bores through the outer bark and into the phloem of the branches and main stem of walnut, butternut, or wingnut trees (Seybold et al. 2013a, b; Hishinuma et al. 2015). This species is characterized by its relatively small size and four to six concentric ridges (asperities) on the upper surface of the pronotum (the shield-like cover behind and over the head) (Fig. 21.11). Like most bark beetles, the larvae are white, C-shaped, and found in the phloem. For this species, the egg galleries created by the adults are generally horizontal (across the grain) and the larval galleries tend to be vertical (along the grain). The male beetle bores into the bark first, creating a push-pin-sized hole in the cracks and furrows or lenticels and leaf scars on the bark surface. Several females then join the male and create the gallery system. The males produce an aggregation pheromone (Seybold et al. 2015), which attracts more males and females to the colonization site and results in a mass attack. The insect appears to be ubiquitous in California, occurring in both walnut orchards and in native black walnut trees growing in windbreaks and surrounding riparian areas. Its distribution reaches from San Diego County in the south to Humboldt and Siskiyou Counties in the north (Fig. 21.12b). It will colonize not only standing live trees, but also recently fallen dead tree stems or branches with fresh phloem.

The discovery of the devastating thousand cankers disease of walnut trees in the western USA (Tisserat et al. 2009, 2011; Utley et al. 2009, 2013; Seybold et al. 2013b) focused attention on the biology and distribution of *P. juglandis* as the disease pathogen's vector. The pathogen, *Geosmithia morbida* Kolařík. Freeland, Utley, & Tisserat, is a mitosporic filamentous fungus that causes restricted necrotic lesions in the phloem of most species of walnut, *Juglans* spp. L. (Tisserat et al. 2009; Utley et al. 2009; Kolařík et al. 2011); butternut, *Juglans cinerea* L. (Serdani et al. 2013); and wingnut, *Pterocarya* spp. Kunth (Hishinuma et al. 2015). Numerous spores (conidia) have been observed on the surface of the wing covers of *P. juglandis* (Fig. 21.13). A group of phoretic mite species (Fig. 21.14) may also be involved in the transfer of the pathogen beneath the bark, as they are with *S. multistriatus* and the Dutch elm disease pathogen, *Ophiostoma novo-ulmi* (Moser et al. 2010). Thus, a plethora of entrance holes created through the outer bark by *P. juglandis* for feeding and/or reproduction result in the transfer of *G. morbida* conidia or yeast propagules to the phloem. The myriad small necrotic areas in the phloem coalesce on the branches and main stem of *Juglans* or *Pterocarya*, likely restricting the flux of carbohydrate within the tree and causing branch dieback and, depending on species, even tree mortality. The time from initial colonization of *Juglans* or *Pterocarya* spp. by *P. juglandis* or initial observations of leaf discoloration in the crown until eventual death of the diseased tree varies with host species, size of the tree, locality, and population density of the vector and pathogen, but crown dieback and sometimes even mortality may occur in a matter of several years (Anonymous 2015b). When the disease has run its course in trees, the xylem surfaces of the branches and even

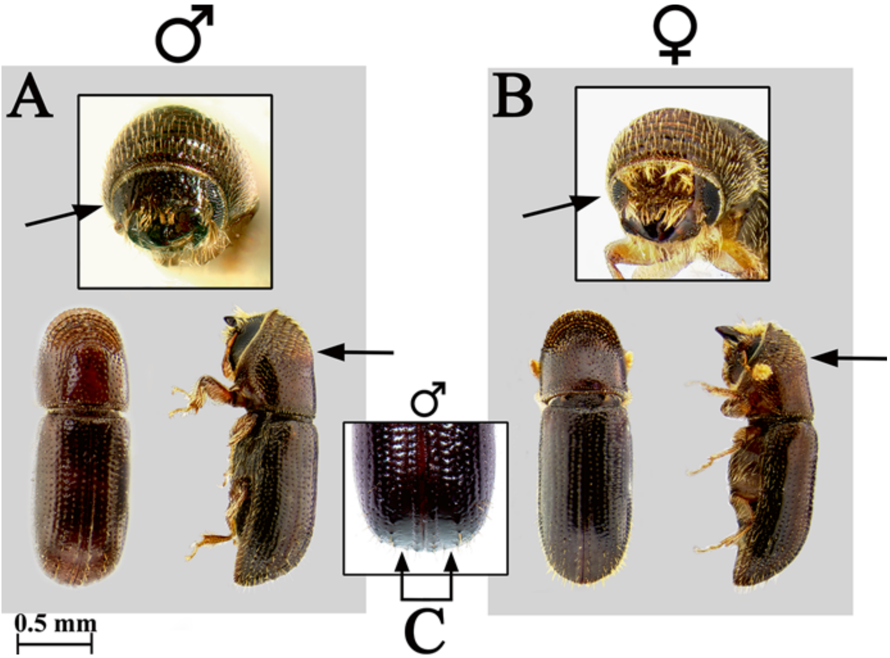


Fig. 21.11 Comparison of morphological characters of male (**a**) and female (**b**) walnut twig beetle, *Pityophthorus juglandis* Blackman. *Arrows* indicate the degree of pubescence on the male and female frons; the apex, which occurs before the midpoint on the anterior half of the pronotum of males and females; and granules on the male elytral declivity (**c**) (Figure by S.M. Hishinuma, UC Davis and ADG, from Seybold et al. 2013a)

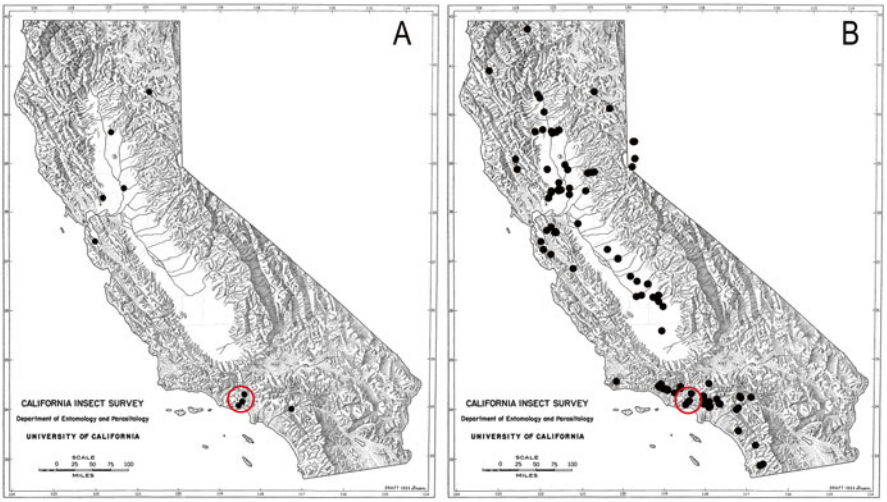


Fig. 21.12 Distribution of the walnut twig beetle, *Pityophthorus juglandis* Blackman in California from the literature and from field survey data and museum records. (**a**) Map from collection records from 1959–1990, with initial collection locations in San Fernando and Tarzana, Los Angeles County (1959 and 1960) *circled* in *red* and (**b**) cumulative collection records from 1959–2015 from field and museum survey by the authors (Note Nevada collection records from Carson City, Genoa, and Reno)

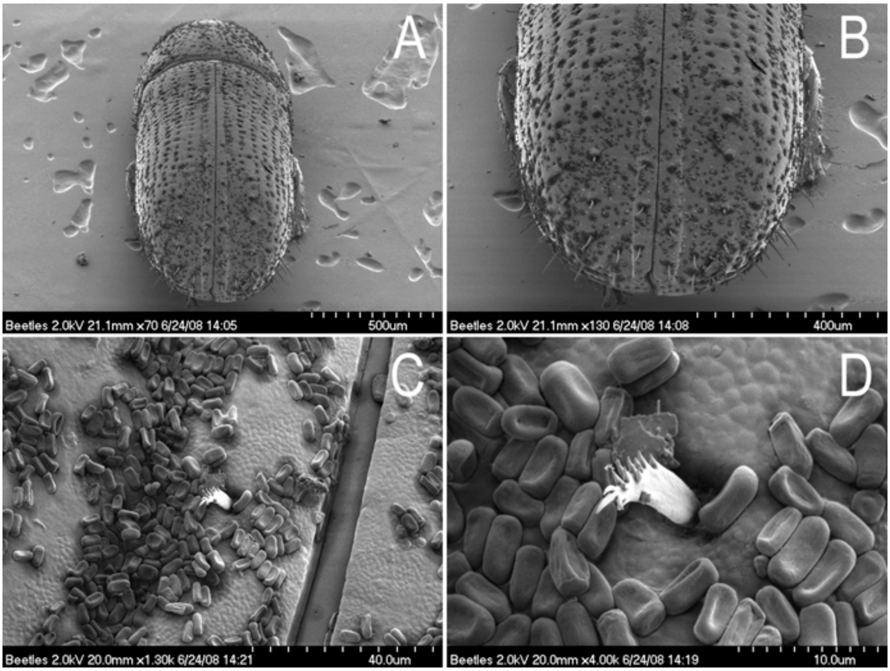


Fig. 21.13 Scanning electron micrographs of the cuticular surface of male walnut twig beetle, *Pityophthorus juglanidis* Blackman, illustrating the presence of conidia likely from *Geosmithia morbida*: (**a**) Posterior perspective of male showing coating of dry spores on surface (scale bar at lower right = 500 μm); (**b**) Posterior perspective of male with the focus on the elytral declivity (scale bar at lower right = 400 μm); (**c**) Enlargement of area around a seta on the elytral suture showing large number of conidia (scale bar at lower right = 40 μm); and (**d**) Enlargement of area around the same seta showing morphology of conidia in and around the setal pit (scale bar at lower right = 10 μm) (Beetles collected in Davis, Yolo County, California, June 13, 2008; photographed June 24, 2008, by ADG and by Delilah F. Wood, USDA Agricultural Research Service Western Regional Research Center, Albany, California)

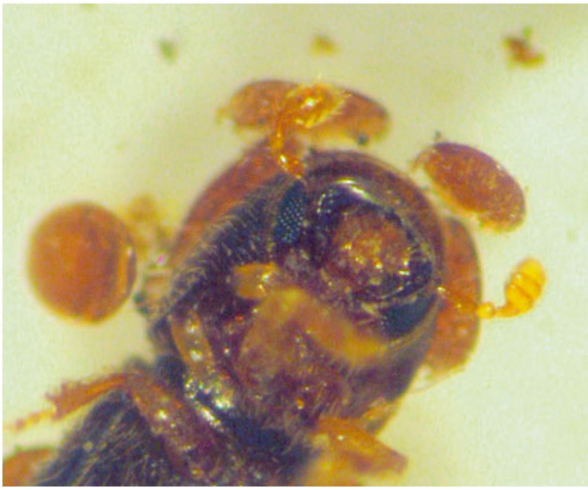


Fig. 21.14 Male walnut twig beetle, *Pityophthorus juglandis* Blackman, with phoretic mites *Saproglyphus* 51939 n. sp. dn, *Tarsonemus minimax* F., and *Trichouropoda* 51943 n. sp. dn that might be involved in the transfer of *Geosmithia morbida* beneath the bark of *Juglans* spp. (Mite identification, John C. Moser, USDA Forest Service, Southern Research Station, Pineville, Louisiana and ADG photo)

the main stem are often marked by the numerous transverse egg galleries created by female *P. juglandis*.

In California, the insect-fungal complex is widespread in endemic native riparian stands of *Juglans hindsii* (in northern California) and *J. californica* (in southern California) (Griffin and Critchfield 1972; Flint et al. 2010), and cases of the disease on various horticultural varieties of *J. regia* in commercial orchards have been numerous (Geiger and Wood s2009; Graves et al. 2009, 2010; Flint et al. 2010; Yaghmour et al. 2014). Urban plantings, trees along rural highways and agricultural lands, and collections of trees in parks and germplasm reserves have all shown disease symptoms. The insect-fungal complex has also been recorded in California from "Royal" hybrid trees, *J. hindsii x nigra*, and from "Paradox," the horticulturally important *J. hindsii x regia* hybrid used widely in the nut industry as a commercial rootstock for *J. regia*.

21.4.2.1 Distribution and Taxonomy

Walnut twig beetle is thought to be native to Arizona, southern California, and New Mexico, USA and Chihuahua, Mexico (Bright 1981; Wood and Bright 1992; Seybold et al. 2013b), however, its status as an invasive or native species in California is confusing. From the first collection in California (Fig. 21.12a), it has expanded its range to cover much of the state (Fig. 21.12b) and to include nine western (Arizona, California, Colorado, Idaho, New Mexico, Nevada, Oregon, Utah, and Washington) and seven eastern (Indiana, Maryland, North Carolina, Ohio, Pennsylvania, Tennessee, and Virginia) U.S. states (Cranshaw 2011; Seybold et al. 2012a, 2013b; University of Maryland Extension 2014; Wiggins et al. 2014; Indiana Department of Natural Resources 2015). This range has expanded nationally from four U.S. counties in 1960 (Fig. 21.15a) to 127 counties in September 2015 (Fig. 21.15b), with the majority of the *P. juglandis* genetic diversity present among purportedly ancestral populations in Arizona and New Mexico (Rugman-Jones et al. 2015). The current U.S. distribution ranges south to north from Cochise and Hildago Counties (southern Arizona and New Mexico, respectively, 31°24′N) to Spokane and Kootenai Counties (northeastern Washington and northern Idaho, respectively, 47°43′N), and west to east from Humboldt and Benton Counties (California, 123°38′W and Oregon, 123°13′W, respectively) to Bucks County (Pennsylvania, 75°89′W) (Seybold et al. 2012a) (Fig. 21.15b). There is only one collection record from northern Mexico in U.S. collections (*CAS*, *USNM*), and neither *P. juglandis* nor *G. morbida* have been detected in Canada as of December 2015 (Troy Kimoto, Canadian Food Inspection Agency, personal communication). The distribution of *P. juglandis* in North America is not continuous within the geographic limits described here. It has likely been governed by the presence of *Juglans* or *Pterocarya* spp. trees in the landscape and by the degree of human-mediated movement of *Juglans* spp. raw logs or barked wood products (Seybold et al. 2012a). Offsite plantings of

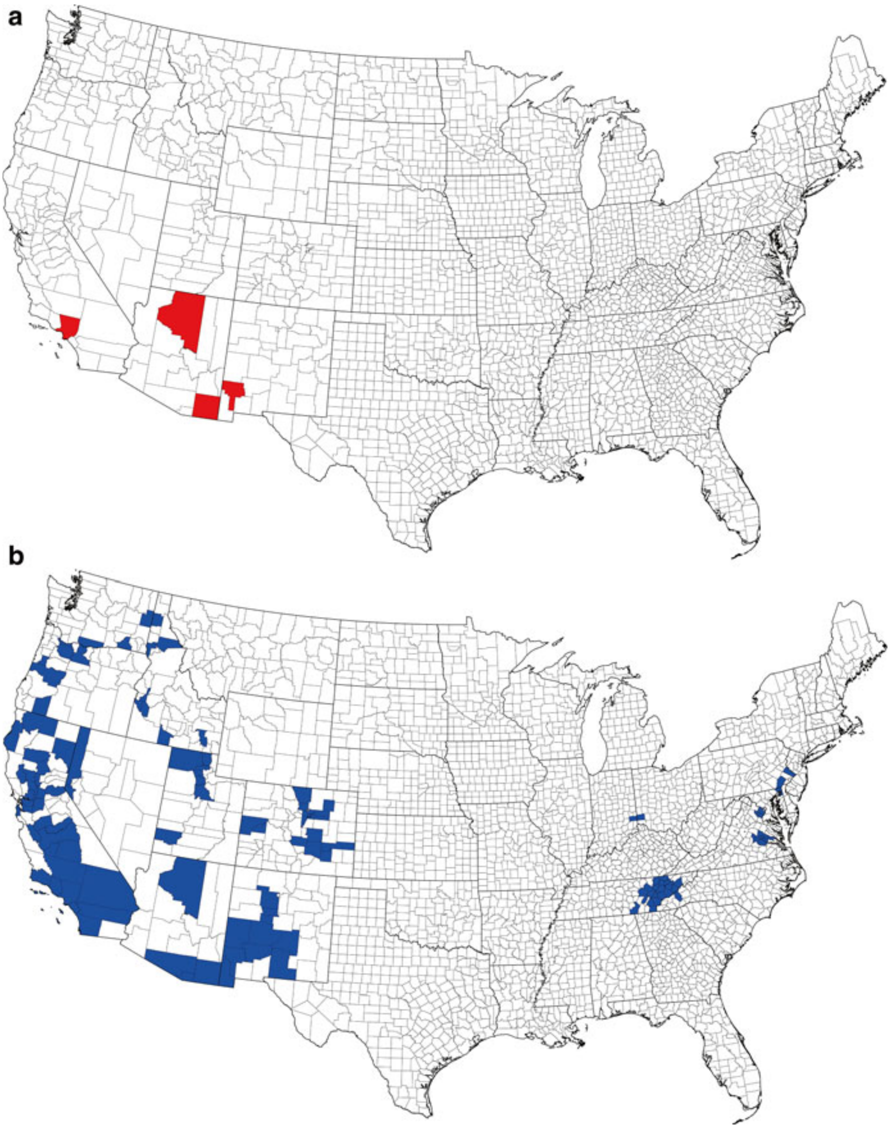


Fig. 21.15 United States of America county distribution records of the walnut twig beetle, *Pityophthorus juglandis* Blackman: (**a**) historic distribution as of 1960 (Bright 1981; Wood and Bright 1992); and (**b**) current distribution (September 2015) based primarily on recent collections by the authors and various cooperators (Figure modified from Rugman-Jones et al. 2015)

eastern black walnut, *J. nigra* L., in the western USA likely facilitated the expansion of the distribution of *P. juglandis* and thousand cankers disease (Tisserat et al. 2011).

Prior to the discovery of thousand cankers disease in the western USA, the North American collection record of *P. juglandis* was sparse. *Pityophthorus juglandis* was initially collected on 15 July 1896 from "black" walnut in Lone Mountain, New Mexico (near Silver City in Grant Co.); this female holotype (*USNM* type No. 41271) was the basis of the species description by Blackman (1928). Blackman (1928) listed little walnut, *Juglans rupestris* Englm. ex Torr., as the host; *J. rupestris* has been synonymized with *Juglans microcarpa* Berland. However, given the locality and our current understanding of native walnut distributions, Arizona walnut, *Juglans major* (Torr. ex Sitsgr.) Heller, was the likely original host for this collection (USGS 2014). Subsequent collections by J.L. Webb (1907), D.J. and J.N. Knull (1947), S.L. Wood (1958–1960) and W.F. Barr (1958) widened the distribution to include Arizona (Cochise and Coconino Cos.) and Chihuahua in Mexico (summarized in Bright 1981). Bright and Stark (1973) reported two records in California: (1) San Fernando, Los Angeles Co. by an unnamed collector on *J. nigra* (specimen reported by Bright and Stark (1973) to be in the California State Collection of Arthropods, Sacramento, CA, *CSCA*) and (2) Tarzana, Los Angeles Co. by an unnamed collector on *J. californica* (specimen reported by Bright and Stark (1973) to be in the *USNM*) (Fig. 21.12a, circled in red). No specific collection dates were reported for these California specimens, but later in their text Bright and Stark (1973) wrote that "It is a recent introduction to the state; the first record is 1959." Bright and Stark (1973) also wrote, "*Geographic distribution and host range*. – *P. juglandis* is distributed in the southwestern states, Arizona, California, and New Mexico where its hosts, walnut trees, are grown," which might suggest that *P. juglandis* was originally native to California. Wood (1977) underscored this uncertainty when he wrote, "Since native potential hosts occur in the area (California), there is a question as to whether an oversight in collecting prior to 1959 occurred or an introduction actually did occur." Indeed, in the Pacific Coast states, the native distributions of *J. californica* and *J. hindsii* extend from southern California (*californica*, Griffin and Critchfield 1972) to southern Oregon (*hindsii*, Griffin and Critchfield 1972; Callahan 2008), and perhaps even into southern Washington for the latter (SJS, pers. observation), suggesting that the ancestoral distribution of *P. juglandis* could have included these states. Nonetheless, population genetics analyses from many collection sites in California, Oregon, and Washington hint at a relatively recent invasion of the Pacific Coast states by *P. juglandis* (Rugman-Jones et al. 2015). Bright (1981) did not report any additions to the California distribution, but listed the specimen documenting the Tarzana locality to be in the *CSCA*, rather than the *USNM*. Wood and Bright (1992) and Bright and Skidmore (1997, 2002) did not report any additions to the western North American distribution of *P. juglandis*; Wood and Bright (1992) listed the host range as *J. californica*, *J. major*, and *J. nigra*. Furniss and Carolin (1977) noted that *P. juglandis* in California and Arizona was one of the few western species in the genus that colonized a hardwood. Cranshaw (2011) and Seybold et al. (2012a) provided updates to the national distribution (Fig. 21.15b).

Pityophthorus juglandis is one of two U.S. representatives of a 19 species subgeneric group of *Pityophthorus* (*Juglandis* group) that is characterized by adults with concentric rows of pronotal asperities; by a generally convex and slightly impressed elytral declivity; by declivital interstriae 1 and 3 that are nearly equal in height; and by glabrous discal elytral interstriae (Bright 1981, 1985; Atkinson 1993). Only *P. juglandis* and *P. pecki* Atkinson (southern Florida, Atkinson and Peck 1994) amongst *Juglandis* group species are known from the USA and only *P. juglandis* is known to colonize walnut. The remaining species in the group have only been collected in Central America or Mexico. Eleven of the nineteen species were described by Wood (1964, 1971, 1976); five by Bright (1985); two by Blackman (1928, 1942); and one by Atkinson (1993). In addition to *P. juglandis*, Blackman (1942) described *P. pudicus* from a specimen collected in the Port of New York from *Sambucus* sp. wood associated with a packing crate originating from Guadalajara, Jalisco, Mexico (Blackman 1942; Bright 1981). Bright (1985) broadened his concept of the *Juglandis* group when he included *P. cracentis*, which has a "distinctly, but slightly impressed" elytral declivity.

Adult *P. juglandis* can be distinguished from most of the other members in the group by the "evenly convex elytral declivity on which interstriae 1 and 3 of the male bear distinct granules, by the broadly flattened, densely pubescent female frons, by the irregular rows of asperities on the anterior surface of the pronotum, by the close, deep punctures on the posterior portion of the pronotum, by the generally distinct rows of punctures in declivital striae 1 and 2, and by the host" (Bright 1981). Bright (1985) modified his key such that *P. juglandis* is now considered to have "punctures in striae 1 and 2 that are indistinct to obsolete," and "declivital interstriae 1 and 3 each with a row of small granules in the male." Bright (1981) considered *P. detentus* Wood to have the most morphological similarity to *P. juglandis*, but the former has a generally shorter body length, declivital interstriae 1 and 3 devoid of granules in both sexes, and pronotal asperities arranged in fairly regular concentric rows. This congener has only been collected in Central America from various shrubs and vines. A Mexican species, *P. insuetus* Bright, collected on the Compositae, also keys out near *P. detentus* (and *P. juglandis*) (Bright 1985), but is smaller with a "more deeply impressed elytral declivity and more distinct strial punctures in striae 1 and 2 on the declivity" (Bright 1985). In the national detection survey, *P. juglandis* has been most frequently confused with *P. crinalis* Blackman and *P. lautus* Eichhoff, two species that can colonize eastern North American hardwoods and *Rhus* spp. (Bright 1981; Atkinson and Peck 1994; Seybold et al. 2013a). These two species are in the *Lautus* subgeneric group; *P. lautus* has been collected on rare occasions from *Juglans*, but *P. crinalis* has not (Bright 1981; Katovich and Ostry 1998).

21.4.2.2 Biology and Community Ecology

Walnut twig beetles overwinter primarily in the larval and adult stages beneath the bark. The beetle is completely dependent on walnut, butternut, or wingnut trees as hosts, and the emerging adult males (and soon thereafter the females) colonize branches of all sizes, but generally not those smaller than 1.5–2 cm (0.5–0.75 in.) in diameter. Unlike many other species of twig beetles (*Pityophthorus*), *P. juglandis* will even attempt to colonize the main stem of trees. These attempts are often successful when the trees are in advanced stages of decline. Entrance holes are not initiated below the soil line. It is never solely a twig-infesting beetle, even in its putative native host (*J. major*) and range (Arizona and New Mexico), where it also colonizes the larger branches and main stem of trees. Dead *J. major* trees with *P. juglandis* galleries on the main stem were observed in this region (Graves et al. 2011, ADG, unpublished data).

In California, adult *P. juglandis* is active in flight nearly year round (Chen and Seybold 2014). It has been caught in pheromone-baited flight traps during every month, although at extremely low levels in December and January. Flight appears to be triggered when ambient air temperatures exceed 65 °F (18–19 °C). Other physical factors such as wind speed, light intensity, and relative humidity also appear to play a role in mediating flight. The beetle prefers to fly when temperature is moderate and wind speed, light intensity, and relative humidity are low; it can be particularly active at dusk (Seybold et al. 2012b; Chen and Seybold 2014). Maximum flight occurs in May and June and then again in September and October. Adult flight activity declines drastically in November (Chen and Seybold 2014). There are three larval instars and likely 2–3 generations per year in California (Dallara et al. 2012, P.L. Dallara, personal correspondence).

In California walnut trees, the only other related insect that might be confused with *P. juglandis* is *X. saxeseni*. Although *X. saxeseni* resembles *P. juglandis* in size and shape, there are clear morphological differences visible under a dissecting microscope or hand lens (Fig. 21.3). Also, as an ambrosia beetle *X. saxeseni* bores into the xylem of walnut trees and feeds on fungi that grow in its galleries. Thus, it colonizes trees that are typically in a later stage of decline than those favored by *P. juglandis*.

Colonization of walnut in California by *P. juglandis* is accompanied by the entry of a series of other subcortical insects that exploit the "carcass" of the declining tree or its insect denizens. The herbivores include the aforementioned *X. saxeseni*, *Cyclorhipidion bodoanum*, and *Hypothenemus eruditus* (Scolytidae); *Rhyncolus cercocarpus* (Thatcher) and *Stenomimus* nr. *pallidus* (Boheman) (both Curculionidae); *Xylotrechus nauticus* (Mannerheim), *Nathrius brevipennis* (Mulsant), and *Phymatodes juglandis* Leng (all Cerambycidae); *Dicerca hornii* Crotch, *Chrysobothris analis* LeConte, *Chrysobothris wintu* Wellso & Manley, and *Anthaxia* sp. (all Buprestidae); *Amphicerus cornutus* (Pallas) and *Scobicia declivis* LeConte (both Bostrichidae); and *Petalium californicum* Fall and *Priobium punctatum* (LeConte) (both Anobiidae). Predaceous insects include *Narthecius simulator* Casey and *Parandrita cephalotes* (LeConte) (both Laemophloeidae), *Temnochila chlorodia* (Mannerheim) (Trogositidae) (rare), and *Agulla* (=*Raphidia*) sp. (Raphidioptera: Raphidiidae), whereas probable parasitoids include *Neocalosoter pityophthori* (Ashmead) (Hymenoptera: Pteromalidae) and *Plastonoxus westwoodi* Kieffer (Hymenoptera: Bethylidae). The pteromalid can be quite abundant when *P. juglandis* are reared from infested branches. Also, the cerambycid *N. brevipennis* has been trapped landing in large numbers (>150) over a 1-week period on live branches or cut branches of *Juglans* in various behavioral assays. *Temnochila chlorodia* has been reared from *Juglans* cut logs under circumstances when both *P. juglandis* and *X. nauticus* have been present. It is likely that *T. chlorodia* had fed on

X. nauticus larvae beneath the bark (Linsley and MacLeod 1942), but in one collection jar in our emergence study, over 20 *P. juglandis* adults were consumed by adult *T. chlorodia*, indicating that this predatory interaction may also occur. It would not be unusual for *T. chlorodia* to be associated with a hardwood bark beetle as Hajek and Dahlsten (1985b) reported that this predator was relatively common in collections of English elm, *Ulmus procera* Salisb. (=*U. minor* cultivar Atinia), that harbored *S. multistriatus* at two sites in northern California. In that survey, however, larval *T. chlorodia* consumed larval *S. multistriatus*.

21.4.2.3 Damage

In addition to the physical damage created by the feeding of the adults and larvae in the phloem, penetration of the bark and transfer of *G. morbida* spores to the phloem by the adults result in an infection of the phloem and necrotic lesions (cankers) that encircle the gallery system. The numerous regions of necrotic tissue from gallery construction and fungal infection may coalesce over time and girdle individual branches and main scaffolds, leading to branch flagging and crown decline (Graves et al. 2009). Presumably the flow of carbohydrates is disrupted as a consequence of the phloem necrosis. In both orchard-grown English walnut trees and landscape black walnut trees, the pattern of decline generally begins in the crown and moves downward as beetles colonize larger and larger diameter portions of the trees. However, in some instances (e.g., in trees previously impacted by crown gall, *Agrobacterium tumefaciens*, shallow bark canker, *Brennaria (=Erwinia) nigrifluens*, or other diseases), *P. juglandis* first colonizes the Paradox or black walnut rootstock or the lower portion of the main trunk of the scion. Although *P. juglandis* appears to have preferences in host selection behavior among species of *Juglans* (S.M. Hishinuma, personal correspondence), all cultivars of English walnut seem to be susceptible to colonization by the beetle. Exhaustive and specific host suitability tests of these cultivars have not been carried out. As the crown is gradually killed in black walnut trees, epicormic branches may sprout from the trunk. This has rarely been observed with *J. regia* trees.

Colonization of walnut trees by *P. juglandis* appears to be a progressive process that can take many years. Trees that are over- or under-watered or that have various root diseases or mistletoe infections may be more susceptible to colonization and may experience an accelerated decline. Ultimately, it appears that colonization by *P. juglandis* and infection by *G. morbida* initiates a decline that is fatal for the tree. The mortality caused by the disease has been largely unquantified in California *J. regia* orchards because in most instances, growers remove the infested walnut trees from orchards before the trees succumb. The decline and mortality have been more obvious in landscape black walnut trees, which are often ignored for many years as their health has waned along California's rural roads and highways. Very little is known of the distribution and impact of *P. juglandis* in wildland forests of the eastern or western USA (Graves et al. 2011; Wiggins et al. 2014). A funnel trapping survey of four national forests of southern California (Angeles, Cleveland, Los Padres, and San Bernardino) revealed limited encroachment of *P. juglandis* on three of the forests (Seybold and Munson 2010), but an extensive distribution and high flight activity in the Los Padres National Forest (Ventura County), which contains the bulk of the native distribution of *J. californica* (Griffin and Critchfield 1972). In an impact survey on national forest lands in Arizona, southern California, and New Mexico, Graves et al. (2011) found cases of dead walnut trees with evidence of *P. juglandis* galleries on six national forests. Of 139 *J. californica* in the southern California survey plots, approximately 5 % were dead and showed evidence of *P. juglandis*; of 194 *J. major* in Arizona and New Mexico, 6.7 % were dead and showed evidence of *P. juglandis*. Crown condition in both regions was worse when *P. juglandis* had been present feeding and reproducing on the trees, which could be interpreted as symptoms of die back occurring in association with the beetle. In the California survey plots, approximately 30 % of the trees had evidence of *P. juglandis*, whereas in the Arizona/New Mexico plots, approximately 50 % of the trees had this evidence (Graves et al. 2011, ADG, unpublished data).

21.4.2.4 Management

Monitoring and Detection

Capturing and identifying the tiny beetle is the key to early detection of the disease in new areas. Detailed guidelines are available for using pheromone-baited traps to detect and monitor *P. juglandis* (Seybold et al. 2013a). A two-page guide for field use and instructional videos are also available at http://www.ipm.ucdavis.edu/thousandcankers. The purpose of this trapping is to detect an incipient population of *P. juglandis* or delimit a known population of *P. juglandis* where it has been recently discovered. The trap and guidelines were developed in northern California native black walnut and English walnut orchard ecosystems with relatively high population densities of *P. juglandis*. The system uses a small multiple-funnel trap baited with the male-produced aggregation pheromone. The trap captures both sexes of the *P. juglandis* while attracting few other insect species, including only low numbers of most other bark or ambrosia beetles (Coleoptera: Scolytidae), making detection of *P. juglandis* easier. The baited traps have been used primarily to detect *P. juglandis* populations. Little information is available on how the traps could be used to assess population levels. If *P. juglandis* is detected in traps, a survey of nearby walnut trees is warranted to assess the extent of beetle infestation and other TCD symptoms. The outer bark can be peeled away to reveal *P. juglandis* galleries in the phloem, a key diagnostic feature for diagnosing the thousand cankers disease complex.

Ideally, pheromone-baited *P. juglandis* traps should be deployed from March through November when ambient air temperatures exceed 65 °F (18–19 °C) (Seybold et al. 2012b; Chen and Seybold 2014). Depending on available resources, more targeted detection protocols may include: (1) Trapping for about 6 weeks from late August through mid-October or late April through mid-June; or (2) Trapping for 3 weeks during May and June and 3 weeks during September and October. A primary consideration when selecting locations for traps and choosing a density of traps in the landscape is whether the objective is to detect an incipient population or delimit a known population. A higher density of traps might be used if the extent of an introduced population is to be assessed. If the goal is to detect a new population of *P. juglandis* over a large land area (e.g., an entire state), only a much lower density of traps would be economically feasible. Whatever the overall goal, traps must be placed near walnut trees.

Control

Currently, sanitation of woody debris is the primary strategy for *P. juglandis* management within orchards. Removal of infested wood piles and prunings should be conducted during the winter months in advance of the primary period of *P. juglandis* emergence and flight activity in the spring (April–June). When possible, infested material should be burned to reduce the build-up of beetle populations. Once a tree becomes infested, no control is available, so it is critically important that growers, practicing arborists, and landscapers be aware of this beetle and the accompanying disease and not move any infested wood. The minute beetles can survive undetected beneath the bark in dry walnut wood; they may emerge later and transmit the disease to other walnut trees. It can take up to 7 months to “clear” infested, firewood-sized pieces of English walnut wood of the *P. juglandis*. It may take longer to disinfest larger pieces of wood with thicker phloem and greater surface area of invaginated bark.

Currently, no insecticides have been shown to reduce mortality rates of trees infested with *P. juglandis*, and chemical control is not recommended at this time. Research is proceeding with systemic insecticides injected into the base of trees, but this will be practical only for valuable shade trees in residential or arboretum settings, but not for forest or orchard applications that involve many trees. Thus, it is important that infested wood is not moved off-site. Infested trees should be taken down, and ground or burned (where allowed) on-site. Because the beetles are very small and difficult to detect, it is important that freshly-cut walnut branches, logs, or burls not be moved or shipped from infested areas, not even for woodworking purposes. Seasoning wood on-site for 2–3 years should allow *P. juglandis* and other woodborers time to emerge at the site of infestation, but it is prudent to have all wood inspected by a knowledgeable entomologist or cooperative extension specialist prior to movement of the material from the site, even when properly seasoned and debarked. The disinfestation of the wood can be accelerated by steam heating the wood to a minimum outer sapwood temperature of 56 °C maintained for 40 min, which is effective for eliminating *P. juglandis* and *G. morbida* from logs of *J. nigra* (Mayfield et al. 2014). However, previously treating barked wood (steam heat or fumigation) does not preclude future attacks by *P. juglandis* if the phloem is still fresh for colonization (Audley 2015; Audley et al. 2016).

21.4.3 *Mediterranean Pine Engraver,* Orthotomicus erosus *(Wollaston)*

The Mediterranean pine engraver, *O. erosus*, is approx. 2.7–3.5 mm long, reddish- to dark brown, and has a moderately concave elytral declivity with four spines on each margin (Fig. 21.16a, b). The second spine is the largest or broadest of the four and is very pronounced in males (Fig. 21.16c, d). Other related species in California that might be confused with *O. erosus* include the pine engraver, *Ips pini* (Say); *Orthotomicus caelatus* (Eichhoff), *Ips latidens* LeConte, and *Ips spinifer* (Eichhoff) (Wood 1982). *Ips pini* also has four declivital spines, but in males the third spine is largest, whereas in females all four spines are similar in size and shape. The other three species only have three declivital spines. Further details on identification of *O. erosus* are available in Cavey et al. (1994) and Lee et al. (2005, 2007).

Aukema et al. (2010) rated *O. erosus* as one of 62 "high impact" nonindigenous, invasive forest insects in the continental USA. These were species of regulatory

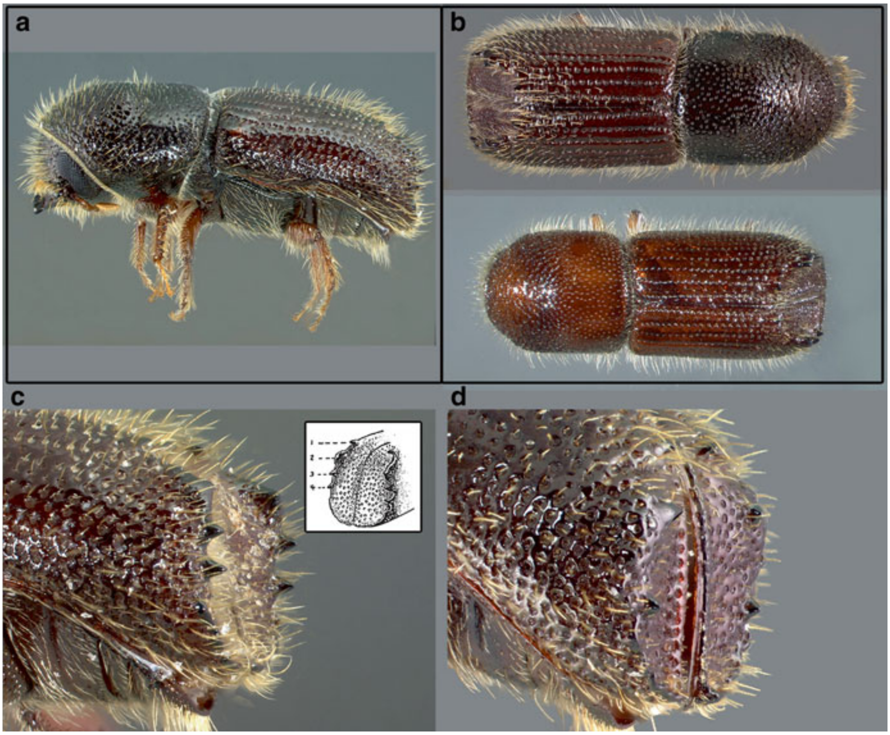


Fig. 21.16 Lateral view of female (**a**) and dorsal views of male (**b**) Mediterranean pine engraver, *Orthotomicus* (*Ips*) *erosus* (Wollaston). The margin of the elytral declivity of males (**c**) is armed with four pronounced spines (inset); the spines are reduced in size on the margin of the elytral declivity of females (**d**) (Photo credits, Dr. Anthony G. Gutierrez (Chief) and Danielle N. Thomas, Molecular Biology Lab, Entomological Sciences Program, U.S. Army CHPPM, Aberdeen Proving Ground, Maryland). Drawing of male elytral declivity (21.16c, *inset*) showing morphology of spines (Cavey et al. 1994)

significance or that had caused notable damage to U.S. forest or urban forest trees. Three hundred and ninety three other invasive forest insects were not considered to be of high impact. *Orthotomicus erosus* was first trapped in California on 25 May 2004 at Chaffee Zoo in the city of Fresno (Fresno Co.) (Fig. 21.17, see red circled collection point), and soon thereafter in five other California counties (Kern, Los Angeles, Madera, Merced, and Tulare), suggesting an established population in the southern Central Valley. At the site of initial detection, 90 % of the 471 specimens were captured in the funnel trap baited with ethanol + α-pinene. In 2005 and 2006, additional survey trapping detected *O. erosus* in Kings, Monterey, San Luis Obispo, and Yolo Cos. Ground checking by the authors and their colleagues at multiple locations in 2004–2007 in Fresno, Tulare, and Kern Cos. revealed large populations of *O. erosus* larvae, pupae, and adults overwintering from December to February. In these areas, *O. erosus* was collected from beneath the bark of several large standing pine stumps (up to approx. 1 m in diameter) and primarily from cut logs (approx. 20 to 50 cm diameter) of widely planted Mediterranean and other non-indigenous pines: *P. halepensis*, *P. pinea*, *P. canariensis*, Scots pine, *P. sylvestris* L., and *P. brutia* (Fig. 21.1). The ground surveys also revealed that *O. erosus* had colonized (and was reared from) cut logs of deodar cedar, *Cedrus deodora* (Roxb.) G. Don, collected in Kingsburg, Tulare Co. The bulk of its current distribution (Fig. 21.17) does not overlap with the distributions of native pines in California, but during the initial surveys vacated galleries were observed on one native species, Monterey pine, *P. radiata* D. Don, in an adventive planting of Christmas trees in Tulare Co., whereas adults were reared from a large cut branch of another native species, gray pine, *P. sabiniana* Douglas ex D. Don, from a green waste pile in Fresno Co. *Orthotomicus erosus* appears to have completely invaded the Central Valley as a specimen was recorded in 2013 from a survey trap in far northern Shasta County (Fig. 21.17).

Several observations in 2004–2007 suggested that *O. erosus* was not an immediately recent introduction, but had been in California for at least 3 years prior to its initial detection. First, the beetle was widely distributed and abundant throughout the eastern half of the southern Central Valley where ornamental pines occur as islands in the landscape. *Orthotomicus erosus* had apparently had sufficient time to locate these trees and debris piles composed of their branches and stems. Second, evidence of *O. erosus* galleries on a weathered and standing, dead tree (*P. halepensis*, approx. 50 cm diameter at breast height) near the community of Arvin in Kern Co. was linked with both a remote location and an older instance of colonization (i.e., at least 3 years prior to the observation in December 2004). Further, in 2004 and 2005, weathered and de-barked, cut pine logs with evidence of *O. erosus* galleries on the wood surface were observed at a golf course in Fresno (Fresno Co.) and at a composting facility south of Visalia (Tulare Co.), both of which indicated older instances of colonization. Thus, the distances between the observation points of some of these remnant galleries, the widespread occurrence of *O. erosus* in the state (Fig. 21.17), and its marked abundance, all suggest that 2000–2001 is a very conservative minimum estimate of the initial introduction of the species to California. The flight trap survey guided by CDFA revealed the presence of these populations; forest entomologists simply would not normally survey the urban forest resources of the southern Central Valley, which is primarily an agroecosystem.

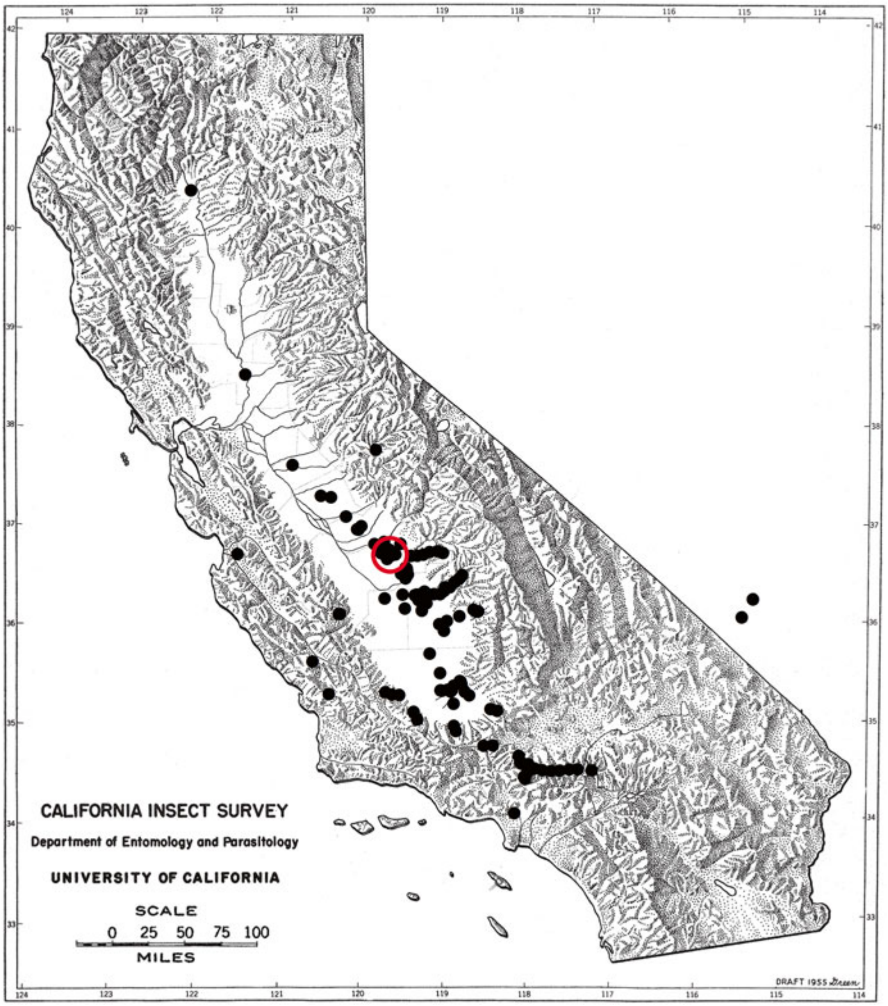


Fig. 21.17 Distribution of the Mediterranean pine engraver, *Orthotomicus* (*Ips*) *erosus* (Wollaston), in California from field survey by the authors (2004-present). Initial collection point *circled* in *red* (V-25-2004, Chaffee Zoo, Fresno, Fresno Co.). Note extreme northern collection point in Shasta Co. (Anderson) and central Sierra Nevada collection point in Tuolumne Co. (Yosemite). The latter is in a region of native coniferous forest. Also note the Clark Co. Nevada collection records from Blue Diamond and Las Vegas (December 2015)

How *O. erosus* entered California is unknown, but it may have arrived with solid wood packing material associated with imported goods. In a survey of 1985–2000 interception records from the USDA APHIS Port Information Network, Haack (2001) concluded that *O. erosus* was the second most frequently intercepted scolytid species at U.S. ports (385 interceptions). The most frequent countries of origin were Spain, Italy, China, Turkey, and Portugal (in descending order). Crating was the most frequently infested type of wooden article, and the associated products were most often tiles, marble, and granite. Ironically, in the analysis, California was not among the top five U.S. states where *O. erosus* had been intercepted. Of the 385 interceptions, only 15 were made at California ports: 14 at Long Beach and one at San Francisco. Of the 15 California interceptions, 12 were made on cargo from China, and one each from France, Korea, and Portugal (RA Haack, pers. comm.). In 2011 it was detected in a survey trap in Cumberland County, North Carolina, but apparently it was not collected again or verified as established by ground survey (NAPIS 2014). In 2015, it was detected with ethanol + α-pinene-baited funnel traps in Blue Diamond and Las Vegas, Nevada (Clark Co.) (Fig. 21.17, JB Knight, Nevada Department of Agriculture, pers. comm.).

Orthotomicus erosus is a well-documented pest of pines and perhaps other conifers throughout its native range in the Mediterranean Basin, the Middle East, Central Asia, and China (Mendel and Halperin 1982; Mendel 1983; Wood and Bright 1992; Yin and Huang 1992; Bright and Skidmore 1997, 2002; Eglitis 2000a; Bright 2014). Very little is known of its occurrence in China, but it has been reported from Anhui, Fujian, Guangdong, Guangxi, Guizhou, Henan, Hunan, Jiangsu, Jiangxi, Liaoning, Qinghai (Hengduan Mountains), Shaanxi, Shandong, Sichuan, Yunnan, and Zhejiang provinces (Yin and Huang 1992; Chen et al. 1998; Bright 2014). In July 2007, this widespread occurrence and host range of the pest in China was confirmed by one of us (SJS), through an examination of the holdings of the Chinese Academy of Sciences insect collection in Beijing. Pfeffer (1994) notes that *O. erosus* is distributed in southern Europe (north to southern Austria), the Crimea, the Caucasus, Asia Minor, the Mediterranean and nearby Atlantic islands (including Madeira Island), Palestine, and North Africa.

Whether its native distribution reaches into central Europe (northern Austria, Germany, Latvia, and Poland) is not clear from the literature (Grüne 1979; Wood and Bright 1992; Yin and Huang 1992; Eglitis 2000a). The species appears to have become otherwise cosmopolitan; it has been reported to have been introduced in Chile (1986), England (1921), Fiji (1985), Finland (1990), South Africa (1976), Swaziland (1983), and Sweden (1988) (Bevan 1984; Browne 1968; Ciesla 1988; Gillerfors 1988; Siitonen 1990; Tribe 1990, 1992; Wood and Bright 1992; Bright and Skidmore 1997, 2002; Eglitis 2000a). Kirkendall (1989) described research on within-family competition between larvae of various bark beetle species in the Ipini, including Norwegian populations of *O. erosus*.

However, the establishment of *O. erosus* in Fiji (1985) (Wood and Bright 1992; Eglitis 2000a) has since been shown to have been incorrect based on a misidentification (Brockerhoff et al. 2006). Furthermore, examination of the records from northern Europe reveals that *O. erosus* is also not likely to be present currently in the British Isles or Scandinavia. Atkinson (1921) reported "large numbers" of all life stages of *O. erosus* in felled *P. sylvestris* in Gloucestershire, England (the "Forest of Dean") and considered the species to be "firmly established." However, Duffy (1953) did not list *O. erosus* among "imported" or "doubtfully indigenous" species of British bark beetles, implying that he considered it indigenous. In contrast, Browne (1968) noted *O. erosus* as established in England, but "too rare to be of any importance," whereas Bevan (1987) ignored *O. erosus* completely in his treatment of forest insects of Britain. Recent collections have only involved interceptions at ports or from cargo without any further evidence of an established population of *O. erosus* in the country (C Tilbury, Forest Research, UK Forestry Commission, Surrey, and MVL Barclay, British Museum of Natural History, London, personal communication, Barclay 2003). In Sweden (Gillerfors 1988; Schroeder 1990) and Finland (Siitonen 1990), reports of *O. erosus* are also from interception records (in this case from imported pulpwood) without any subsequent evaluation of the biology, ecology, impact, or establishment of the species. Siitonen (1990) describes the interception of *O. erosus* in pine pulpwood imported to Finland from Siberia. Since Siberia or any eastern portion of the former Soviet Union has not been documented previously as part of the native range of *O. erosus* (Wood and Bright 1992), there is a strong likelihood that this report of *O. erosus* may also have been a misidentification. Finally, upon further examination, the Norwegian population of *Orthotomicus* used in the competition studies turned out to be *O. proximus* (Eichhoff) rather than *O. erosus* (LR Kirkendall, University of Bergen, pers. comm.), and there are no current records of indigenous or introduced populations in Norway (K Thunes, Norwegian Forest Research Institute, pers. comm.). The cold temperature tolerances of *O. erosus* from California were studied in the laboratory in the Minnesota Department of Agriculture-University of Minnesota BL2 Quarantine Facility in St. Paul, Minnesota, and the mean supercooling point for adult *O. erosus* was approximately −17 °C (1.4 °F) in October, −22 °C (−7.6 °F) in December and January, and −16 °C (3.2 °F) in March (Venette et al. 2009). When adults were cooled to different temperatures and examined for mortality, no significant mortality was observed until temperatures approached the mean supercooling point (Venette et al. 2009). These authors stated that, "From 1964–2004, winter temperatures in the north central U.S. were never warm enough to allow adult *O. erosus* to successfully overwinter." Thus, the potential for establishment, and the biology, ecology, and impact of *O. erosus* in northern climates worldwide bears further scrutiny.

In its native and introduced range, *O. erosus* is considered to be a secondary pest that infests standing pine trees under some form of stress, or recently fallen trees, broken branches, or slash (Bevan 1984; Eglitis 2000a). One report from Zhejiang province in China suggests that it can colonize living, healthy pines and it is the primary colonizer and cause of death of these trees (Jiang et al. 1992). In this instance, a 20 % loss of standing *Pinus massoniana* Lambert was reported from the Zhejiang University Forest (Jiang et al. 1992). *Orthotomicus erosus* has a strong preference for portions of pine logs that are above the soil surface (Tribe 1992). In California we observed it to attack and develop in the stems of standing, declining trees (December 2004 in Fresno, Fresno Co., and July and August 2006 in Visalia, Tulare Co.), and have found galleries on dead branches (approx. 10 cm in diameter) removed from a standing live *P. brutia* (February 2005, near Kingsburg, Tulare Co.). In Israel, where its biology has been the most studied, outbreaks of *O. erosus* have occurred after thinning events, followed by winters with low rainfall or after fires in adjoining stands (Mendel and Halperin 1982; Halperin et al. 1983; Mendel 1983; Mendel et al. 1992). Interactions with fire or hail have also been reported in South Africa (Bevan 1984; Baylis et al. 1986; Tribe 1990; Zwolinski et al. 1995).

For example, Zwolinski et al. (1995) suggested that in South Africa, *O. erosus* has a higher rate of infestation in pines that were previously wounded by hail and infected with fungi through the wounds.

21.4.3.1 Biology and Community Ecology

In most locations throughout its native and introduced range, *O. erosus* has been observed to have two to four generations per year (Grüne 1979; Mendel 1983; Bevan 1984; Tribe 1990; Jiang et al. 1992; Eglitis 2000a). Based on developmental times taken during various seasons, Mendel (1983) estimated that *O. erosus* may have up to seven generations per year in Israel's coastal plain. This prediction has not been confirmed by observation anywhere in the distribution of *O. erosus*. In California, it appeared most active in flight in June and July based on the trapping survey records in Fresno and Kern Cos. Flight at these sites continued into mid-October in 2004 and 2005. Other trapping data from 2005 to 2006 suggested that flight begins in early February and continues into December in Fresno and Tulare Cos. (Lee et al. 2016). In our initial ground surveys in California, new galleries initiated by overwintering adults were first observed in March. First generation adult beetles from spring broods began emerging in June, whereas newly initiated galleries continued to be found in summer and fall to as late as early November. From these observations, *O. erosus* likely develops from egg to adult in 3 months in spring, and likely within 2 months in summer and fall. Given that beetle flight and brood activity were observed continuously from June to October, *O. erosus* likely completes three generations per year in California's Central Valley, possibly initiating a fourth generation in November that overwinters in the immature stages. As expected, the seasonal pattern of development that we have observed in California (three to four generations per year, active from February to November) is the inverse of the pattern for introduced populations in the Southern Hemisphere (Bevan 1984).

An analysis of the host range of *O. erosus* suggests that it can colonize all pines and a few nonpines (Appendix 21.I). Males construct a nuptial chamber, and emit an aggregation pheromone, which consists primarily of 2-methyl-3-buten-2-ol (Giesen et al. 1984; Seybold et al. 2006a, b; Lee et al. 2016). Two or three females mate with him; each female excavates an egg gallery in opposite directions laying 26–75 eggs. Larvae, white to cream-colored, legless grubs and up to approx. 3 mm long, mine away from the egg galleries in the phloem and can score the outer xylem. Thus, the nuptial chamber and egg galleries comprise the central tunnel; each is approximately 1.2–12.5 cm long with numerous larval tunnels extending outwards. Adults may initiate a new gallery in another location.

Interactions of *O. erosus* with various pathogenic and sapstaining fungi have been noted in South Africa (Zhou et al. 2001, 2002a, b) and Tunisia (Ben Jamaa et al. 2007), and some of the ophiostomoid fungi isolated from *O. erosus* may contribute to its impact on trees or wood products. For example, *Ophiostoma ips* (Rumb.) Nannf. [previously *Ceratocystis ips* Rumbold] was associated with 60 % of 665 samples of adult *O. erosus* or its galleries on trap logs of Mexican weeping pine, *P. patula*, and slash pine, *P. elliottii* (Zhou et al. 2001). Of six other fungi recovered in this study, none were present in more than 1.7 % of the samples. *Ophiostoma ips* was also isolated from *O. erosus* and from cambium associated with new bark beetle galleries in cut logs and standing trees of maritime pine, *Pinus pinaster* Ait., and *P. radiata*, both of which had been previously infected with the fungus *Verticladiella alacris* Wingfield & Marasas (Wingfield and Marasas 1980). *Orthotomicus erosus* has also been associated with several other fungal species including *Graphium pseudormiticum* M. Mouton & M.J. Wingfield, and *Leptographium lundbergii* Lagerb. & Melin (Wingfield and Marasas 1980; Mouton et al. 1994; Zhou et al. 2001). *Graphium pseudormiticum* was isolated from adult *O. erosus* recovered from *Pinus* sp. bait logs (tree species not reported); *L. lundbergii* was isolated from adult *O. erosus* or its galleries in *P. patula* and *P. elliottii* trap logs (Zhou et al. 2001). In South Africa, an analysis of resin exudation, sapwood discoloration, and lesion length in 2-year old pines (*P. radiata*, *P. elliottii*, and *P. elliottii x caribaea*) caused by inoculations of *O. ips*, *L. lundbergii*, and *Leptograpium serpens* (Goid.) M.J. Wingfield suggested that *O. ips* gave rise to longer lesions than the other two fungi, but that none of these fungi should be considered as serious pathogens of aboveground portions of young pines (Zhou et al. 2002a, b). In Spain a small proportion of a sample population of *O. erosus* were reported to carry the pitch canker fungus, *Fusarium circinatum* Nirenberg and O'Donnell (Romón et al. 2007). In California, the mycoflora of *O. erosus* overwintering in *P. canariensis* and *P. halepensis* was heavily dominated by *Ophiostoma ips* (S. Kim et al. unpublished data, Iowa State University), which agrees with phytopathological studies of *O. erosus* in South Africa (see above) and North Africa (Ben Jamaa et al. 2007).

A variety of natural enemies and subcortical competitors regulate the populations of *O. erosus* in its native and introduced range (Mendel and Halperin 1981; Mendel 1985, 1986). A life table analysis in *P. massoniana* in Guangxi province in China showed that mortality is distributed as egg (23 %), larvae (19 %), pupae (14 %) and adult (8 %), and natural enemies included spiders, staphylinids, mites, parasitoids, ants, and fungi (Chen et al. 1998). Yang (1996) listed *Rhopalicus tutela* (Walker)*, Roptrocerus xylophagorum* (Ratzeburg), *Eurytoma blastophagi* Hedqvist, and *Metacolus unifasciatus* Förster as hymenopterous parasitoids of *O. erosus* in China. Kfir (1986) released Israeli populations of *Dendrosoter caenopachoides* Rusch. (Braconidae) and *Metacolus unifasciatus* Förster (Pteromalidae) in South Africa to enhance the biological control of *O. erosus*. Documented predators in the Mediterranean have included birds (Mendel 1985) and colydiid beetles (Mendel et al. 1990; Podoler et al. 1990). Several species of Histeridae and Tenebrionidae (both Coleoptera) may also feed on *O. erosus* (Mendel et al. 1990). Amezaga and Rodríguez (1998) have studied resource partitioning by *O. erosus* and three other scolytids in northern Spain. With cut stems of *P. radiata* and *P. sylvestris* (18–30 years old) they found that the pine shoot beetle, *Tomicus piniperda* L., generally flew earlier in the season than *O. erosus* and occupied a greater portion of the niche of *O. erosus* than vice versa. *Orthotomicus erosus* tended to colonize thinner barked portions of the cut stems and these authors suggested that bark thickness appeared to be a good segregation factor for the four species along the tree stems. In California, however, we have observed colonization by *O. erosus* in logs with a range of bark thicknesses, including extremely thick bark (e.g., in lower stem sections of *P. canariensis* and *P. pinea* from very large trees). In these instances the larvae and pupae may not reside immediately on the surface of the xylem, but may be found on the outer bark side of the phloem or almost in the outer bark itself.

In multiple instances in California field surveys, active and old galleries in cut logs suggested extremely large populations of the insect without much evidence of either natural enemies or interspecific competition. Hand collecting and subsequent funnel trapping experiments with more targeted lures (Lee et al. 2016) have so far revealed only 11 species of Coleoptera and two species of Hymenoptera associated with *O. erosus*. One fairly common associate that is a likely predator of immature stages is *Microprius rufulus* (Motschulsky) (Coleoptera: Colydiidae), which is also apparently an exotic species to the USA, but has been well established in the desert areas of Southern California for at least 65 years (Ivie et al. 2001). We have observed this colydiid nearly ubiquitously in the galleries of *O. erosus* and caught it in *O. erosus* pheromone-baited flight traps in the southern Central Valley, which reflects a California range-extension for *M. rufulus* (Ivie et al. 2001). In several instances we have also found larvae of *T. chlorodia* (Trogositidae) beneath the bark in *O. erosus* galleries and have trapped adults in *O. erosus* pheromone-baited traps. These adult predators consumed adult *O. erosus* in the trap cups. We have not recovered any larvae or adults of predaceous checkered beetles (Cleridae) from beneath the bark of infested logs or from survey traps or pheromone-baited traps in the currently infested area. We have observed odorous house ants, *Tapinoma sessile* (Say) and thief ants, *Solenopsis molesta* (Say) (Hymenoptera: Formicidae) feeding on larvae of *O. erosus* beneath the bark of colonized logs that had been subjected to flooding in Tulare Co. Argentine ants, *Linepithema humile* (Mayr), which occur in sympatry with *O. erosus* both in the Mediterranean Basin and in California, did not appear to negatively impact the colonization success of *O. erosus* in Portugal (Henin and Paiva 2004). We have noted only two other scolytids beneath the bark in association with *O. erosus* in California: the California fivespined ips, *Ips paraconfusus* Lanier and *X. saxeseni*. Both of these associates were found in *P. halepensis*, but they have been rare in our rearings from *O. erosus*-infested logs. Late stage coleopteran associates of *O. erosus* include *Cossonus crenatus* Horn (Curculionidae) in old galleries (*P. brutia* and *P. pinea*); a bark anobiid, likely *Ernobius mollis* (L.) (Seybold and Tupy 1993), in *P. brutia* branches that were previously colonized and vacated by *O. erosus*; and a longhorned woodborer, *Eucrossus villicornis* LeConte (Cerambycidae), reared from *O. erosus*-infested *P. halepensis* logs. Interestingly, two stored products beetles, *Cryptolestes ferrugineus* (Stephens) and *Tribolium castaneum* (Herbst) have been collected both beneath the bark with *O. erosus* and in pheromone-baited flight traps. Sokoloff (1974) notes that *Tribolium* spp. are often found beneath the bark as semi-predators and scavengers, and that this may have been the ancestral habitat.

21.4.3.2 Chemical Ecology and Future Impacts of *O. erosus* in California

The pheromone system of *O. erosus* has been studied in Europe, Israel, and South Africa (reviewed in Seybold et al. 2006a). Males produce both ipsdienol and 2-methyl-3-buten-2-ol, which are active synergistically to elicit flight from both sexes. Research questions that needed to be addressed with the invasive population in California included (1) what are the optimal release rates of the two terpene alcohols?; (2) what is the optimal enantiomeric composition of the ipsdienol?; and (3) what is the effect, if any, of release rate and enantiomeric composition of host monoterpene co-attractants (e.g., α-pinene) on the flight response? (Seybold et al. 2006a; Lee et al. 2016). The answers to these questions were a necessary first step to improving the detection lure for *O. erosus*. The question of the co-attractant effect of monoterpenes was prompted by the relatively high catches of *O. erosus* at the original detection site in Fresno Co. to traps baited with the second detection lure (i.e., ethanol + α-pinene). The other two detection traps in the survey (neither of which contained α-pinene in the lure) only accounted for 10 % of the specimens. Thus, we hypothesized that α-pinene may play a role in the flight response of *O. erosus*.

An improved lure [2-methyl-3-buten-2-ol, (−)-ipsdienol, and α-pinene] was developed (Seybold and Downing 2009; Lee et al. 2016), and the host monoterpene co-attractant was very important to the ultimate efficacy of the lure. The release rate of the monoterpene appeared to be more important than its enantiomeric composition in the flight assays (Lee et al. 2016). Note that the enantiomeric composition of the ipsdienol was reported erroneously to be (+)-ipsdienol (Seybold and Downing 2009). The improved lure was used to both estimate the innate dispersal distance of *O. erosus* at two Central Valley locations and to install and monitor extensive trapping transects that penetrated the U.S. National Forest System in the Sierra Nevada and the Transverse Mountain Range (Seybold et al. 2008a, 2010). This work indicated dispersal distances of up to 10 km by a very small percentage of the released population and considerable invasion of the wild land forested area in California (Fig. 21.18). One specimen was even trapped in 2012 responding to (α)-pinene and ethanol at one of the entrances to Yosemite National Park in Tuolumne Co. (Fig. 21.17). Lee et al. (2008) provided an analysis of which native pines might be impacted by *O. erosus* once its populations expanded from their Central Valley point of introduction. Expansion of the range to the Sierra Nevada, Coastal, and Transverse mountain ranges would likely lead first to feeding and reproduction in native *Pinus sabiniana* Douglas *ex* D. Don*,* which encircles the Central Valley at foothill elevations (500–1000 m) (Griffin and Critchfield 1972). Lee et al. (2008) further speculated that at higher elevations, *O. erosus* could potentially reproduce in native populations of *P. contorta murrayana, P. jeffreyi, P. lambertiana,* and *P. ponderosa,* although harsher high elevation climates may restrain its invasion into these ecotones (Venette et al. 2009). These authors also predicted that *O. erosus* would spread easily to the Los Angeles Basin and Inland Empire regions of California where the weather is warm and exotic *Pinus* spp. are planted widely. Urban Las Vegas, Nevada (Clark Co.) has a comparable habitat and urban host type. Catches in trapping transects in 2009 and 2010 revealed that this expansion had already occurred as had expansions into the Antelope Valley area (Lancaster, Palmdale,

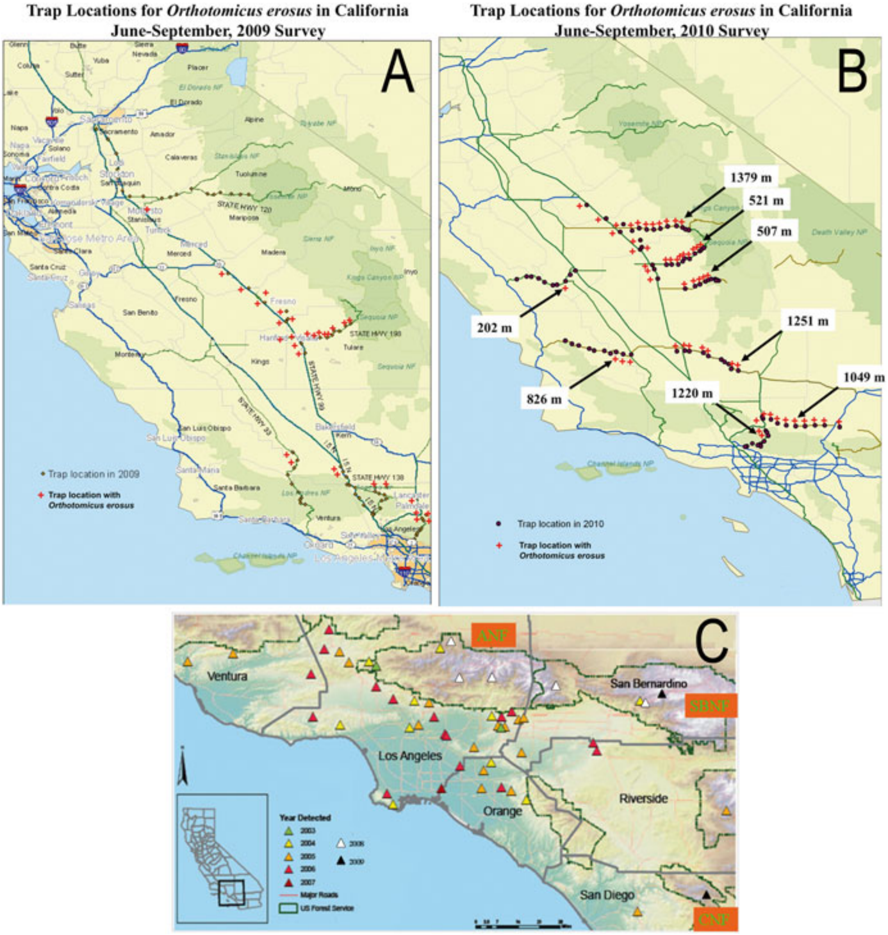


Fig. 21.18 Trap locations (*dots*) and detections (*red crosses*) of the Mediterranean pine engraver, *Orthtomicus* (*Ips*) *erosus* (Wollaston) from long transect surveys in 2009 (**a**) and 2010 (**b**) in California's Central Valley and surrounding foothill and mountane ecosystems (Seybold et al. 2008a). Elevations at the end of some transects are indicated because higher elevations are associated with California native conifers (Griffin and Critchfield 1972). (**c**) Similar survey for the red-haired pine bark beetle, *Hylurgus ligniperda* (F.) was carried out on U.S. National Forest Lands (Angeles, Cleveland, and San Bernardino) with positive detections in 2008 (*white triangles*) and 2009 (*black triangles*) (Seybold 2008)

Victorville) and into areas with native *P. monophylla* on the Tehachapi mountain range and adventive stands of *P. radiata* in the coastal locations to the west of the Central Valley (Fig. 21.18a, b). In all of these instances, collection of *O. erosus* in these California native hosts has not yet occurred and the impact of *O. erosus* on these trees in native forest areas has not been quantified.

The probability of introduction of *O. erosus* to California and Las Vegas, Nevada may have been enhanced by climate and by the ubiquitous plantings of exotic Mediterranean pines, which are familiar hosts for *O. erosus*. For example, Niemelä and Mattson (1996) noted a similar phenomenon with the successful introduction of the pine shoot beetle, *T. piniperda*, and the ornamental plantings of *P. sylvestris* and *Pinus nigra* in the lower Great Lakes region of North America. However, the ultimate success of *O. erosus* in California will depend on its capacity to co-occur with a rather dense pre-existing guild of subcortical insects in pines (Seybold et al. 2006a). In California's Central Valley, the Mediterranean pines tend not to be colonized frequently by native bark beetles (particularly obvious by its relative absence is *I. paraconfusus*), so newly introduced populations of *O. erosus* may have encountered an optimal scenario for establishment that included favorable climate, extremely suitable hosts, limited predation, and limited interspecific competition. In the various California native forest ecosystems, *O. erosus* will likely encounter anywhere from two to ten other pine-infested bark beetles or woodborers that also have a strong preference for the main stem of declining pines, and the allomonal effects of these competitors may limit the access of *O. erosus* to suitable phloem for feeding and reproduction. The redhaired pine bark beetle, *H. ligniperda* (see immediately below), will face the same crowded *niche* as it expands its invading populations into native California pines.

21.4.4 Redhaired Pine Bark Beetle, **Hylurgus ligniperda** *(Fabricius)*

The redhaired pine bark beetle, *H. ligniperda*, is a relatively long and narrow black beetle (Fig. 21.19a, b) about 6 mm long by 2 mm wide. Coarse, reddish to golden hairs are particularly noticeable on the posterior slope of the wing covers (elytra), and it lacks teeth, spines, or bumps on the posterior margins of the elytra (Fig. 21.19c) (Liu et al. 2007). It is unique morphologically among the California fauna and the only member of its genus in the State. Males and females can be differentiated by the morphology of the sixth and seventh abdominal tergites, which is likely related to the stridulation by the male (Liu et al. 2008).

The first established and overwintering population of *H. ligniperda* in North America was found in 2000 in Monroe County, New York near the city of Rochester (Petrice et al. 2004 and references therein). In 2001, the beetle was found in the two adjacent counties of Ontario and Wayne. In 2003, it was detected at two locations in Los Angeles County, California in multiple funnel traps; in 2005 and 2006 it was collected from stumps and woody debris from the frequently planted Mediterranean pines, *P. halepensis* and *P. canariensis* in the southern California urban landscape. It was especially abundant in cut logs in contact with the soil surface in and around green waste piles. When detected in survey traps, the majority of specimens responded to ethanol and (−)-α-pinene, which supports a survey of various baits conducted in New York (Petrice et al. 2004). The first detections in California occurred in 2003 at Bear Divide Guard Station, Angeles National Forest, and at the Frank G. Bonelli Regional County Park (both Los Angeles County) (Fig. 21.20, see red circles), which are both located near heavily urbanized areas. However,

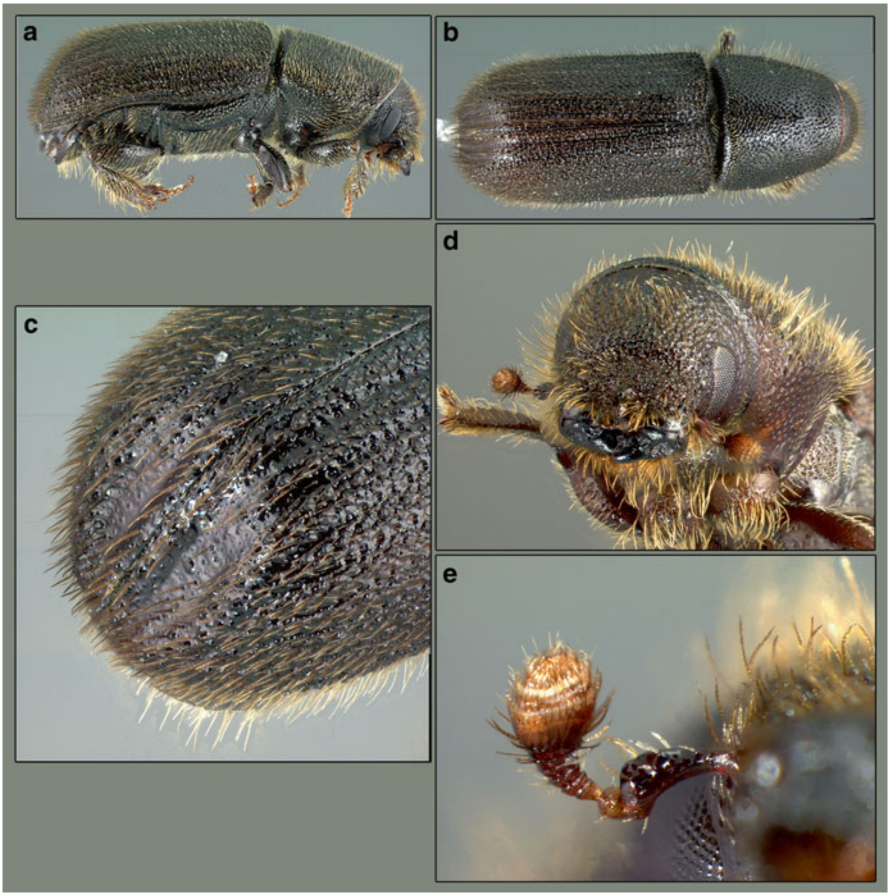


Fig. 21.19 Lateral (**a**) and dorsal (**b**) views of adult male redhaired pine bark beetle, *Hylurgus ligniperda* (F.). Dense, red setae on the elytral declivity (**c**) and longitudinal tubercle (projection) on the frons of the head (**d**). Male antennal club (**e**) (Photo credits, Dr. Anthony G. Gutierrez (Chief) and Danielle N. Thomas, Molecular Biology Lab, Entomological Sciences Program, U.S. Army CHPPM, Aberdeen Proving Ground, Maryland)

specimens have also been trapped on USDA National Forest lands in more remote locations in Los Angeles, Orange, Riverside, and San Bernardino Counties. Ground checking for this species on 10 March 2005, and 7 March and 13 April, 2006 at Bonelli Park and Descanso Gardens (Los Angeles Co.) revealed that *H. ligniperda* was frequently found in large dimensional (minimum 15–20 cm diameter) cut or broken logs of *P. halepensis* and *P. canariensis.* At these times the beetles were newly colonizing and ovipositing in this fresh host material. Egg galleries were about 6 cm in length. Most of the galleries were on the undersides of the logs that were in contact with soil or, in one case, concrete, and beetles often tunneled into the logs from the cut ends. Mating pairs of *H. ligniperda* were also collected on

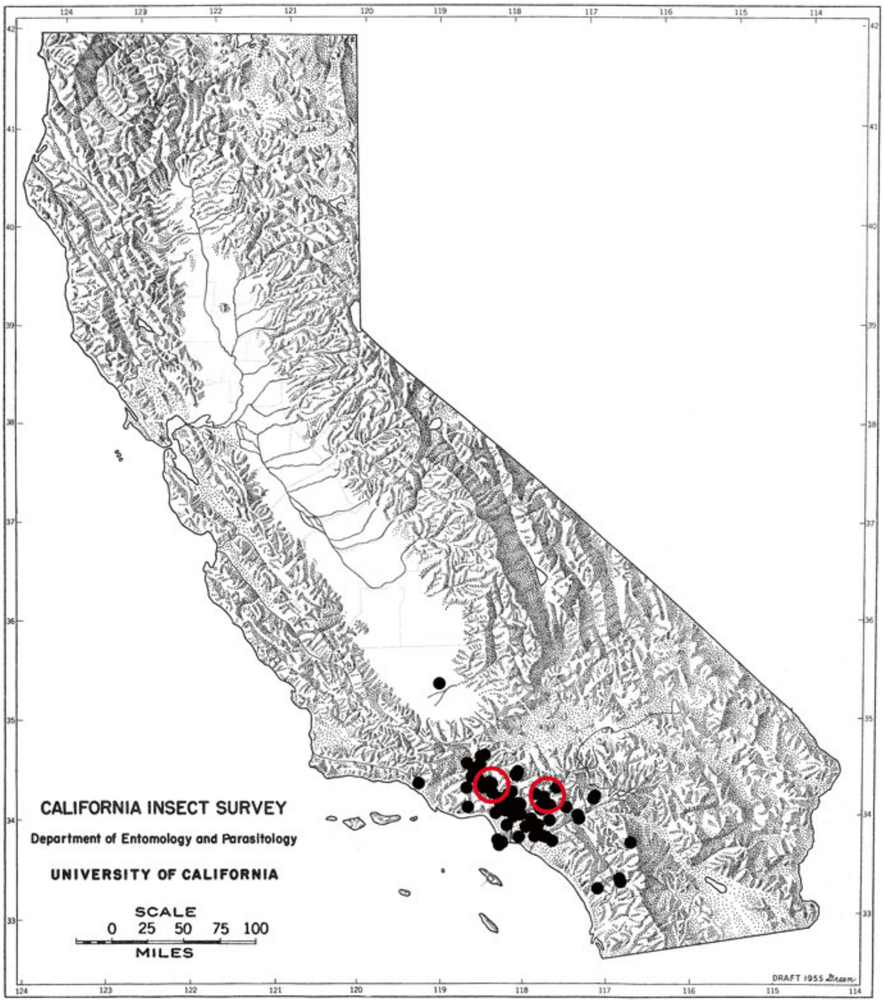


Fig. 21.20 Distribution of the redhaired pine bark beetle, *Hylurgus ligniperda* (F.), in California from field and museum survey by the authors (2003-present). The two initial Los Angeles Co. collection points are *circled* in *red* (VII-10-2003, F.G. Bonelli Regional Park, San Dimas and VIII-8-2003, Bear Divide Guard Station, Angeles National Forest)

10 March 2005 at Bonelli Park from a stump of a *P. halepensis* tree that had broken during a major storm on 27 December 2004. In the same logs and stumps, *H. ligniperda* were frequently found adjacent to larval mines of the invasive roundheaded woodborer, *Arhopalus syriacus*, and to more advanced galleries of *Ips paraconfusus* Lanier, which was generally absent from the undersides of the logs. In contrast to its near absence on Mediterranean pines in the southern Central Valley, *I. paraconfusus* is quite abundant in these pines planted in the Los Angeles Basin. Another native scolytid associated with *H. ligniperda*, *Carphoborus simplex* LeConte, was also

collected on several occasions in the Los Angeles Basin in smaller diameter logs and branches of *P. halepensis* and *P. canariensis*.

By May 2007, *H. ligniperda* had been collected by hand or in attractant-baited survey traps in six counties in southern California (Los Angeles, Orange, Riverside, San Bernardino, San Diego, and Ventura) (Fig. 21.20) Liu et al. 2007). The northernmost collection point at the time was near the community of Castaic in Los Angeles County on the southern base of the transverse Tehachapi Mountain Range. In August of 2009, *H. ligniperda* was detected in a survey trap near Lebec, California in southern Kern County, which represented a breach of the natural montane barrier (Penrose 2010). On the same date, survey entomologists collected a specimen of *H. ligniperda* in a funnel trap even further north near the Kern County Museum in Bakersfield (Penrose 2010). In 2009 and 2010, D.-G. Liu (UC Davis Department of Entomology) discovered that *H. ligniperda* was also established to the southeast of these locations in a native stand of singleleaf pinyon pine, *Pinus monophylla* Torr. & Frém., near the northern boundary of the Angeles National Forest and the southern edge of Lancaster/Palmdale and the Antelope Valley (Los Angeles County) (Fig. 21.18). The dispersal of the invasive population into native forest type, and particularly into *P. monophylla*, is significant because the primary concern in western North America is that *H. ligniperda* might become a highly effective vector of the pathogen for blackstain root disease, *Leptographium wageneri*, which is a serious native pest of conifers (Cobb 1988).

Specimens in the *CSCA* (Sacramento, California) indicated that *H. ligniperda* had been intercepted and collected at the Port of Oakland on several occasions on *P. radiata* lumber or dunnage from New Zealand (1995, 1996). In an assessment of pest risk associated with importation of *P. radiata* logs from Chile into the USA, *H. ligniperda* was considered to have the highest risk potential among ten insects in the analysis (USDA Forest Service 1993). In an analysis of national records from the Port Information Network, Haack (2001) reported 217 interceptions of *H. ligniperda* in the USA between 1985 and 2000. As was the case with *O. erosus*, California did not rank among the top five U.S. states for interception (11 records). These interceptions occurred at Long Beach (8), San Francisco (2) and San Diego (1), and they originated from Portugal (5), New Zealand (3), France (2), and Belgium (1) (RA Haack, pers. comm.). The population in New York has not appeared to have expanded beyond the area of the original discovery and has not dispersed into southern Canada as of December 2015 (Troy Kimoto, Canadian Food Inspection Agency, personal communication).

Wood and Bright (1992) list Europe (including western Russia), the Mediterranean (including North Africa and associated Atlantic and Mediterranean Islands), and Asia (China) as the native range of *H. ligniperda*. Pfeffer (1994) notes that it is distributed in central and southern Europe, the Crimea, the Caucasus, Asia Minor, and Algeria. Whether the native distribution includes China is not substantiated elsewhere in the literature. Indeed, a review of the Chinese literature reveals that although it has been intercepted many times at Chinese ports, it is apparently not yet established in China (Wei and Shao 1991; Yang and An 2002; Liang et al. 2003; Hu et al. 2004; Wang et al. 2005). For example, Liang et al. (2003) specifically documented 65 records of interception in 2002 on Monterey pine, *Pinus radiata* D. Don, imported from New Zealand to Guangdong Province, China. *Hylurgus ligniperda* appears to have achieved an invasive distribution quite similar to *O. erosus*. Introduced locations include Australia, Japan, New Zealand (1974), St. Helena Island, Sri Lanka (=Ceylon), South Africa, South America (Brazil, Chile, Uruguay), Swaziland (Browne 1968; Bain 1977; Neumann 1979; Zondag 1979; MacKenzie 1992; Wood and Bright 1992), and the eastern USA (USDA Forest Service 2002). Like *O. erosus*, its presence in northern climates is questionable. Duffy (1953) reported *H. ligniperda* as neither "imported" nor "doubtfully indigenous," whereas Browne (1968) considered it "reported in Britain, but not as a breeding species." Recent collections have only involved interceptions at ports or from cargo without any further evidence of an established population (C Tilbury, Forest Research, UK Forestry Commission, Surrey, and MVL Barclay, BMNH, London, personal communication). There are no current records of indigenous or introduced populations in Norway (K Thunes, Norwegian Forest Research Institute, pers. comm.), and in Sweden it was detected on multiple pulpwood log shipments from Chile (10 of 14 shipments) and France (3 of 6 shipments), but is apparently not yet established (Schroeder 1990). Collection records from the Baltic countries of Estonia and Latvia (Bright and Skidmore 2002) are also likely not of established populations.

The beetle feeds in the phloem of the basal portion of pine stems, large roots, or woody debris on the soil surface. Throughout its native and introduced range, *H. ligniperda* infests fresh stumps, logging debris, the basal stems of standing trees, or large, exposed roots of unhealthy trees in the genus *Pinus*. Records of pine species colonized so far are listed in Appendix 21.I. It has a strong proclivity to colonize cut logs in association with soil (Tribe 1992; Mausel 2002; Mausel et al. 2007), even locating and colonizing logs buried 40 cm below the surface (Tribe 1992). Based on observations in Chile, Ciesla (1988, 1993) reported that it can also cause seedling mortality by feeding on root collars and roots. Similar observations were made in Australia (Victoria) in *P. radiata* nurseries and second rotation sites (Neumann 1979; Neumann and Marks 1990). In southeastern Australia, Neumann (1987) described mortality caused by *H. ligniperda* to *P. radiata* ranging in age from 4 to 14 years. In Spain, Garcia de Viedma (1966) reported that *H. ligniperda* colonized and killed only pines up to 15 cm diameter at the base and that adults overwintered in groups of 30 to 40 beneath the bark at the root collar and in the larger roots. However, in New Zealand, *H. ligniperda* does not appear to kill seedlings (MacKenzie 1992; Reay and Walsh 2001; Brownbridge et al. 2010). In South Africa, apparently *Hylastes angustatus* (Herbst) is considered more aggressive than *H. ligniperda* because it is *H. angustatus* (and by inference not *H. ligniperda*) that damages pine seedlings during maturation feeding (Zhou et al. 2002a, b). A similar situation pertains in New Zealand with *Hylastes ater* (Paykull) vs. *H. ligniperda* (Brownbridge et al. 2010). In South Africa *H. ligniperda* colonized *P. radiata* logs at greatest frequency during the fall months (April/May in the Southern Hemisphere), and, in contrast to *O. erosus*, was generally more active during the cooler months of the year (Tribe 1991a). Southern Hemisphere winter flight activity was also documented in mature *P. radiata* stands in Victoria (Neumann 1978), but was not observed in *P. radiata* plantations in Chile (Mausel 2002) or New Zealand (Reay and Walsh 2001).

The greatest impact of *H. ligniperda* in western North America may be as a vector of fungal pathogens or agents of sapstain (MacKenzie 1992; USDA Forest Service 1993). In New Zealand, *Leptographium truncatum* (= *L. lundbergii*) and *L. procerum* (W.B. Kendr.) M.J. Wingfield have been isolated from *H. ligniperda* (Wingfield et al. 1988; MacKenzie 1992). In South Africa 11 fungal species in various genera have been isolated from beetles or their galleries in *P. patula* and *P. elliottii* trap logs (Zhou et al. 2001), with 21.6 % of 199 samples carrying *L. lundbergii*, 21.1 % carrying *L. serpens*, and 12.6 % carrying *Ophiostoma ips* (Wingfield et al. 1985; Tribe 1991a, b; Zhou et al. 2001). In Chile, *O. ips*, *O. galeiformis* (Bakshi) Mathiesen-Käärik, *Ceratocystiopsis minuta* (Siemaszko) Upadhyay & Kendrick were isolated from 80 specimens of *H. ligniperda* or its galleries in felled *P. radiata* in log decks (Zhou et al. 2004). No relative frequencies of occurrence of the three fungi were provided in the latter study. In New York, *H. ligniperda* appears to be associated with a syndrome called white pine root decline (USDA Forest Service 2002), which involves *L. procerum* (Zhou et al. 2001), but to our knowledge this fungal species has not been reported from New York populations of the beetle. In the western USA, *L. wageneri* (Kendrick) M. J. Wingfield, which is the causal agent of black stain root disease (Cobb 1988), may become associated with *H. ligniperda*, with potentially negative consequences for western pines and perhaps other conifers. This disease is prevalent in the coniferous forests of the Tranverse (San Bernardino) Mountain Range (Wagener and Mielke 1961; Merrill 1997 and LD Merrill, pers. comm.), which overlaps with the current distribution of *H. ligniperda* in California (Figs. 21.18 and 21.20). An analysis of the fungal associates of specimens of *H. ligniperda* collected from Mediterranean pine logs at two locations in Los Angeles County revealed eight species of Ophiostomatales and seven unidentified species (Kim et al. 2011). The most frequently isolated species were *Ophiostoma ips* and *Grosmannia galeiforme*, which were isolated respectively from 31 % to 23 % of the 118 beetles. The other species isolated included *O. piceae* (isolated from 9 % of the beetles), *O. querci* (8 %) and *Leptographium tereforme* sp. nov. (6 %). *Grosmannia huntii*, *L. serpens*, three *Sporothrix* species, *O. floccosum*, *O. stenoceras*, two unidentified *Hyalorhinocladiella* sp. and a sterile fungus each were isolated from fewer then 5 % of beetles. Most of the identified species already were known in USA and have been found in association with *H. ligniperda* in other countries. However the new species, *L. tereforme*, and *G. galeiforme* were recorded from the USA for the first time, and this was the first report of *L. serpens* from western North America.

Limited studies have been conducted to identify attractants or pheromones for *H. ligniperda* (Reay and Walsh 2002; Mausel 2002; Petrice et al. 2004). Mausel (2002) did not find any evidence for an aggregation or sex pheromone in field studies, but Reay and Walsh (2002) and Petrice et al. (2004) found that host compounds such as α-pinene, β-pinene, and ethanol can affect flight behavior. Petrice et al. (2004) found that baits containing α- or β-pinene and ethanol were the most attractive to *H. ligniperda* among the four treatments of α-pinene (high release rate) plus ethanol, α-pinene (low release rate) plus ethanol, β-pinene (high release rate) plus ethanol, and α-pinene (low release rate) alone. Reay and Walsh (2002) reported that both α- and β-pinene were attractive to *H. ligniperda*, and ethanol had a synergistic effect on the attraction to α-pinene or β-pinene. Both studies had limitations of either not including appropriate controls or not reporting the enantiomeric composition of the monoterpenes.

A year-long field bioassay (2006–2007) of the flight response of both sexes of *H. ligniperda* in Los Angeles County by our lab group demonstrated that ethanol and (−)-α-pinene functioned synergistically for both sexes as an attractant (Liu et al. 2016). Ethanol was not attractive alone, but (−)-α-pinene was moderately attractive to both sexes. Seasonal flight activity data from the bioassay and from the statewide survey suggested that the flight of *H. ligniperda* occurred year round in Southern California with major peaks in the spring (March to early May) and summer (late July), but was relatively low from August to late January. A wide range of other subcortical Coleoptera from urban forests of Southern California were trapped in the experiment, i.e., 22 species of Scolytidae (including eight of the invasive species covered in this chapter), six species of Bostrichidae, three species of Colydiidae, and 5 species of Cerambycidae. *Xyleborinus saxeseni* and both sexes of three native species of false powderpost beetles [*Amphicerus cornutus*, *Scobicia declivis*, and *S. suturalis* (Horn) (Coleoptera: Bostrichidae)] responded significantly to either treatment containing ethanol. Both sexes of the invasive roundheaded borer, *Arhopalus syriacus*, and a native root-feeding bark beetle, *Hylastes tenuis* Eichhoff, responded to treatments similarly to *H. ligniperda*, i.e., with a significant and synergistic response to ethanol and α-pinene. Peak flight activities of these subcortical beetles were variable depending on localities and seasons. This study represented the first report of flight dynamics in California for *A. syriacus*, *Am. cornutus*, *H. tenuis*, *S. declivis*, *S. suturalis*, and *X. saxeseni*, as well as for *H. ligniperda*. The diversity of bark and woodboring beetles caught, and synergism of (−)-α-pinene and ethanol from the year-long flight bioassay confirmed the utility of including both (−)-α-pinene and ethanol in monitoring or early detection programs for invasive species (Rabaglia et al. 2008).

21.4.5 Miscellaneous Indigenous Exotic Species in California

The peach bark beetle, *Phloeotribus liminaris* (Harris), is an eastern North American species that was first collected on November 8, 2002 in Fullerton, California (Orange Co.) from a dying ornamental Catalina cherry tree, *Prunus licifolia* spp. *lyonii* (Eastw.) Raven. It has since been collected several times in funnel traps from sites in Los Angeles, San Bernardino, and San Diego Cos. This species, *Ips calligraphus* (Germar), and two ambrosia beetles previously reported in California, *Monarthrum mali* (Fitch) and *Xyleborus xylographus* Say (Wood 1982), are all examples of “indigenous” exotic bark and ambrosia beetle species (Dodds et al.

2010) that have likely come to California from eastern North America (Table 21.2). *Ips calligraphus* has not been reported from the State in many years, but at one time had a fairly substantial population in the central Sierra Nevada in ponderosa pine, *Pinus ponderosa* (Herbert 1916; Wood and Stark 1968; Connor and Wilkinson 1983; Lanier et al. 1991). Another subcortical species of note from eastern North America that is relatively new to California (Duckles and Švihra 1995; Dreistadt et al. 2004) and Nevada (Carlos et al. 2002) is the bronze birch borer, *Agrilus anxius* Gory, which is a flatheaded borer that attacks the main stem of ornamental birches. It was first detected in 1992 in Marin and Sonoma Counties in northern California (Dreistadt et al. 2004). Its distribution and current status in California need further attention. In 2003, one of us (RLP) also confirmed the presence of another eastern U.S. woodborer species in California: the redheaded ash borer, *Neoclytus acuminatus* (F.) (Coleoptera: Cerambycidae). As of late 2007, it was only known from Sacramento Co., but it was subsequently reared from *Juglans* (likely *J. regia*) in Tulare Co. (southern Central Valley) (Dennis Haines, CDFA, Tulare County, pers. comm., 10 April 2014) and trapped in July and August 2015 in surveys of the walnut twig beetle in *J. regia* orchards in Colusa, Solano, and Yolo Cos. (northern Central Valley).

21.5 Summary and Future Expectations

Over a decade of intensive survey has revealed a greater than 100 % increase in invasive Scolytidae in California (from 10 to 22 species) (Table 21.2), bringing the exotic species composition in the State to approx. 10 % of the native fauna. Five of the species are indigenous exotics from eastern North America or the desert Southwest. This increase in the number of invasive bark and ambrosia beetles is a reflection of both commitment of resources and research effort to the discovery and characterization of newly established populations of species as well as enhanced awareness of which "native" species may have been actually invasive (e.g., *C. bodoanum*, *H. eruditus*, *P. juglandis*, and *X. saxeseni*). The extra-continental invasive scolytids in California comprise nearly 30 % of the 58 documented invasive species in the USA (Haack 2001, 2006; Lee et al. 2007; Haack and Rabaglia 2013). Given the dictum that invasive species often re-associate themselves with their hosts of origin (i.e., in this case adventive populations of trees) in the invaded habitat (Mattson et al. 1992; Niemelä and Mattson 1996; Langor et al. 2009 for Canada), it is not surprising that some of the key invasive bark beetles are of Mediterranean origin (Mifsud and Knížek 2009). However, there is also a trend toward introduction and establishment of Asian invasive species in California (e.g., polyphagous shot hole borer and banded elm bark beetle, *Scolytus schevyrewi*). Invasive bark and ambrosia beetles present new management challenges for urban foresters and public and private land managers evoking a need for outreach and publicly accessible IPM literature (Dreistadt et al. 2004; Lee et al. 2005, 2006, 2007; Liu et al. 2007; Seybold et al. 2008b, 2013a, b; Flint et al. 2010; Coleman et al. 2013).

Southern California appears to have been a particularly fertile area for the introduction and establishment of exotic Scolytidae. Factors enhancing this immigration include favorable and diverse climate, diverse and exotic (tropical and temperate) vegetation, large human population centers and extreme ethnic diversity, poor air quality that stresses plants (Grulke et al. 2002), and high levels of commercial and military port traffic. The compatibility of California's Mediterranean climate with the native climate of some of these invaders cannot be overlooked. Despite a relatively even distribution of survey traps across the northern and southern portions of the state, the majority of the ten new records of Scolytidae reported here were exclusively or partially from southern California. We anticipate that this trend will continue.

Climate change is exerting a broad impact on the population biology of native scolytids in North America (Bentz et al. 2010), with the most obvious effects at higher elevations and latitudes. There also appears to be a trend whereby southern populations of indigenous exotic subcortical species are invading and expanding their populations generally northward. Examples of this include the Mexican pine beetle, *Dendroctonus mexicanus* Hopkins (Moser et al. 2005), the Mexican soapberry borer, *Agrilus prionurus* Chevrolat (Billings et al. 2014), the walnut twig beetle, *P. juglandis* (Rugman-Jones et al. 2015), the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleman et al. 2015, see Chap. 22), and two other newly discovered flatheaded borers in California, *Chrysobothris analis* LeConte (Westcott et al. 2016) and *C. costifrons costifrons* Waterhouse (Basham et al. 2015). Whether or not this trend will continue to manifest itself in the urban, peri-urban, and wildland forests on the North American continent, and in California in particular, remains to be seen. As a counterexample to the south to north invasion trend, a historically significant southern outbreak of a defoliator was recently documented when Douglas-fir tussock moth, *Orgyia pseudotsugata*, for the first time in the forest entomological record, killed large numbers of white fir, *A. concolor*, trees in the San Bernardino Mountains (Coleman et al. 2014b).

It is highly likely that continued survey in the next few years will detect additional immigrant scolytid species in California. Based on available host type, climate, importation pathways, and geographic proximity, highly probable immigrant scolytid species to California include: *Gnathotrichus materiarius* (Fitch)*, Hylastes opacus* Erichson, *Monarthrum fasciatum* (Say), *Xyleborinus alni* (Niisima), *Xylosandrus crassiusculus* (Motschulsky), and *Xyloterinus politus* Say (all introduced in neighboring Oregon, Mudge et al. 2001; LaBonte et al. 2005); *Hylurgopinus rufipes* (Eichhoff), *Hylurgops palliatus* (Gyllenhal), *Pityogenes bidentatus* (Herbst), *T. piniperda*, *Xyleborus glabratus* Eichhoff, and *Xylosandrus compactus* (Eichhoff) (all present in eastern North America); *Carphoborus minimus* F., *Crypturgus mediterraneus* Eichhoff, *Hylastes linearis* Erichson, *Hylurgus micklitzi* Wachtl., *Pityogenes calcaratus* Eichh., and *Tomicus destruens* (Woll.) (all associated with *O. erosus* in the Mediterranean, Mendel 1987; Mendel et al. 1991; Mifsud and Knížek 2009); *Hylastes angustatus* (Herbst) (associated with *H. ligniperda* in South Africa); and *Hylastes ater* (Paykull), *Ips duplicatus* (Sahlberg), *Ips sexdentatus* (Boerner), *Ips typographus*, *Pityogenes chalcographus* (L.), *Scolytus intricatus* (Ratzeburg), and *Scolytus scolytus* (Fab.) (major Eurasian pest species with frequent North American interception histories, Haack 2006). A Mediterranean cypress bark beetle, *Phloeosinus aubei* (Perris) (Mendel 1984, 1987; Bel Habib et al. 2007) has recently invaded Central Europe (Gabor Szocs, Plant Protection Institute CAR HAS, Budapest, Hungary, personal correspondence), and could represent a strong threat to California's many urban species and cultivars in the Cupressaceae as well as to the California endemics in the forested landscape. Another Mediterranean species, *Scolytus amygdali*, could already be present in California in crypsis with *S. rugulosus* (as was apparently the case in the Maltese Islands, Mifsud and Knížek 2009), which underscore the importance of investigating the complexity of populations of *S. rugulosus* in North America. Two final Eurasian species of concern because of their potential pest status are *Dendroctonus armandi* Tsai and Li and *D. micans* (Kugelann). Watchlists like this have merit when considering how to structure detection surveys, however, it has been the case that relatively obscure and unpredictable species [e.g., *S. schevyrewi*, the goldspotted oak borer, *A. auroguttatus*, or the Eucalyptus longhorned borers, *Phoracantha recurva* Newman and *P. semipunctata* (F.)] can also have relatively profound impacts on trees in the invaded habitat because of the lack of host resilience in the new environment. Also, the lists provide outreach specialists with a planning framework for the advent of key species through publications and presentations [e.g., Dreistadt et al. (2004) discussed the potential arrival of *X. crassiasculus* and its impact on California shade tree resources].

21.6 Acknowledgements

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Fig. 21.21 Richard Lynn Penrose (11 January, 1943–17 March 2011) at the California Department of Food and Agriculture Plant Health and Pest Prevention Services, Pest Exclusion Branch, Meadowview Field Office, circa 2009 (SJS photo)

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Appendix 21.I: Host Ranges of Selected Invasive Bark and Ambrosia Beetles in California Mediterranean Forest Systems

For more details on the host ranges of these species, the reader is referred to the World Catalog of the Scolytidae (Wood and Bright 1992) as well as to the three catalog supplements (Bright and Skidmore 1997, 2002; Bright 2014).

Fruit-Tree Pinhole Borer or Lesser Shothole Borer, **Xyleborinus saxeseni** *(Ratzeburg)*

Possibly no species is exempt from invasion (Bright and Stark 1973). Chamberlin (1939) only listed hardwoods (*Quercus*, *Fagus*, *Betula*, *Acer,* etc.), but Wood and Bright (1992) also list conifers such as *Abies*, *Chamaecyparis*, *Cryptomeria*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga*, and *Tsuga* among many other tree species. We have reared this species from *Alnus rhombifolia*, *Juglans californica*, *J. hindsii*, *J. mollis*, *J. regia*, *J. hindsii* x *nigra*, *J. hindsii* x *regia*, *Pinus radiata*, and *Prunus cerasifera* (SJS, unpublished data) and *Pterocarya fraxinifolia* (Hishinuma et al. 2015).

Spermophagous Bark Beetles, **Coccotrypes** *Eichhoff and* **Dactylotrypes** *Eggers*

Coccotrypes advena Blandford is thought to be native to Asia (Indonesia) and breeds in either bark or large seeds of a variety of tropical hosts (Wood 1977). Wood and Bright (1992) list these hosts, which include *Albizzia* sp., *Ficus bracteata*, *F. xylophylla*, *Pterocarpus indicus*, and *Theobroma cacao*. Bright and Skidmore (1997) listed four additional hosts: *Calophyllum brasiliense*, *Eugenia jambos*, *Pouteria multiflora*, and *Sloanea berteriana*, whereas Bright and Skidmore (2002) added the petioles of *Cecropia insignis* and *C. peltata* to the list. Bright (2014) cataloged references for seven new hosts, which included logs of *Pinus caribea* and *Sloanea berteroana*, as well as seeds of *Persea americana*.

Coccotrypes carpophagus (Hornung) likely originated in Africa, but was named for betel nuts from India (Wood 1977). Wood (1977) also suggest that it breeds in a wide variety of nuts and other large seeds, and Wood and Bright (1992) listed 27 genera or species of hosts. These included *Cassia grandis, Coccothrinix argentea, Diospyros spp., Neowashingtonia robusta, Phoenix dactylifera, Sabal palmetto, Theoborma cacao*, and *Washingtonia filifera*. Bright and Skidmore (1997) listed *Acacia mangium* and *Quercus variabilis*, whereas Bright and Skidmore (2002) listed four new host records, including *Washingtonia robusta* (presumably as a correction for *Neowashingtonia* in Wood and Bright 1992). Bright (2014) listed seeds of *Persea americana* and *Prestoea montana*, as well as fruits of *Dillenia indica* as additional host records.

Coccotrypes dactyliperda (F.) also likely originated in Africa, and frequently colonizes and breeds in date pits (Wood 1977). Wood (1977) also suggests that it "may breed in a wide variety of nuts, and buttons or other objects made from vegetable ivory." Wood and Bright (1992) listed 24 genera or species of hosts. This list overlaps with that of *C. carpophagus*, but also includes *Coccos* spp.*, Olea europaea, Phoenix* spp., and *Persea gratissima.* Bright and Skidmore (1997); Bright and Skidmore (2002); and Bright (2014) provide summaries of only distributional records (including Hawaii, Malta, New Zealand), but no new host records.

Dactylotrypes longicollis (Wollaston) has been recorded from the following hosts (presumably on the seeds) in its native Atlantic Island distribution (or in invaded regions of France): *Butia eriospatha, Chamaerops humilis*, *Dracsena draco* (L.), *Phoenix canariensis*, *Phoenix pumila*, and *Trachycarpus excelsus* (Wood and Bright 1992). Bright and Skidmore (1997) reported an expanded distribution into Italy and Spain and added date palm, *Phoenix dactylifera* as a host. Whitehead et al. (2000) reported that it was collected in seeds of *P. canariensis* in Croatia and transported to Slovakia. It was found later in the Maltese Islands but no host of collection was reported (Mifsud and Colonnelli 2010). LaBonte and Takahashi (2012) report that it only attacks the seeds of palms and related plants; they found dead specimens of *D. longicollis* in the fallen seeds of Brazilian needle palm, *Trithrinax brasiliensis* Martius (Arecaceae) in a southern California arboretum (Fullerton, Orange Co.). It was collected in funnel traps at this site and at the Los Angeles County Arboretum.

Hypothenemus eruditus *Westwood*

The host range is enormous (Wood and Bright 1992; Bright and Skidmore 1997, 2002; Bright 2014). Wood (2007) noted that "hundreds of host species have been recorded including fungal fruiting bodies, twigs, weeds, pods, seeds, and other unexpected places." "The original series was removed from active tunnels in the cover of an old book."

Shothole Borer, Scolytus rugulosus *(Müller)*

Scolytus rugulosus has been described as cosmopolitan and occurring wherever the hosts (*Malus* spp., *Prunus* spp., *Pyrus* sp., and less frequently *Crataegus* spp., *Cydonia* sp., *Ulmus* sp., etc.) are cultivated (Wood 1982) or as "occurring in most fruit-growing areas of the United States and Canada" (Furniss and Carolin 1977). The latter authors also list mountain mahogany (*Cercocarpus*) amongst the hosts. Michalski (1973), Wood and Bright (1992), and Bright and Skidmore (1997) provide much more comprehensive host lists, which include species of significance to urban and wild land forestry, such as *Acer*, *Betula*, *Castanea*, *Fagus*, *Taxus*, *Tilia*, *Ulmus* (*carpinifolia*), as well as *Amelanchier*, *Celtis*, *Corylus*, *Cotoneaster*, *Morus*, *Sorbus*, *Juglans regia* L., and many others. Whether these are truly developmental hosts or just chance collections on these plants or plant misidentifications needs to be verified. The primary hosts noted by Furniss and Carolin (1977) and Wood (1982) appear to be the only confirmed hosts so far in California, as Dreistadt et al. (2004) list English laurel, fruit trees, and hawthorn as hosts. In our museum survey, we found specimens with host labels that included *Cupressus* (Santa Clara Co., V-1985, *SDMC*, doubtful developmental host record); *Pyracantha* spp. (Rosaceae, Contra Costa Co., VI-1953, *EMEC*); and loquat, *Eriobotrya japonica* (Rosaceae, Orange Co., IV-1915, *EMEC*).

European Elm Bark Beetle, Scolytus multistriatus *(Marsham)*

Wood and Bright (1992) note that this species colonizes *Ulmus* spp. as hosts and is rare in other hosts. Baker (1972) reports that *S. multistriatus* attacks and colonizes all native and introduced species of elms (*Ulmus* spp., slippery, American, English, Japanese, etc.) in North America as well as the related Japanese zelkova, *Zelkova serrata* (Thunb.) Makino.

Banded Elm Bark Beetle, Scolytus schevyrewi *Semenov*

Scolytus schevyrewi has been reported to colonize elms (*Ulmus* spp., American, big fruit, chalked bark, English, European white, field, Japanese, rock, Siberian, smooth-leaved, winged); various trees in the rose family (Rosaceae, almond, apricot, cherry, paradise apple, peach, pear, other *Prunus* spp.); Oleaster (Elaeagnaceae); pea shrub (Fabaceae); Russian olive; and weeping willow (Salicaceae) (Latin names provided in Negrón et al. 2005 and host range summarized in Lee et al. 2007). However, in North America, the only confirmed hosts are in the *Ulmus*. In the laboratory, *S. schevyrewi* readily colonized bolts of American elm, *Ulmus americana* L., but not Chinese elm, *Ulmus parvifolia* Jacq.; Siberian peashrub, *Caragana arborescens* Lam.; a cherry, *Prunus fontanesiana* (Spach) C. K. Schneid.; or Russian olive, *Elaeagnus angustifolia* L. (2011).

Walnut Twig Beetle, Pityophthorus juglandis *Blackman*

Pityophthorus juglandis colonizes all species of *Juglans* (walnuts, butternuts, and their hybrids) as well as several species of *Pterocarya* (wingnut) (reviewed in Hishinuma et al. 2015).

Mediterranean Pine Engraver, Orthotomicus *(*Ips*)* erosus *(Wollaston)*

The principal species of pines colonized by *O. erosus* in its native range are *Pinus armandii* Franchet, *P. brutia*, *P. canariensis*, *P. halepensis*, *P. kesiya* Royle ex Gordon var. *langbianensis* (Chevalier) Cheng & Fu, *P. massoniana*, *P. nigra* Arnold, *P. pinaster* (= *P. maritima* Ait.), *P. pinea*, *P. sylvestris*, *P. tabuliformis* Carrière, and *P. yunnanensis* Franchet (Yin et al. 1984; Jiang et al. 1992; Wood and Bright 1992; Yin and Huang 1992; Bright and Skidmore 1997, 2002; Chen et al. 1998; Eglitis 2000a). In introduced areas it has colonized *P. caribaea* Morelet, *P. echinata* Mill., *P. elliottii* Engelmann, *P. patula* Scheide & Deppe, *P. radiata*, and *P. taeda* L. (Bevan 1984; Eglitis 2000a). Reports of *O. erosus* in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, spruce, *Picea* spp., fir, *Abies* spp., cypress, *Cupressus* spp., and cedar, *Cedrus* spp. (Grüne 1979; Mendel and Halperin 1982; Wood and Bright 1992; Bright and Skidmore 1997, 2002; Eglitis 2000a) are considered by us in most cases to likely be instances of maturation feeding, collection from adult overwintering sites, or accidental associations rather than developmental records (Chararas and M'Sadda 1970). This hypothesis has been substantiated in part by a laboratory no-choice physiological host range study with the introduced California population where, Lee et al. (2008) identified potentially vulnerable native and adventive hosts in North America among 22 conifer species. The beetle reproduced on four pines from its native Eurasian range: Aleppo, Canary Island, Italian stone, and Scots pines; 11 native North American pines: eastern white, gray, jack, Jeffrey, loblolly, Monterey, ponderosa, red, Sierra lodgepole, singleleaf pinyon, and sugar pines; and four native nonpines: Douglas-fir, black and white spruce, and tamarack. Among nonpines, fewer progeny developed and they were of smaller size on Douglas-fir and tamarack, but sex ratios of progeny were nearly 1:1 on all hosts. Beetles did not develop on white fir, incense cedar, or coast redwood (Lee et al. 2008). With loblolly pine, the first new adults emerged 42 days after parental females were introduced into host logs at temperatures of 20–33 °C and 523.5 or 334.7 accumulated degree-days based on lower development thresholds of 13.6 °C or 18 °C, respectively. Laboratory studies of walking and boring behavior as a prelude to host selection (Walter et al. 2010a, b) showed slightly broader ranges of suitability or short-range acceptability, with the angiosperm non-host *Betula papyrifera* Marsh eliciting a higher walking response than would be expected by chance (Walter et al. 2010b) and extracts of the marginal host tamarack, *Larix laricina* (Du Roi) Koch, eliciting an increase in the initiation and extent of boring by *O. erosus* on a filter paper substrate (Walter et al. 2010a).

Redhaired Pine Bark Beetle, Hylurgus ligniperda *(Fabricius)*

Pine species colonized by *H. ligniperda* include *P. brutia, P. canariensis, P. elliottii, P. halepensis, P. montezumae* Lamb*., P. nigra, P. patula, P. pinaster, P. pinea, P. radiata, P. strobus* L.*,* and *P. sylvestris* (Browne 1968; Bain 1977; Pfeffer 1994; Bright and Skidmore 1997; Eglitis 2000b; USDA Forest Service 2002). Its host range may extend to other species in the Pinaceae (USDA Forest Service 2002), but we could not confirm this in the primary literature or on the ground in California.

References

Amezaga I, Rodríguez MÁ (1998) Resource partitioning of four sympatric bark beetles depending on swarming dates and tree species. For Ecol Manag 109:127–135

Anonymous (2015a) Major urban parks of California, Balboa, Golden Gate, and Griffith Parks. https://en.wikipedia.org/wiki/Balboa_Park_(San_Diego); https://en.wikipedia.org/wiki/Golden_Gate_Park; and https://en.wikipedia.org/wiki/Griffith_Park. Accessed 4 July 2015

Anonymous (2015b) Thousand cankers disease. https://en.wikipedia.org/wiki/Thousand_cankers_disease. Accessed 8 July 2015

Armitage HM (1951) Current insect notes. Bull Calif Dept Agric 40:111–118

Atkinson DJ (1921) *Ips* (*Tomicus*) *erosus* Woll. in Britain. Entomol Mon Mag 57:253–255

Atkinson TH (1993) A new species of *Pityophthorus* Eichhoff (Coleoptera: Scolytidae) from southern Florida with a key to the Florida species. Fla Entomol 76:608–616

Atkinson TH, Peck SB (1994) Annotated checklist of the bark and ambrosia beetles (Coleoptera: Platypodidae and Scolytidae) of tropical southern Florida. Fla Entomol 77:313–329

Audley J (2015) Assessment of *Pityophthorus juglandis* colonization characteristics and implications for further spread of thousand cankers disease. M.S. thesis, University of Tennessee, Knoxville, TN, 88 pp

Audley J, Mayfield AE, Meyers SW et al (2016) Phytosanitation methods influence post-treatment colonization of *Juglans nigra* logs by *Pityophthorus juglandis* (Coleoptera: Curculionidae: Scolytinae). J Econ Entomol. doi:10.1093/jee/tov252

Aukema JE, McCullough DG, Von Holle B et al (2010) Historical accumulation of nonindigenous forest pests in the continental United States. BioScience 60:886–897

Bain J (1977) *Hylurgus ligniperda* (Fabricius) (Coleoptera: Scolytidae), vol 18, Forest and timber insects in New Zealand. Forest Research Institute, New Zealand Forest Service, Rotorua, 7 pp

Bain A (1998) A seventeenth-century beetle fauna from colonial Boston. Hist Archaeol 32:38–48

Baker WL (1972) Eastern forest insects, Misc Publ No. 1175. U.S. Department of Agriculture, Forest Service, Washington, DC, 642 pp

Bakker ES (1984) An island called California: an ecological introduction to its natural communities, 2nd edn. University of California Press, Berkeley/Los Angeles. 484 pp

Barclay MVL (2003) A record of *Uloma culinaris* (Linnaeus) (Tenebrionidae: Ulominae) from the British Isles, with a discussion of its European biology. Entomol Rec 115:181–186

Barger JH, Hock WK (1971) Distribution of Dutch elm disease and the smaller European elm bark beetle in the United States as of 1970. Plant Dis Rep 55:271–272

Basham JP, Waayers RJ, Westcott RL (2015) Discovery of *Chrysobothris costifrons costifrons* Waterhouse, 1887 (Coleoptera: Buprestidae) in southern California, U.S.A. Pan Pac Entomol 91:200–202

Baylis NT, de Ronde C, James DB (1986) Observations of damage of a secondary nature following a wild fire at the Otterford State Forest. South Afr For J 137:36–37

Beede RH, Hasey JK (1997) The history of the walnut in California. In: Ramos DD (ed) Walnut production manual. Publication No. 3373 (University of California (System) Division of Agriculture and Natural Resources). University of California Division of Agriculture and Natural Resources, Oakland, CA, pp 8–15, 328 pp

Beh MM, Metz MR, Seybold SJ et al (2014) The novel interaction between *Phytophthora ramorum* and wildfire elicits elevated ambrosia beetle landing rates on tanoak, *Notholithocarpus densiflorus*. For Ecol Manag 318:21–33

Bel Habib R, Ben Jamâa ML, Nouira S (2007) Biological characteristics of the cypress bark beetle *Phloeosinus aubei* in the Kessra forest, center of Tunisia. Tunisian J Plant Prot 2:99–108

Ben Jamaa ML, Lieutier F, Yart A et al (2007) The virulence of phytopathogenic fungi associated with the bark beetles *Tomicus piniperda* and *Orthotomicus erosus* in Tunisia. For Pathol 37:51–63

Bentz BJ, Régnière J, Fettig CJ et al (2010) Climate change and bark beetles of the western US and Canada: direct and indirect effects. Bioscience 60:602–613

Ben-Yehuda S, Tolasch T, Francke W et al (2002) Aggregation pheromone of the almond bark beetle *Scolytus amygdali* (Coleoptera: Scolytidae). IOBC/WPRS Bull 25:1–12

Bevan D (1984) *Orthotomicus erosus* (Wollaston) in Usutu pine plantations, Swaziland. Forest Research report number 64. Usutu Pulp Company Limited, 34 pp

Bevan D (1987) Forest insects: a guide to insects feeding on trees in Britain, vol 1, Forestry Commission handbook. HMSO, London, UK

Billings RF, Grosman DM, Pase HA III (2014) Soapberry borer, *Agrilus prionurus* (Coleoptera: Buprestidae): an exotic pest threatens western soapberry in Texas. Southeastern Naturalist, 13:105–116

Blackman MW (1928) The genus *Pityophthorus* Eichh. In North America: a revisional study of the *Pityophthorini*, with descriptions of two new genera and seventy-one new species. Bull NY State Coll For 1(3–6):183 pp

Blackman MW (1942) New species of bark beetles (*Pityophthorini*) from Mexico and tropical America (Coleoptera: Scolytidae). Proc US Natl Mus 92(3147):177–227

Bloomfield H (1979) Elms for always. Am For 85:24–26, 48–50

Borchert D, Newton L, Culliney T et al (2011) Risk assessment of the movement of firewood within the United States. Plant Epidemiology and Risk Analysis Laboratory Center for Plant Health Science and Technology Plant Protection and Quarantine United States Department of Agriculture Animal and Plants Health Inspection Service, Report Rev.1 20110105, Raleigh, NC, 1 May 2011, 122 pp. http://www.emeraldashborer.info/files/USDA_APHIS_firewood_pathway_assessment_May_2010.pdf. Acessed 4 July 2015

Bousquet Y, Bouchard P, Davies AE et al (2013) Checklist of beetles (Coleoptera) of Canada and Alaska, 2nd edn. Pensoft Publishers, Sofia, 402 pp

Bright DE Jr (1968) A review of the tribe Xyleborini in America north of Mexico (Coleoptera: Scolytidae). Can Entomol 100:1288–1323

Bright DE Jr (1981) Taxonomic monograph of the genus *Pityophthorus* Eichhoff in North and Central America, vol 118, Memoirs Entomological Society of Canada. Entomological Society of Canada, Ottawa, 378 pp

Bright DE Jr (1985) New species and new records of North American *Pityophthorus* (Coleoptera: Scolytidae): part V: the *juglandis* group. Great Basin Natl 45:476–482

Bright DE Jr (2014) A catalog of Scolytidae and Platypodidae (Coleoptera), Supplement 3 (1999–2010), with notes on subfamily and tribal reclassification. Insecta Mundi 0356:1–336

Bright DE Jr, Skidmore RE (1997) A catalog of Scolytidae and Platypodidae (Coleoptera), Supplement 1 (1990–1994). NRC Research Press, Ottawa, 368 pp

Bright DE Jr, Skidmore RE (2002) A catalog of Scolytidae and Platypodidae (Coleoptera), Supplement 2 (1995–1999). NRC Research Press, Ottawa, 523 pp

Bright DE Jr, Stark RW (1973) The bark and ambrosia beetles of California, Coleoptera: Scolytidae and Platypodidae, vol 16, Bull California Insect Survey. University of California Press, Berkeley, 169 pp

Brockerhoff EG, Bain J, Kimberley MO et al (2006) Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. Can J For Res 36:263–268

Brown LR (1965) Seasonal development of the smaller European elm bark beetle in southern California. J Econ Entomol 58:176–177

Brownbridge M, Reay SD, Cummings NJ (2010) Association of entomopathogenic fungi with exotic bark beetles in New Zealand pine plantations. Mycopathol 169:75–80

Browne FG (1968) Pests and diseases of forest plantation trees: an annotated list of the principal species occurring in the British Commonwealth. Clarendon, Oxford, UK, 1330 pp

Browne LE (1972) An emergence cage and refrigerated collector for wood-boring insects and their associates. J Econ Entomol 65:1499–1501

Buth JL, Ellis RA (1981) Trapping elm bark beetles in the city of Winnipeg, with a new record for *Scolytus multistriatus* (Coleoptera: Scolytidae) in Manitoba. Can Entomol 113:263–264

Callahan F (2008) Hinds walnut (*Juglans hindsii*) in Oregon. Kalmiopsis 15:42–52

Canadian Food Inspection Agency [CFIA] (2007) Plant protection survey report. (http://www.inspection.gc.ca/english/plaveg/pestrava/surv/sit2007e.shtml)

Carlos WJ, Johnson WS, Skelley J et al (2002) The bronze birch borer, University of Nevada Cooperative Extension Fact Sheet 02–38, University of Nevada, Reno, NV, 4 pp

Cavey J, Passoa S, Kucera D (1994) Screening aids for exotic bark beetles in the Northeastern United States. NA-TP-11-94. Northeastern Area: U.S. Department of Agriculture, Forest Service

Chamberlin WJ (1939) The bark and timber beetles of North America, north of Mexico. Oregon State College Co-Op Association, Corvallis, OR, 513 pp

Chapman JW (1910) The introduction of a European scolytid (The smaller elm bark beetle, *Scolytus multistriatus* Marsh) into Massachusetts. Psyche 17:63–68

Chararas C, M'Sadda K (1970) Attraction chimique et attraction sexuelle chez *Orthotomicus erosus* Woll. (Coléoptère Scolytidae). C R Acad Sci Paris 271:1904–1907

Chen Y, Seybold SJ (2014) Crepuscular flight activity of an invasive insect governed by interacting abiotic factors. PLoS One 9(8):e105945. doi:10.1371/journal.pone.0105945

Chen Y, Dallara PL, Nelson LJ et al (2016) Comparative morphometric and chemical analyses of phenotypes of two invasive ambrosia beetles (*Euwallacea* spp.) in the United States of America. Insect Sci (in review)

Chen S-W, Huang J-J, Long H-J (1998) Preliminary studies on the life table of *Orthotomicus erosus* natural populations. Entomol Knowl 35:352–353 (in Chinese)

Ciesla WM (1988) Pine bark beetles: a new pest management challenge for Chilean foresters. J For 86:27–31

Ciesla WM (1993) Recent introductions of forest insects and their effects: a global overview. FAO Plant Prot Bull 41:3–13

Claflin LE, Dooling OJ (1973) Dutch elm disease in Montana. Plant Dis Rep 57:701

Cobb FW Jr (1988) *Leptographium wageneri*, cause of black-stain root disease: a review of its discovery, occurrence and biology with emphasis on pinyon and ponderosa pine. In: Harrington TC, Cobb FW Jr (eds) *Leptographium* root diseases on conifers. APS Press, St. Paul, pp 41–62

Coleman TW, Seybold SJ (2008) Previously unrecorded damage to oak, *Quercus* spp., in southern California by the goldspotted oak borer, *Agrilus coxalis* Waterhouse (Coleoptera: Buprestidae). Pan Pac Entomol 84:288–300

Coleman TW, Eskalen A, Stouthamer R (2013) New pest complex in California: the polyphagous shot hole borer, *Euwallacea* sp., and Fusarium Dieback, *Fusarium euwallaceae*. USDA Forest Service, Pest Alert, R5-PR-032, 4 Nov 2013, 5 pp

Coleman TW, Chen Y, Graves AD et al (2014a) Developing monitoring techniques for the invasive goldspotted oak borer (Coleoptera: Buprestidae) in California. Environ Entomol 43:729–743. doi:10.1603/EN13162

Coleman TW, Jones MI, Courtial B et al (2014b) Impact of the first recorded outbreak of the Douglas-fir tussock moth, *Orgyia pseudotsugata*, in southern California and the extent of its distribution in the Pacific Southwest region. For Ecol Manag 329:295–305. http://dx.doi.org/10.1016/j.foreco.2014.06.027

Coleman TW, Jones MI, Smith SL et al (2015) Goldspotted oak borer, *Agrilus auroguttatus*. USDA Forest Service, Forest Insect and Disease Leaflet No. 183, Mar 2015, 16 pp. http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprd3833276.pdf

Connor MD, Wilkinson RC (1983) *Ips* bark beetles in the South, USDA Forest Service Forest Insect and Disease Leaflet No. 129, U.S. Department of Agriculture, Forest Service, Washington, DC, 8 pp

Cranshaw W (2011) Recently recognized range extensions of the walnut twig beetle, *Pityophthorus juglandis* Blackman (Coleoptera: Curculionidae: Scolytinae), in the western United States. Coleop Bull 65:48–49

Dallara PL, Flint ML, Seybold SJ (2012) An analysis of the larval instars of the walnut twig beetle, *Pityophthorus juglandis*, in northern California black walnut, *Juglans hindsii*, and a new host record for *Hylocurus hirtellus*. Pan Pac Entomol 88:338–366

Davidson AG, Newell WR (1957) Atlantic Provinces forest disease survey. Annual report of the forest insect and disease survey 1957. Canada Department of Agriculture, Forest Biology Division, Science Service, Ottawa, ON

Davidson AG, Pomerleau R, Dance BW et al (1964) A review of the Dutch elm disease. For Entomol Pathol Branch, Bi-Mon Prog Rep 20(4):1–8

Dodds KJ, Gilmore DW, Seybold SJ (2010) Assessing the threat posed by indigenous exotics: a case study of two North American bark beetle species. Ann Entomol Soc Am 103:39–49

Doerr MD, Brunner JF, Smith TJ (2008) Biology and management of bark beetles (Coleoptera: Curculionidae) in Washington cherry orchards. J Entomol Soc Br Columb 105:69–81

Douglas H, Bouchard P, Anderson RS et al (2013) New Curculionoidea (Coleoptera) records for Canada. ZooKeys 309:13–48

Dreistadt SH, Clark JK, Flint ML (2004) Pests of landscape trees and shrubs: an integrated pest management guide, vol 3359, 2nd edn, Statewide Integrated Pest Management Program. University of California, Division of Agriculture and Natural Resources, Oakland, CA, 501 pp

Duckles B, Švihra P (1995) Bronze birch borer discovered in California. HortScript, Aug 1995, No. 16. University of California Cooperative Extension, Novato, CA, 4 pp

Duffy EAJ (1953) Handbook for identification of British insects, Coleoptera: Scolytidae and Platypodidae. R Entomol Soc Lond 5(15):20

Eglitis AE (2000a) Mediterranean pine engraver beetle. USDA Animal and Plant Health Inspection Service and Forest Service Pest Risk Assessment for Importation of Solid Wood Packing Materials into the United States, Washington, DC, pp 190–193, 275 pp

Eglitis AE (2000b) Red-haired pine bark beetle. USDA Animal and Plant Health Inspection Service and Forest Service Pest Risk Assessment for Importation of Solid Wood Packing Materials into the United States, Washington, DC, pp 183–185, 275 pp

Eskalen A, Stouthamer R, Lynch SC et al (2013) Host range of *Fusarium* dieback and its ambrosia beetle (Coleoptera: Scolytinae) vector in southern California. Plant Dis 97:938–951

Essig EO (1915) Injurious and beneficial insects of California, 2nd edn, Supplement to the monthly bulletin of the California, State Commission of Horticulture. California State Print, Sacramento, CA, 541 pp

Essig EO (1926) Insects of Western North America. Macmillan, New York, NY, 511 pp

Flint ML, Graves AD, Seybold SJ (2010) Thousand cankers disease of walnuts spreads in California. CAPCA Advis Mag 8(3):36–39

Furniss RL, Carolin VM (1977) Western forest insects, Miscellaneous publication No. 1339. U.S. Department of Agriculture, Forest Service, Washington, DC, 654 pp

Garcia de Viedma M (1966) *Hylurgus ligniperda*, a pest of pine reafforestation: symptoms of attack. Rev Appl Entomol 54:128–129

Garrison RW (1993) New agricultural pest for southern California: a cypress bark beetle (*Phloeosinus armatus*). Los Angeles County Agricultural Commissioner's Office Note, Feb 1993, 2 pp

Geiger J, Woods M (compilers) (2009) California forest pest conditions-2008. California Forest Pest Council, California Department of Forestry and Fire Protection, Sacramento, CA, June 2009, 65 pp

Giesen H, Kohnle U, Vité JP et al (1984) Das Aggregationspheromon des Mediterranen Kiefernborkenkäfers *Ips* (*Orthotomicus*) *erosus*. Z Angew Entomol 98:95–97

Gillerfors G (1988) Skalbaggar införda till Sverige med importerad massaved (Beetles introduced into Sweden with imported pulpwood). Entomol Tidskr 109:42–45

Graves AD, Coleman TW, Flint ML et al (2009) Walnut twig beetle and thousand cankers disease: field identification guide, UC-IPM website publication, 21 Nov 2009, 2 pp. http://www.ipm.ucdavis.edu/PDF/MISC/thousand_cankers_field_guide.pdf

Graves AD, Flint ML, Coleman TW et al (2010) Thousand cankers disease of walnuts: a new disease in California, UC-IPM website publication, 4 pp. http://www.ipm.ucdavis.edu/EXOTIC/thousandcankers.html

Graves AD, Coleman TW, Seybold SJ (2011) Monitoring walnut health and decline in response to thousand cankers disease and infestation by the walnut twig beetle, *Pityophthorus juglandis*, in southern California and New Mexico. Year one progress report for USDA Forest Service Forest Health Monitoring project INT-EM-B-11-03. http://fhm.fs.fed.us/em/funded/12/INT-EM-B-11-03.pdf. Accessed 18 June 2015

Griffin JR, Critchfield WB (1972) The distribution of forest trees in California. USDA Forest Service. Research paper PSW-82. Pacific Forest and Range Experiment Station, 114 pp. (reprinted with supplement, 1976). Available: http://www.fs.fed.us/psw/publications/documents/psw_rp082/psw_rp082.pdf. Accessed 4 Apr 2015

Grulke NE, Preisler HK, Rose C et al (2002) O_3 uptake and drought stress effects on carbon acquisition of ponderosa pine in natural stands. New Phytol 154:621–631

Grüne S (1979) Brief illustrated key to European bark beetles. M&H Schaper, Hannover, 182 pp

Haack RA (2001) Intercepted Scolytidae (Coleoptera) at U.S. ports of entry: 1985–2000. Integr Pest Manag Rev 6:253–282

Haack RA (2006) Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can J For Res 36:269–288

Haack RA, Rabaglia RJ (2013) Exotic bark and ambrosia beetles in the USA: potential and current invaders. In: Peña J (ed) Potential invasive pests of agricultural crops. CAB International, Wallingford/Boston

Haack RA, Petrice TR, Wiedenhoeft AC (2010) Incidence of bark and wood-boring insects in firewood: a survey at Michigan's Mackinac Bridge. J Econ Entomol 103:1682–1692

Hajek AE, Dahlsten DL (1985a) Factors influencing the mortality of *Scolytus multistriatus* (Coleoptera: Scolytidae) in elm branches in California. Can Entomol 117:819–828

Hajek AE, Dahlsten DL (1985b) Insect and mite associates of *Scolytus multistriatus* (Coleoptera: Scolytidae) in California. Can Entomol 117:409–421

Halperin J, Mendel Z, Golan Y (1983) On the damage caused by bark beetles to pine plantations: preliminary report. La-Yaavan 33:46

Harrington TC, McNew D, Steimal J et al (2001) Phylogeny and taxonomy of the *Ophiostoma piceae* complex and the Dutch elm disease fungi. Mycologia 93:111–136

Henin J-M, Paiva MR (2004) Interactions between *Orthotomicus erosus* (Woll.) (Col., Scolytidae) and the Argentine ant *Linepithema humile* (Mayr) (Hym., Formicidae). J Pest Sci 77:113–117

Herbert FB (1916) Biological notes on certain western species of the genus *Ips* (DeGeer). U.S. Department of Agriculture Bureau of Entomology, Forest Entomology, Los Gatos, CA, Dec 1916, 44 pp

Hickman JC (ed) (1996) The Jepson manual: higher plants of California. University of California Press, Berkeley, CA, 1400 pp

Hishinuma SM, Dallara PL, Yaghmour MA et al (2015) Wingnut (Juglandaceae) as a new generic host for *Pityophthorus juglandis* (Coleoptera: Curculionidae) and the thousand cankers disease pathogen, *Geosmithia morbida* (Ascomycota: Hypocreales). Can Entomol. doi:10.4039/tce.2015.37

Hobson KR, Bright DE Jr (1994) A key to the *Xyleborus* of California, with faunal comments (Coleoptera: Scolytidae). Pan Pac Entomol 70:267–268

Holzman J, Bohonak AJ, Kirkendall LR et al (2009) Inbreeding variability and population structure in the invasive halplodiploid palm-seed borer (*Coccotrypes dactyliperda*). J Evol Biol 22:1076–1087

Hopkins AD (1899) Preliminary report on the insect enemies of forests of the Northwest. USDA Division of Entomology Bulletin No. 21, USDA Division of Entomology, Washington, DC, 27 pp

Hu X-N, Wu J-J, Liang F et al (2004) Study on the biological control of *Steinernema feltiae* against *Hylurgus ligniperda* on the entry log. Plant Quarantine 18:269–272 (in Chinese)

Humble LM, John E, Smith J et al (2010) First records of the banded elm bark beetle, *Scolytus schevyrewi* Semenov (Coleoptera: Curculionidae: Scolytinae), in British Columbia. J Entomol Soc Br Columb 107:21–24

Indiana Department of Natural Resources (2015) Walnut twig beetle detected in Indiana. Available from http://www.in.gov/activecalendar_dnr/EventList.aspx?view=EventDetails&eventidn=7823&information_id=15952&type=&syndicate=syndicate. Accessed 26 Apr 2015

Ives WGH, Petty J (1976) Prairies region. Annual report of the forest insect and disease survey, 1975. Canadian Forestry Service, Ottawa, ON, pp 69–74

Ivie MA, Slipinski SA, Wegrzynowicz P (2001) New records and synonyms in the Colydiinae and Pycnomerini (Coleoptera: Zopheridae). Insecta Mundi 15:185–188

Jacobi WR, Koski RD, Harrington TC et al (2007) Association of *Ophiostoma novo-ulmi* with *Scolytus schevyrewi* (Scolytidae) in Colorado. Plant Dis 91:245–247

Jacobi WR, Hardin JG, Goodrich BA et al (2012) Retail firewood can transport live tree pests. J Econ Entomol 105:1645–1658

Jacobi W, Koski R, Negrón JF (2013) Dutch elm disease pathogen transmission by the banded elm bark beetle *Scolytus schevyrewi* (Curculionidae subfamily Scolytinae). For Pathol 43:232–237

Jiang Y-P, Huang Z-Y, Huang X-C (1992) Studies on *Orthotomicus erosus*. J Zhejiang Norm Univ (Nat Sci) 15:79–81 (in Chinese)

Johnson PL, Hayes JL, Rinehart RE et al (2008) Characterization of two non-native invasive bark beetles, *Scolytus schevyrewi* and *Scolytus multistriatus* (Coleoptera: Curculionidae: Scolytinae). Can Entomol 140:527–538

Jones MI, Coleman TW, Graves AD et al (2013) Sanitation options for managing oak wood infested with the invasive goldspotted oak borer (Coleoptera: Buprestidae) in southern California. J Econ Entomol 106:235–246

Jurc M, Bojović S, Komjanc B et al (2009) Xylophagous entomofauna in branches of oaks (*Quercus* spp.) and its significance for oak health in the Karst region of Slovenia. Biologia 64:130–138

Katovich SA, Ostry ME (1998) Insects associated with butternut and butternut canker in Minnesota and Wisconsin. Great Lakes Entomol 31:97–108

Kfir R (1986) Releases of natural enemies against the pine bark beetle *Orthotomicus erosus* (Wollaston) in South Africa. J Entomol Soc South Afr 49:391–392

Kim S, Harrington TC, Lee JC et al (2011) *Leptographium tereforme*, *sp. nov*. and other Ophiostomatales isolated from the redhaired pine bark beetle, *Hylurgus ligniperda*, in California. Mycologia 103:152–163. doi:10.3852/10-096

Kirkendall LR (1989) Within-harem competition among *Ips* females, an overlooked component of density-dependent larval mortality. Holarct Ecol 12:477–487

Kolařík M, Freeland E, Utley C et al (2011) *Geosmithia morbida* sp. nov., a new phytopathogenic species living in symbiosis with the walnut twig beetle (*Pityophthorus juglandis*) on *Juglans* in USA. Mycologia 103:325–332

Krivolutskaya GO (1983) Ecological and geographical characteristics of the northern Asian bark beetle fauna (Coleoptera: Scolytidae). Entomol Rev 62:52–67

LaBonte JR (2010) The banded elm bark beetle, *Scolytus schevyrewi* Semenov (Coleoptera, Curculionidae, Scolytinae) in North America: a taxonomic review and modifications to the Wood (1982) key to the species of *Scolytus* Geoffroy in North and Central America. ZooKeys 56:207–218

LaBonte JR, Takahashi CY (2012) *Dactylotrypes longicollis* (Wollaston) (Coleoptera: Curculionidae: Scolytinae): an exotic bark beetle new to California and North America. Pan Pac Entomol 88:222–230

LaBonte JR, Mudge AD, Johnson KJR (2005) Non-indigenous woodboring Coleoptera (Cerambycidae, Curculionidae: Scolytinae) new to Oregon and Washington, 1999–2002: consequences of the intracontinental movement of raw wood products and solid wood packing materials. Proc Entomol Soc Wash 107:554–564

Langor DW, DeHass LJ, Footit RG (2009) Diversity of non-native terrestrial arthropods on woody plants in Canada. Biol Invasions 11:5–19

Lanier GN, Teale SA, Pajares JA (1991) Biosystematics of the genus *Ips* (Coleoptera: Scolytidae) in North America of the *Ips calligraphus* group. Can Entomol 123:1103–1124

Lanner RM (1999) Conifers of California. Cachuma Press, Los Olivos, CA

Lee JC, Seybold SJ (2010) Host acceptance and larval competition in the banded and European elm bark beetles (Coleoptera: Scolytidae): potential mechanisms for competitive displacement between invasive species. J Insect Behav 23:19–34. http://dx.doi.org/10.1007/s10905-009-9192-1

Lee JC, Smith SL, Seybold SJ (2005) The Mediterranean pine engraver, *Orthotomicus erosus*. USDA Forest Service, Pest Alert, R5-PR-016, 4 pp. http://entomology.ucdavis.edu/files/215004.pdf or http://www.treesearch.fs.fed.us/pubs/48537. Accessed 21 December 2015

Lee JC, Negrón JF, McElwey SJ et al (2006) Banded elm bark beetle – *Scolytus schevyrewi*. USDA Forest Service, Pest Alert, R2-PR-04-06, 2 pp. http://www.na.fs.fed.us/pubs/palerts/banded_elm_beetle/beb.pdf. Accessed 13 June 2015

Lee JC, Haack RA, Negrón JF et al (2007) Invasive bark beetles. Forest Insect and Disease Leaflet, No. 176. USDA Forest Service, Washington, DC, 12 pp

Lee JC, Flint ML, Seybold SJ (2008) Suitability of pines and other conifers as hosts for the invasive Mediterranean pine engraver (Coleoptera: Scolytidae) in North America. J Econ Entomol 101:829–837

Lee JC, Aguayo I, Aslin R et al (2009) Co-occurrence of the invasive banded and European elm bark beetles (Coleoptera: Scolytidae) in North America. Ann Entomol Soc Am 102:426–436

Lee JC, Hamud SM, Negrón JF et al (2010) Semiochemical-mediated flight strategies of two invasive elm bark beetles: a potential factor in competitive displacement. Environ Entomol 39:642–652. doi:10.1603/EN09327

Lee JC, Negrón JF, McElwey SJ et al (2011) Biology of the invasive banded elm bark beetle (Coleoptera: Scolytidae) in the western United States. Ann Entomol Soc Am 104:705–717. doi:10.1603/AN10150

Lee JC, Jiroš P, Liu D-L et al (2016) Pheromone production and flight response to semiochemicals by the Mediterranean pine engraver (Coleoptera: Scolytidae), a recently invasive bark beetle in California. J Chem Ecol (in prep.)

Liang Q-C, Chen S-Y, Liu Z-C et al (2003) Interception records of harmful beetles in imported *Pinus radiata* logs from New Zealand. Plant Quarantine 17:352–353 (in Chinese)

Lindgren BS (1983) A multiple funnel trap for scolytid beetles (Coleoptera). Can Entomol 115:299–302

Linsley EG (1963) The Cerambycidae of North America. Part IV. Taxonomy and classification of the subfamily Cerambycinae, tribes Elaphidionini through Rhinotragini, vol 21, University of California publications in entomology. University of California Press, Berkeley, CA, 165 pp

Linsley EG, Chemsak JA (1997) The Cerambycidae of North America, Part VIII: bibliography, index, and host plant index, vol 117, University of California publications in entomology. University of California Press, Berkeley, CA, 534 pp

Linsley EG, MacLeod GF (1942) Ambrosia beetles attacking deciduous fruit trees in California. J Econ Entomol 35:601

Liu H-P, Haack RA (2003) *Scolytus schevyrewi*. Pest report from the exotic forest pest information system for North America. http://www.spfnic.fs.fed.us/exfor/data/pestreports.cfm?pestidval=163&langdisplay=english. Accessed 25 June 2015

Liu D-G, Bohne MJ, Lee JC et al (2007) New introduction in California: the redhaired pine bark beetle, *Hylurgus ligniperda* Fabricius. USDA Forest Service, Pest Alert, R5-PR-07, Nov 2007, 3 pp. http://entomology.ucdavis.edu/files/215005.pdf. Accessed 16 June 2015. or http://www.treesearch.fs.fed.us/pubs/48536. Accessed 7 Aug 2015

Liu D-G, Flint M, Seybold SJ (2008) A secondary sexual character in the redhaired pine bark beetle, *Hylurgus ligniperda* Fabricius (Coleoptera: Scolytidae). Pan Pac Entomol 84:26–28

Liu D-G, Chen Y, Lee JC et al (2016) Responses of the invasive redhaired pine bark beetle, *Hylurgus ligniperda* (Coleoptera: Scolytidae), and associated subcortical Coleoptera to host volatiles in the southern California urban landscape. Biol Invasions (in prep)

MacKenzie M (1992) Potential forest exports and pests from New Zealand. In: Filip GM (ed) Log imports and introduced forest pests into the Pacific Northwest, Corvallis, OR, 21–23 April. Oregon State University, Department of Forest Science, College of Forestry, Corvallis, OR, Unpaginated

Mattson WJ, Lawrence RK, Haack RA et al (1988) Defensive strategies of woody plants against different insect-feeding guilds in relation to plant ecological strategies and intimacy of association with insects. In: Mattson WJ, Levieux J, Bernard-Dagan C (eds) Mechanisms of woody plant defenses against insects: search for patterns. Springer, New York, pp 3–38

Mattson WJ, Niemela P, Millers I et al (1992) Immigrant phytophagous insects on woody plants in the United States and Canada: an annotated list, USDA Forest Service, North Central Forest Experiment Station General Technical Report NC-169, St. Paul, MN, 27 pp

Mausel DL (2002) Harvesting, transporting, and storing of *Pinus radiata* logs in Chile to minimize the movement of *Hylurgus ligniperda* and *Hylastes ater* (Coleoptera: Scolytidae) to ports of embarkation. M.S. Thesis, University of Washington, Seattle, WA, 121 pp

Mausel DL, Gara RI, Lanfranco D et al (2007) The introduced bark beetles *Hylurgus ligniperda* and *Hylastes ater* (Coleoptera: Scolytidae) in Chile: seasonal flight and effect of *Pinus radiata* log placement on colonization. Can J For Res 37:156–169

Mayfield AE, Fraedrich SW, Taylor A et al (2014) Efficacy of heat treatment for the thousand cankers disease vector and pathogen in small black walnut logs. J Econ Entomol 107:174–184. http://dx.doi.org/10.1603/EC13390

McPherson BA, Erbilgin N, Wood DL et al (2008) Attraction of ambrosia and bark beetles to coast live oaks infected by *Phytophthora ramorum*. Agric For Entomol 10:315–321

Mendel Z (1983) Seasonal history of *Orthotomicus erosus* (Coleoptera: Scolytidae) in Israel. Phytoparasit 11:13–24

Mendel Z (1984) Life history of *Phloeosinus armatus* Reiter and *P. aubei* Perris (Coleoptera: Scolytidae) in Israel. Phytoparasit 12:89–97

Mendel Z (1985) Predation of *Orthotomicus erosus* (Col., Scolytidae) by the Syrian woodpecker (*Picoides syriacus*, Aves, Picidae). Z Angew Entomol 100:355–360

Mendel Z (1986) Hymenopterous parasitoids of bark beetles [Scolytidae] in Israel: relationships between host and parasitoid size, and sex ratio. Entomophaga 31:127–137

Mendel Z (1987) Major pests of man-made forests in Israel: origin, biology, damage and control. Phytoparasit 15:131–137

Mendel Z, Halperin J (1981) Parasites of bark beetles [Col.: Scolytidae] on pine and cypress in Israel. Entomophaga 26:375–379

Mendel Z, Halperin J (1982) The biology and behavior of *Orthotomicus erosus* in Israel. Phytoparasit 10:169–181

Mendel Z, Podoler H, Livne H (1990) Interactions between *Aulonium ruficorne* (Coleoptera: Colydiidae) and other natural enemies of bark beetles (Coleoptera: Scolytidae). Entomoph 35:99–105

Mendel Z, Boneh O, Shenhar Y et al (1991) Diurnal flight patterns of *Orthotomicus erosus* and *Pityogenes calcaratus* in Israel. Phytoparasit 19:23–31

Mendel Z, Boneh O, Riov J (1992) Some foundations for the application of aggregation pheromone to control pine bark beetles in Israel. J Appl Entomol 114:217–227

Mendel Z, Ben-Yehuda S, Marcus R et al (1997) Distribution and extent of damage by *Scolytus* spp. to stone and pome fruit orchards in Israel. Int J Trop Insect Sci 17:175–181

Merrill LD (1997) San Bernardino National Forest mortality aerial survey report. USDA Forest Service, San Bernardino National Forest, Supervisor's Office, San Bernardino, CA, 26 Aug 1997

Michalski J (1973) Revision of the Palearctic species of the genus *Scolytus* Geoffroy (Coleoptera: Scolytidae). Polska Akademia Nauk, Zakład Zoologh Systematycznej I Doświadczalnej, Państwowe Wydawnictwo Naukowe, Warszava, 214 pp

Mifsud D, Colonnelli E (2010) The Curculionoidea of the Maltese Islands (Central Mediterranean) (Coleoptera). Bull Entomol Soc Malta 3:55–143

Mifsud D, Knížek M (2009) The bark beetles (Coleoptera: Scolytidae) of the Maltese Islands (Central Mediterranean). Bull Entomol Soc Malta 2:25–52

Moser JC, Fitzgibbon BA, Klepzig KD (2005) The Mexican pine beetle, *Dendroctonus mexicanus*: first record in the United States and co-occurrence with the southern pine beetle-*Dendroctonus frontalis* (Coleoptera: Scolytidae or Curculionidae: Scolytinae). Entomol News 116:235–243

Moser JC, Konrad H, Blomquist SR et al (2010) Do mites phoretic on elm bark beetles contribute to the transmission of Dutch elm disease? Naturwissenschaften 97:219–227

Mouton M, Wingfield MJ, Van Wyk PS et al (1994) *Graphium pseudormiticum* sp. nov.: a new hyphomycete with unusual conidiogenesis. Mycol Res 98:1272–1276

Mudge AD, LaBonte JR, Johnson KJR et al (2001) Exotic woodboring Coleoptera (Micromalthidae, Scolytidae) and Hymenoptera (Xiphydriidae) new to Oregon and Washington. Proc Entomol Soc Wash 103:1011–1019

Muller KK, Broder RE, Beittel W (1974) Trees of Santa Barbara. Santa Barbara Botanic Garden, Santa Barbara/West Berlin, Germany: Brüder Hartmann

National Agricultural Pest Information System (NAPIS) (2014) Survey status of Mediterranean pine engraver-*Orthotomicus erosus* 2006–2014. http://pest.ceris.purdue.edu/map.php?code=INBQQEA#. Accessed 25 June 2015

Negrón JF, Witcosky JJ, Cain RJ et al (2005) The banded elm bark beetle: a new threat to elms in North America. Am Entomol 51:84–94

Neumann FG (1978) Insect populations in Eucalypt and pine forests in northeastern Victoria. Aust For Res 8:13–24

Neumann FG (1979) Insect pest management in Australia radiata pine plantations. Aust For 42:30–38

Neumann FG (1987) Introduced bark beetles on exotic trees in Australia with special reference to infestations of *Ips grandicollis* in pine plantations. Aust For 50:166–178

Neumann FG, Marks GC (1990) Status and management of insect pests and diseases in Victorian softwood plantations. Aust For 53:131–144

Niemelä P, Mattson WJ (1996) Invasion of North American forests by European phytophagous insects. Bioscience 46:741–753

Parker KG, Collins DL, Tyler LJ et al (1947) The Dutch elm disease: association of *Ceratostomella ulmi* with *Scolytus multistriatus*, its advance into new areas, method of determining its distribution, and control of the disease. Cornell Experiment Station Memoir No. 275, pp 5-44

Penrose RL (2010) Final report on the Exotic Woodborer Survey for the period of January 1, 2009 through December 31, 2009. California of Department Food and Agricultural Integrated Pest Control Branch Biological Control Program, 14 Apr 2010, USDA contract no. 09-8523-0478-CA, 12 pp

Petrice TR, Haack RA, Poland TM (2004) Evaluation of three trap types and five lures for monitoring *Hylurgus ligniperda* (Coleoptera: Scolytidae) and other local scolytids in New York. Great Lakes Entomol 37:1–9

Pfeffer A (1994) Zentral- und westpaläarktische borken- und kernkäfer (Coleoptera, Scolytidae, Platypodidae). Entomol Basil 17:5–310

Podoler H, Mendel Z, Livne H (1990) Studies on the biology of a bark beetle predator, *Aulonium ruficorne* (Coleoptera: Scolytidae). Environ Entomol 19:1010–1016

Rabaglia RJ, Dole SA, Cognato AI (2006) Review of American Xyleborina (Coleoptera: Curculionidae: Scolytinae) occurring north of Mexico, with an illustrated key. Ann Entomol Soc Am 99:1034–1056

Rabaglia R, Duerr D, Acciavatti R et al (2008) USDA Forest Service early detection and rapid response project for non-native bark and ambrosia beetles, summary of the 2001–2005 pilot project. USDA Forest Service, Forest Health Protection, Washington, DC, 12 pp

Ranger CM, Schultz PB, Frank SD et al (2015) Non-native ambrosia beetles as opportunistic exploiters of living but weakened trees. PLoS One 10(7):e0131496. doi:10.1371/journal.pone.0131496 (accessed July 4, 2015)

Readio PA (1935) The entomological phases of Dutch elm disease. J Econ Entomol 28:341–353

Reay SD, Walsh PJ (2001) Observations of the flight activity of *Hylastes ater* and *Hylurgus ligniperda* (Curculionidae: Scolytinae) in *Pinus radiata* forests in the central North Island, New Zealand. N Z Entomol 24:79–85

Reay SD, Walsh PJ (2002) Relative attractiveness of some volatiles to the introduced pine bark beetles, *Hylastes ater* and *Hylurgus ligniperda* (Curculionidae: Scolytinae). N Z Entomol 25:51–56

Romón P, Iturrondobeitia JC, Gibson K et al (2007) Quantitative association of bark beetles with pitch canker fungus and effects of verbenone on their semiochemical communication in Monterey pine forests in northern Spain. Environ Entomol 36:743–750

Rugman-Jones PF, Seybold SJ, Graves AD et al (2015) Phylogeography of the walnut twig beetle, *Pityophthorus juglandis*, the vector of thousand cankers disease in North American walnut trees. PLoS One 10(2):e0118264. doi:10.1371/journal.pone.0118264

Schroeder LM (1990) Occurrences of insects in coniferous roundwood imported to Sweden from France and Chile. Bull OEPP 20:591–596

Scriven GT, Reeves EL, Luck RF (1986) Beetle from Australia threatens eucalyptus. California Agriculture, Oakland, CA, July–Aug, pp 4–6

Serdani M, Vlach J, Wallis K et al (2013) First report of *Geosmithia morbida* and *Pityophthorus juglandis* causing thousand cankers disease in butternut [online]. Plant Health Prog. doi:10.1094/PHP-2013-1018-01-BR. Available from http://www.plantmanagementnetwork.org/pub/php/brief/2013/butternut. Accessed 4 Mar 2015

Seybold SJ (2008) Monitoring invasive bark and woodboring beetles in periurban forests following wildfire. Forest Health Monitoring Fire Monitoring project no. WC-F-08-01, 2008–2010. http://fhm.fs.fed.us/em/funded/09/wc-f-08-01.pdf. Accessed 9 July 2015

Seybold SJ, Downing M (2009) What risk do invasive bark beetles and woodborers pose to forests of the western U.S.?: a case study of the Mediterranean pine engraver, *Orthotomicus erosus*, pp 111–134, In: Hayes JL, Lundquist JE (compilers) The Western bark beetle research group: a unique collaboration with forest health protection. Proceedings of a symposium at the 2007 Society of American Foresters conference, 23–28 Oct 2007, Portland. USDA Forest Service general technical report, GTR–PNW–784, 134 pp

Seybold SJ, Munson AS (2010) Implementing detection and trapping technology for the walnut twig beetle, *Pityophthorus juglandis*, in Idaho, Utah, and Southern California. Special Technology Development project no. R4-2011-01, 2011–2013

Seybold SJ, Tupy JL (1993) *Ernobius mollis* (L.) (Coleoptera:Anobiidae) established in California. Pan Pac Entomol 69:36–40

Seybold SJ, Huber DPW, Lee JC et al (2006a) Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. Phytochem Rev 5:143–178

Seybold SJ, Lee JC, Luxová A et al (2006b) Chemical ecology of bark beetles in California's urban forests. In: Hoddle MS, Johnson MW (eds) Proceedings of the 5th annual meeting of the California conference on biological control, Riverside, 27–28 July 2006, pp 87–94, 198 pp

Seybold SJ, Munson AS, Venette RC (2008a) Improved early detection for the Mediterranean pine engraver, *Orthotomicus erosus*, an invasive bark beetle. USDA Forest Service, Special Technology Development project no. R4-2008-01, 2008–2011

Seybold SJ, Paine TD, Dreistadt SH (2008b) Bark beetles: integrated pest management for home gardeners and landscape professionals, vol 7421, Agricultural National Resources pest notes. University of California Statewide IPM Program, Oakland, CA, 7 pp

Seybold SJ, Liu D-G, Venette RC et al (2010) Detection of low density invasive populations of the Mediterranean pine engraver, *Orthotomicus erosus*, in California with pheromone-baited traps, p 368. In: Parrotta JA, Carr MA(eds) Forests for the future: sustaining society and the environment. XXIII IUFRO World Congress; 23–28 Aug 2010, Seoul, Republic of Korea. Int For Rev 12(5):368, 508 pp. Commonwealth Forestry Association. www.cfa-international.org. (Abstract)

Seybold SJ, Coleman TW, Dallara PL et al (2012a) Recent collecting reveals new state records and the extremes in the distribution of the walnut twig beetle, *Pityophthorus juglandis* Blackman (Coleoptera: Scolytidae), in the United States. Pan Pac Entomol 88:377–380

Seybold SJ, King JA, Harris DR et al (2012b) Diurnal flight response of the walnut twig beetle, *Pityophthorus juglandis*, to pheromone-baited traps in two northern California walnut habitats. Pan Pac Entomol 88:231–247

Seybold SJ, Dallara PL, Hishinuma SM et al (2013a) Detecting and identifying the walnut twig beetle: monitoring guidelines for the invasive vector of thousand cankers disease of walnut. University of California Agriculture and Natural Resources, Statewide Integrated Pest Management Program, Oakland, CA, 13 Mar 2013, 13 pp. http://www.ipm.ucdavis.edu/PMG/menu.thousandcankers.html

Seybold SJ, Haugen D, O'Brien J et al (2013b) Thousand cankers disease. USDA Forest Service, Northeastern Area State and Private Forestry Pest Alert, NA-PR-02-10, originally published May, 2010, reprinted Aug 2010, Oct 2011, and Feb 2013, 2 pp. http://www.na.fs.fed.us/pubs/detail.cfm?id=5225. Accessed 31 Jan 2015

Seybold SJ, Dallara PL, Nelson LJ et al (2015) Methods of monitoring and controlling the walnut twig beetle, *Pityophthorus juglandis*. US Patent 9,137,990 B2, 12 pp. + 7 Figs., 22 Sept 2015

Siitonen J (1990) Potential forest pest beetles conveyed to Finland on timber imported from the Soviet Union. Silva Fenn 24:315–321

Smith LM (1932) The shot hole borer, vol 64, Circular (University of California Agricultural Extension Service). College of Agriculture, University of California, Berkeley, CA, 13 pp

Smith LM (1945) Control of the shot-hole borer, vol 4047, Leaflet. University of California, College of Agriculture, Agricultural Experiment Station, Berkeley, CA, 4 pp

Sokoloff A (1974) The biology of *Tribolium* with special emphasis on genetic aspects, vol 2. Clarendon, Oxford, UK, 610 pp

Solomon JD (1995) Guide to insect borers in North American broadleaf trees and shrubs, Agriculture Handbook No. 706. U.S. Department of Agriculture, Forest Service, Washington, DC, 735 pp

Švihra P (1987) Suitability of elm firewood to bark beetle attack stored under polyethylene sheeting. J Arboric 13:164–166

Švihra P (1998) An unusual attack pattern of *Scolytus multistriatus* beetles in Chinese elm. J Arboric 24:322–331

Švihra P, Koehler CS (1981) Attraction of flying *Scolytus multistriatus* to cut wood of three elm species in California. Environ Entomol 10:565–566

Švihra P, Volney WJA (1983) Effect of English, Siberian, and Chinese elms on the attack behavior and brood survival of *Scolytus multistriatus* (Coleoptera:Scolytidae). Can Entomol 115:513–522

Tisserat N, Cranshaw W, Leatherman D et al (2009) Black walnut mortality in Colorado caused by the walnut twig beetle and thousand cankers disease. Plant Health Prog. doi:10.1094/PHP-2009-0811-01-RS

Tisserat N, Cranshaw W, Putnam M et al (2011) Thousand cankers disease is widespread on black walnut, *Juglans nigra*, in the western United States. Online Plant Health Prog. doi:10.1094/PHP-2011-0630-01-BR

Tribe GD (1990) Phenology of *Pinus radiata* log colonization and reproduction by the European bark beetle, *Orthotomicus erosus* (Wollaston) (Coleoptera: Scolytidae) in the south-western Cape Province. J Entomol Soc South Afr 53:117–126

Tribe GD (1991a) Phenology of *Pinus radiata* log colonization by the red-haired pine bark beetle *Hylurgus ligniperda* (Fabricus) (Coleoptera: Scolytidae) in the south-western Cape Province. J Entomol Soc South Afr 54:1–7

Tribe GD (1991b) Phenology of three exotic pine bark beetle species (Coleoptera: Scolytidae) colonising *Pinus radiata* logs in the south-western Cape Province. South Afr For J 257:27–31

Tribe GD (1992) Colonisation sites on *Pinus radiata* logs of the bark beetles, *Orthotomicus erosus*, *Hylastes angustatus*, and *Hylurgus ligniperda* (Coleoptera: Scolytidae). J Entomol Soc South Afr 55:77–84

United States Geological Survey (USGS) (2014) Digital representations of tree species range maps from "Atlas of United States Trees" by Elbert L. Little, Jr. (and other publications). Available from http://esp.cr.usgs.gov/data/little/. Accessed 19 June 2015

University of California Integrated Pest Management Guidelines (UC-IPM) (2015) Shothole borer, *Scolytus rugulosus* on cherry, peach, and plum. UC ANR publications 3440, 3454, and 3462. http://www.ipm.ucdavis.edu/PMG/r105301611.html; http://www.ipm.ucdavis.edu/PMG/r602301511.html; and http://www.ipm.ucdavis.edu/PMG/r611302711.html Accessed 6 July 2015

University of Maryland Extension (2014) Thousand cankers disease: thousand cankers disease found in mid-Atlantic. Available from http://extension.umd.edu/ipm/thousand-cankers-disesase. Accessed 25 Aug 2014

USDA Forest Service (1993) Pest risk assessment of the importation of *Pinus radiata*, *Nothofagus dombeyi*, and *Laurelia philippiana* logs from Chile, vol 1517, Miscellaneous publication. U.S. Department of Agriculture, Forest Service, Washington, DC, 248 pp

USDA Forest Service (2002) New introduction: the red-haired bark beetle, *Hylurgus ligniperda* Fabricius (Coleoptera: Scolytidae), Pest alert NA-PR-03-02. U.S. Department of Agriculture, Forest Service, Northeastern Area, Washington, DC, 2 pp

USDA Forest Service (2015) Forest inventory and analysis. www.fs.fed.us/pnw/fia/statewide_results/ca.shtml. Accessed 4 Apr 2015

USDA Forest Service and APHIS (2000) Pest risk assessment for importation of solid wood packing materials into the United States, 275 pp

USDA Forest Service Hopkins U.S. System Index (HUSSI) (1929–1955). *Scolytus rugulosus* (Hopkins records Nos. 19352, 20901, 20902, 20913, 20931–20933, 21172, 37595) and *Xyleborinus saxeseni* (Hopkins records Nos. 15802, 18312, 33920) in California

Utley C, Cranshaw W, Seybold SJ et al (2009) Susceptibility of *Juglans* and *Carya* species to *Geosmithia*; a cause of thousand cankers disease [Abstract]. Phytopathol Suppl 99:S133

Utley C, Nguyen T, Roubtsova T et al (2013) Susceptibility of walnut and hickory species to *Geosmithia morbida*. Plant Dis 97:601–607. http://dx.doi.org/10.1094/PDIS-07-12-0636-RE, "First Look" posted 5 Dec 2012

Vandenberg NJ, Rabaglia RJ, Bright DE Jr (2000) New records of two *Xyleborus* (Coleoptera: Scolytidae) in North America. Proc Entomol Soc Wash 102:62–68

Venette RC, Walter AJ, Seybold SJ (2009) Comparing risks from native and exotic bark beetles to the health of Great Lakes forests. In: Proceedings Society of American Foresters 2008 annual meeting, Reno, NV. CD-ROM. Society of American Foresters, Bethesda, MD

Wagener WW, Mielke JL (1961) A staining-fungus root disease of ponderosa, Jeffrey, and pinyon pines. Plant Dis Rep 45:831–835

Walter AJ, Venette RC, Kells SA et al (2010a) Boring in response to bark and phloem extracts from North American trees does not explain host acceptance by the Mediterranean pine engraver, *Orthotomicus erosus* (Coleoptera: Scolytidae). Environ Entomol 39:661–669. doi:10.1603/EN09320

Walter AJ, Venette RC, Kells SA et al (2010b) Walking response of the Mediterranean pine engraver, *Orthotomicus erosus*, to novel plant odors host in a laboratory olfactometer. J Insect Behav 23:251–267. doi:10.1007/s10905-010-9211-2

Wang Z-T (1992) *Scolytus schevyrewi* Semenov. In: Xiao G (ed) Forest insects of China, 2nd edn. (trans: Dr. Houping Liu). China Forum Publishing House, Beijing, China, pp 633–634

Wang F, Chen S-L, Zhou W-C (2005) Recognition and diagnosis of *Hylurgus ligniperda*. Plant Quarantine 20:30–31 (in Chinese)

Webber JF (1990) The relative effectiveness of *Scolytus scolytus, S. multistriatus* and *S. kirschii* as vectors of Dutch elm disease. Eur J For Pathol 20:184–192

Webber JF (2000) Insect vector behavior and the evolution of Dutch elm disease. In: Dunn CP (ed) The elms: breeding, conservation, and disease management. Kluwer, Boston, MA, pp 47–60

Webber JF (2004) Experimental studies on factors influencing the transmission of Dutch elm disease. Investig Agraria: Sistemas y Recursos Forestales 13:197–205

Webber JF, Brasier CM (1984) Transmission of Dutch elm disease: a study of the processes involved. In: Anderson J, Rayner ADM, Walton D (eds) Invertebrate-microbial interactions. Cambridge University Press, Cambridge, UK, pp 271–306

Weber BC, McPherson JE (1983) Life history of the ambrosia beetle *Xylosandrus germanus* (Coleoptera: Scolytidae). Ann Entomol Soc Am 76:455–462

Wei H-D, Shao P-Z (1991) Methods for quarantine of imported wood infested with *Hylurgus ligniperda*. Plant Quarantine 5:199–200 (in Chinese)

Westcott RL, Haines RD, Hishinuma SM et al (2016) *Chrysobothris analis* LeConte, 1860 (Coleoptera: Buprestidae) discovered in California with notes on *Chrysobothris wintu* Wellso & Manley, 2007. Pan Pac Entomol (In Press)

Whitehead PF, Zach P, Kulfan J et al (2000) *Dactylotrypes longicollis* (Wollaston 1864) (Coleoptera, Scolytidae) introduced to the Slovak Republic. J Pest Sci 73:17–18

Wiggins GJ, Grant JF, Lambdin PL et al (2014) Discovery of walnut twig beetle, *Pityophthorus juglandis*, associated with forested black walnut, *Juglans nigra*, in the eastern U.S. Forests 5:1185–1193

Wingfield MJ, Marasas WFO (1980) *Ceratocystis ips* associated with *Orthotomicus erosus* (Coleoptera: Scolytidae) on *Pinus* spp. in the Cape Province of South Africa. Phytophyl 12:65–69

Wingfield MJ, Strauss LA, Tribe GD (1985) Fungi associated with three pine bark beetles in South Africa. Phytopathology 75:1338

Wingfield MJ, Capretti P, MacKenzie M (1988) *Leptographium* spp. as root pathogens of conifers: an international perspective. In: Harrington TC, Cobb FW Jr (eds) Leptographium root diseases on conifers. APS Press, St. Paul, MN, pp 113–128

Wood SL (1964) New species of North American *Pityophthorus* Eichhoff (Coleoptera: Scolytidae). Great Basin Natl 24:59–70

Wood SL (1971) New species of bark beetles (Coleoptera: Scolytidae) from western North America. Great Basin Natl 31:69–76

Wood SL (1976) New synonymy and new species American bark beetles (Coleoptera: Scolytidae). Great Basin Natl 36:347–365

Wood SL (1977) Introduced and exported American *Scolytidae* (*Coleoptera*). Great Basin Natl 37:57–74

Wood SL (1982) The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Natl Mem 6:1–1359

Wood SL (1992) Nomenclature changes and new species in Platypodidae and Scolytidae (Coleoptera), Part II. Great Basin Natl 52:78–88

Wood SL (2007) Bark and ambrosia beetles of South America (Coleoptera, Scolytidae). Brigham Young University, M.L. Bean Life Science Museum, Provo, UT, 900 pp

Wood SL, Bright DE Jr (1992) A catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: taxonomic index, vol 13, Great Basin naturalist memoirs. Brigham Young University, Provo, UT, 1553 pp

Wood DL, Stark RW (1968) The life history of *Ips calligraphus* (Coleoptera: Scolytidae) with notes on its biology in California. Can Entomol 100:145–151

Yaghmour MA, Nguyen TL, Roubtsova TV et al (2014) First report of Geosmithia morbida on English walnut and its Paradox rootstock in California. Plant Dis 98:1441 (published online at http://dx.doi.org/10.1094/PDIS-06-14-0569-PDN)

Yang Z-Q (1996) Parasitic wasps on bark beetles in China. Science Press, Beijing

Yang X-J, An Y-L (2002) Diagnosis of *Hylurgus ligniperda* in imported pines during interceptions at ports of entry. Plant Quarantine 16:288–289 (in Chinese)

Yin H-F, Huang F-S (1992) Scolytidae: *Orthotomicus erosus* Wollaston. In: Peng J-W, Liu Y-Q (eds) Iconography (atlas) of forest insects in Hunan China. Hunan Science and Technology Press, Changsha, p 635. (in Chinese)

Yin H-F, Huang F-S, Li Z-L (1984) Economic insect fauna of China, Fasicle 29, Coleoptera: Scolytidae. Science Press, Beijing, China, pp 138–139. (in Chinese)

Zhou X-D, de Beer ZW, Wingfield BD et al (2001) Ophiostomatoid fungi associated with three pine-infesting bark beetles in South Africa. Sydowia 53:290–300

Zhou X-D, Burgess T, de Beer ZW et al (2002a) Development of polymorphic microsatellite markers for the tree pathogen and sapstain agent, *Ophiostoma ips*. Mol Ecol Notes 2:309–312

Zhou X-D, de Beer ZW, Wingfield BD et al (2002b) Infection sequence and pathogenicity of *Ophiostoma ips*, *Leptographium serpens* and *L. lundbergii* to pines in South Africa. Fung Divers 10:229–240

Zhou X-D, de Beer ZW, Ahumada R et al (2004) *Ophiostoma* and *Ceratocystiopsis spp*. associated with two pine-infesting bark beetles in Chile. Fung Divers 15:261–274

Zondag R (1979) Breeding of the clerid *Thanasimus formicarius* for the control of the bark beetles *Hylastes ater* and *Hylurgus ligniperda* in New Zealand. N Z J For Sci 9:125–132

Zwolinski JB, Swart WJ, Wingfield MJ (1995) Association of *Sphaeropsis sapinea* with insect infestation following hail damage of *Pinus radiata*. For Ecol Manag 72:293–298

Chapter 22
Goldspotted Oak Borer in California: Invasion History, Biology, Impact, Management, and Implications for Mediterranean Forests Worldwide

Tom W. Coleman and Steven J. Seybold

Abstract In 2008, the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), was first linked to elevated levels of oak mortality in southern California (CA), but it appears to have impacted oak woodlands and mixed conifer forests across all land ownerships in this region for nearly two decades. This unexpectedly damaging indigenous exotic phloem- and wood-boring pest is hypothesized to have been introduced in the late 1990s to early 2000s *via* infested firewood from southeastern Arizona to San Diego County, CA. The life history and impact of *A. auroguttatus* on oaks were unknown in its native range prior to 2008, and confusion surrounding its taxonomic placement further complicated the status of this emerging pest problem. The primary tree species infested in CA are coast live oak, *Quercus agrifolia* Née, and California black oak, *Quercus kelloggii* Newb. As the invaded range expands, *A. auroguttatus* may interact with the broader community of other exotic and native pests of oaks in CA and continue to cause ecological and economic impacts. Early detection of *A. auroguttatus* is an imperative prerequisite for managing this invasive species and preventative and suppression treatments have been developed to protect high-value oaks. The movement of infested firewood will likely result in additional satellite infestations across the range of susceptible hosts from Baja California Norte, Mexico to southern Oregon. *Agrilus auroguttatus* currently represents the most significant insect threat to oaks in CA, but, if they are introduced, other European and eastern North American *Agrilus* species also threaten these Mediterranean forest ecosystems.

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22.1 Threats to Oak Woodlands in Mediterranean Ecosystems

Oak savannas and woodlands are ecologically and economically vital components of Mediterranean forest ecosystems in northern Africa, southern Europe, and southwestern North America. Deciduous and evergreen oak species dominate and co-dominate the canopy cover in flood plains, riparian corridors, coastal habitats, semi-arid foothills and mixed-conifer forests in these regions (Brasier and Scott 1994; Pavlik et al. 1996). These savannas and woodlands provide habitat and a food source for wildlife, and they support grazing (Brasier 1996; Pavlik et al. 1996). Wood or oak bark from these Mediterranean forest ecosystems are valued for lumber, fuel, and cork [e.g., cork oak, *Quercus suber* L. (Section *Cerris*)] (Brasier 1996).

Since the end of the nineteenth century, oak declines impacting several species have been reported from Central Europe and the Mediterranean region (Brasier and Scott 1994; Gibbs and Greig 1997; Fuhrer 1998; Thomas et al. 2002; Jurc et al. 2009; Sallé et al. 2014). A complex of abiotic and biotic factors, including air pollution, drought stress, flooding, warming climate, frost damage, defoliation by insects, bark beetles, wood borers, pathogenic fungi, bacterial infection, and anthropogenic disturbances have been suggested as catalysts or contributors in oak declines in Europe (Brasier and Scott 1994; Fuhrer 1998; Moraal and Hilszczański 2000; Thomas et al. 2002; Jurc et al. 2009; Sallé et al. 2014; Brown et al. 2015). In general, exotic insects and pathogens have not been reported as primary aggressors in these European oak declines. However, a range expansion of the oak splendor beetle, *Agrilus biguttatus* (F.) (Coleoptera: Buprestidae), may be a new component of oak decline in Europe (Gibbs and Greig 1997; Moraal and Hilszczański 2000; Jurc et al. 2009), and *Phytophthora cinnamomi* Rands (Pythiales: Pythiaceae), an exotic root pathogen, has been linked to oak decline in the Iberian region (Brasier et al. 1993; Thomas et al. 2002). In the oak woodlands of California (CA), where a Mediterranean climate prevails in North America, oak declines have not been a common occurrence historically. However, over the last several decades widespread oak mortality along the central coast of CA and north to Oregon has been associated with infection of red oaks (*Quercus* section *Lobatae*, Nixon 1993; Manos et al. 1999) by *Phytophthora ramorum* Werres et al., the causal agent of sudden oak death (Rizzo and Garbelotto 2003; Grünwald et al. 2008, 2012). Urbanization, and wildfire are also threatening deciduous and evergreen oak species in CA oak savannas and woodlands.

22.2 Indigenous Exotic Species

The number of non-indigenous (alien, exotic) forest insect species continues to rise in North America commensurate with increasing levels of international trade (Haack 2006; Langor et al. 2009; Klepzig et al. 2010), and phloem- and wood-boring species have increased dramatically within the United States of America (USA) (Aukema et al. 2010). The establishment and impact of non-indigenous species in naïve ecosystems may depend on several factors, including the size of the founding population, absence of co-evolved natural enemies, insufficient plant resistance, and absence of competitors for host resources (Liebhold et al. 1995; Brockerhoff et al. 2006). The spread of non-indigenous insects is dictated by population growth and dispersal, but the ultimate invaded range of a species is also dictated by the available ecological *niche* and accessibility of habitats suitable for existing populations (Liebhold et al. 1995; Venette et al. 2010). Oceans, deserts, and mountain ranges have acted as natural barriers to limit the spread of populations and influence species divergence and speciation (Mayr 1963). The movement of *indigenous* species across these natural barriers into naïve ecosystems *via* range expansion or human-assisted dispersal can also result in urban tree and forest management concerns. The organisms that partake in this phenomenon have been referred to as "indigenous exotic" or "intracontinental invasive" species (Dodds et al. 2010; Coleman and Seybold 2011).

In the USA, examples of indigenous exotic forest insects include the Mexican soapberry borer, *Agrilus prionurus* Chevrolat (Coleoptera: Buprestidae) (Billings and Pase 2008); the bronze birch borer, *Agrilus anxius* Gory (Carlos et al. 2002); two other flatheaded borers, *Chrysobothris costifrons costifrons* Waterhouse, and *C. analis* LeConte (Basham et al. 2015; Westcott et al. 2015); the locust borer, *Megacyllene robiniae* (Forster) (Coleoptera: Cerambycidae) (Galford 1984); the longhorned beetle, *Neospondylis upiformis* (Mannerheim) (Cerambycidae) (Smith and Hurley 2005); the sixspined ips, *Ips calligraphus* (Germar) (Wood and Stark 1968), the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Dodds et al. 2010), the walnut twig beetle, *Pityophthorus juglandis* Blackman (Seybold et al. 2013) (all Coleoptera: Scolytidae) (Bright 2014); and the Nantucket pine tip moth, *Rhyacionia frustrana* (Scudder) (Lepdioptera: Tortricidae) (Yates et al. 1981). The fir bark beetle, *Polygraphus proximus* Blandford (Scolytidae) (Baranchikov et al. 2010) and *A. biguttatus* (Pederson and Jørum 2009), are international examples of "indigenous exotics" in western Eurasia and Europe, respectively. The transportation of some of these species has been attributed to discrete pathways of trade within the nursery industry and movement of raw wood materials, whereas others have undergone more continuous range expansions from historical collection records that had been defined by the native distributions of their hosts. Tree injury and mortality associated with these species may be restricted to their native hosts in new ecosystems due to ornamental or off-site plantings. However, some species may colonize and injure novel hosts in the new habitats.

22.3 The Goldspotted Oak Borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae)

In 2004, the goldspotted oak borer, *A. auroguttatus*, was first detected in San Diego Co., CA, approximately 670 km from its native historic range in southeastern Arizona (AZ), USA, representing another example of an indigenous exotic species

(Westcott 2005) (Fig. 22.1). The population has since spread to Riverside, Orange, and Los Angeles Cos., CA (Jones et al. 2013; Coleman et al. 2015). The spread of the established population in CA can likely be attributed to natural dispersal by the beetle and movement of firewood cut from infested trees (Coleman and Seybold 2011).

We hypothesized that infested firewood was also likely the pathway by which *A. auroguttatus* was introduced originally into southern CA (Coleman and Seybold 2008b, 2011). Infested firewood has been associated with the movement of other exotic species in the USA, including the emerald ash borer, *A. planipennis* Fairmaire (Haack et al. 2010). It is less likely that *A. auroguttatus* has expanded its range westward into CA through natural dispersal. *Agrilus auroguttatus* would have had to cross the natural barriers of the Mojave and Sonoran Deserts, which bisect CA and AZ and extend from southern Nevada to Sinaloa, Mexico. Annual plant species and low shrubs dominate these deserts (Shreve and Wiggins 1964), thus isolating the oak hosts of *A. auroguttatus* in each region. Differences between the habitats in CA and AZ are not restricted solely to plant species assemblages, but also extend to other *Agrilus* and the subcortical community of other wood-boring insect species on oaks (Coleman and Seybold 2011). Furthermore, the rainfall regimes are dissimilar between the two regions (Westcott 2005). Arizona is characterized by monsoonal precipitation with rainfall occurring primarily during the summer months, whereas CA is characterized by precipitation that falls primarily during the winter months.

Since 2002, elevated levels of oak mortality occurred continuously in eastern San Diego Co. (USDA FHM 2014). However, *A. auroguttatus* was not linked to tree

Fig. 22.1 Goldspotted oak borer, *Agrilus auroguttatus*, adults feeding on foliage of coast live oak, *Quercus agrifolia*

injury and mortality until 2008 in San Diego Co., CA (Coleman and Seybold 2008a, b). For years oak mortality was thought to be associated with drought, and referred to colloquially as “oak croak,” following several failed investigations to associate the continuing tree mortality with infection by pathogens. Coleman et al. (2011) reported that old growth oaks had the most favorable water status when compared to smaller and mature oaks in the uninfested and infested areas of San Diego Co. Thus, although this largest size class of oaks typically showed the highest probability of infestation by *A. auroguttatus*, these oaks did not appear to be under drought stress. Furthermore, in the same study, early summer plant water status (e.g., branchlet xylem water potential and water use efficiency) was similar for uninfested and newly infested trees, suggesting that *A. auroguttatus* was not pre-selecting drought-stressed trees. It appears that drought stress is not required for *A. auroguttatus* injury and mortality in CA, but drought may increase host susceptibility to this invasive species.

22.4 History of *Agrilus auroguttatus* in Its Native Region and Similar Species

The taxonomic status of *A. auroguttatus* has been in a state of flux for decades. Schaeffer (1905) initially described *A. auroguttatus* from populations in southeastern AZ, but Hespenheide (1979) synonymized *A. auroguttatus* with a similar species, *A. coxalis* Waterhouse, collected only from central and southern Mexico and Guatemala (Fig. 22.2). Following discovery of the invasive population in CA (Westcott 2005; Coleman and Seybold 2008b) and morphological scrutiny of the specimens, Hespenheide and Bellamy (2009) assigned subspecific status to the populations from AZ/CA (*Agrilus coxalis auroguttatus* Schaeffer) and Mexico/Guatemala (*Agrilus coxalis coxalis* Waterhouse). Hespenheide et al. (2011) returned *A. auroguttatus* and *A. coxalis* to species status based on the morphology of the male genitalia. The common name of Mexican goldspotted oak borer has been assigned to *A. coxalis*. Prior to 2008, no life history information was known about either *A. auroguttatus* in AZ or *A. coxalis* in Mexico (Furniss and Carolin 1977; Cibrian et al. 1995; Solomon 1995). Tree mortality was never associated with these two species in their native ranges until the discovery of *A. auroguttatus* in CA.

Molecular analyses of mitochondrial and nuclear ribosomal DNA (mtDNA and rDNA) supported the morphologically-based species status of *A. auroguttatus* and *A. coxalis* (Coleman et al. 2012b). The COI (mtDNA) gene sequences of *A. coxalis* from southern Mexico differed by 11 % from the homologous sequences from *A. auroguttatus* from AZ and CA (Coleman et al. 2012b). Additional analyses revealed that the invasive CA population of *A. auroguttatus* was similar to AZ populations, sharing two mtDNA haplotypes (Lopez et al. 2014c). In addition, examination of the D2 domain of 28S rDNA sequences revealed that the AZ and CA populations were identical, whereas sequences from the Mexican *A. coxalis* population differed from sequences from the AZ–CA populations by 8 base pairs (Coleman et al.

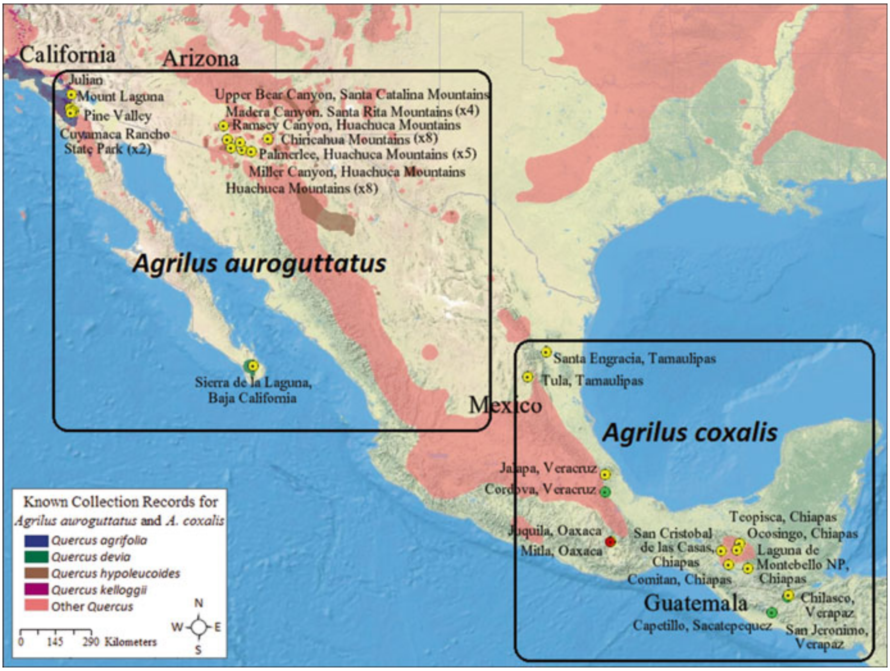

Fig. 22.2 Recorded distributions of the goldspotted oak borer, *Agrilus auroguttatus*, the Mexican goldspotted oak borer, *A. coxalis*, and associated oaks, *Quercus* sp., in North and Central America (Coleman and Seybold 2011). Previous collection sites are noted in *yellow*; the lectotype and paralectotypes for *A. coxalis* are designated in *red* and *green*, respectively. Locality data were derived from the literature and from a survey of museum specimens (Modified from Coleman and Seybold 2008b). Extreme southern collection localities for *A. coxalis* (San Lorenzo, Zacapa, San Lorenzo, San Marcos, Guatemala; and Montaña del Malacate, Olancho, Honduras) are not depicted

2012b). Additional surveys and collections of *A. auroguttatus* across the mountain ranges of the Coronado National Forest in southeastern AZ further confirmed that all of the populations were *A. auroguttatus* and that populations from the Dragoon Mountains in AZ may be the source of the populations in southern CA (Lopez et al. 2014c) (Fig. 22.3).

22.5 *Agrilus auroguttatus* Life History and Biology

Agrilus auroguttatus adults are a dull metallic green with golden-colored pubescent spots on the surface of the thorax and abdomen (Fig. 22.1). Adults are 9.4 (±0.1) mm long and 2.1 (±0.1) mm wide (both mean ± s.e.) (Coleman and Seybold 2008b). Adult males can be distinguished from females by the presence of a median ventral groove on the first abdominal segment, and females are generally larger than males (Coleman and Seybold 2010). Adults feed minimally along the margins of oak

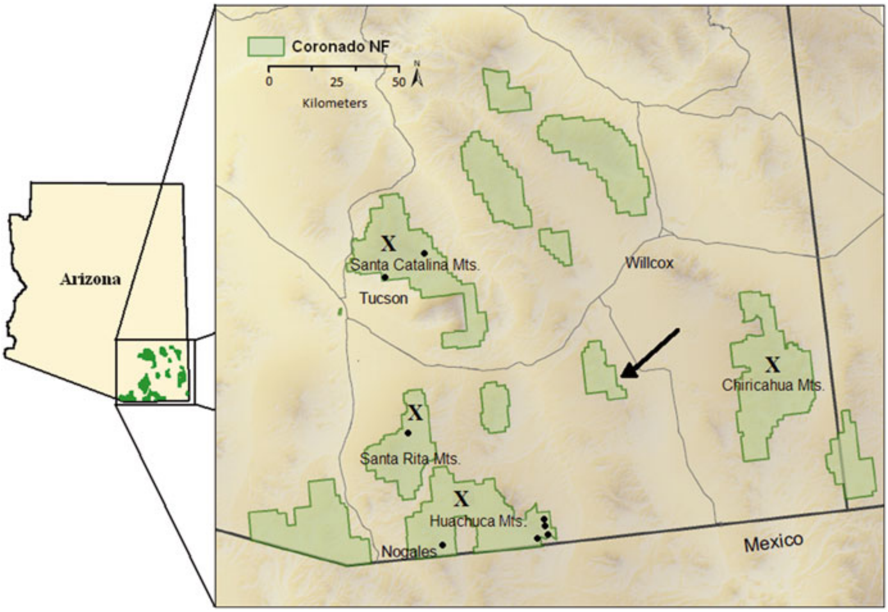

Fig. 22.3 Historical collection records of the goldspotted oak borer, *Agrilus auroguttatus*, from four mountain ranges (Santa Catalina, Santa Rita, Huachuca, and Chiricahua) in the Coronado National Forest in southeastern Arizona (Modified from Coleman and Seybold 2011). General collection localities are denoted by an X, whereas specific locations from collection labels are indicated by *black dots* (•). *Arrow*: Dragoon Mountains-the putative origin of the population of *A. auroguttatus* that has been introduced into California (Lopez et al. 2014c)

leaves, and females must feed to become sexually mature. Females, when paired with a single male, become sexually mature after 8 days with a food source of water and leaves; can have an ovipositional period of 43.6 (±7.4) days; survive for 72.1 (±6.3) days in a laboratory setting; and lay approximately 200 eggs (Lopez and Hoddle 2014). Adult males can survive for 37.1 (±6.0) days under the same conditions. As is the case with other species of *Agrilus*, adult *A. auroguttatus* likely mate in the canopy of host trees or along the main stem (Carlson and Knight 1969; Haack and Acciavatti 1992; Lelito et al. 2007; Rodriguez-Saona et al. 2007). Females of *A. auroguttatus* lay eggs from June to September singly or in clusters on the bark surface or in bark cracks along the main stem and larger branches of oak trees (Flint et al. 2013). Adults begin to emerge in late May and the main flight period extends to September (Coleman et al. 2014a). Peak flight occurs from late June to early July in southern CA. This period of adult activity has been supported by collection dates on numerous specimen records (Coleman and Seybold 2011) and seasonal emergence from infested wood (Jones et al. 2013 and see Management-monitoring techniques below). *Agrilus auroguttatus* is believed to be univoltine, but the life cycle may take 2 years in healthier host trees (Flint et al. 2013; Haavik et al. 2013). In flight mill studies, adults flew a mean distance of 790 m in 24 h (Lopez et al. 2014b).

Eggs of *A. auroguttatus* are tan in color, oval, and less than 0.25 mm in diameter (Flint et al. 2013). Eggs have rarely been observed in the field due to their small size and the inconspicuous oviposition sites. Larvae hatch from eggs approximately 10–15 days after oviposition (Lopez and Hoddle 2013) and likely complete four larval instars (Haavik et al. 2013). Larvae are white in color and legless; they possess C-shaped spiracles along the lateral sides of the abdomen, and two urogomphi at the tip of the abdomen (Fig. 22.4). First instar larvae are about 2 mm long, whereas fourth instar larvae are 20 mm long and 4 mm wide (Flint et al. 2013). After hatching, larvae tunnel through the bark and phloem to the interface of the phloem and xylem. Feeding occurs primarily in this cambial region, and the larvae injure the cambium and phloem

Fig. 22.4 Larva of goldspotted oak borer, *Agrilus auroguttatus*, feeding at the phloem/xylem interface of California black oak, *Quercus kelloggii*, in southern California. This feeding destroys the meristematic cambium and causes necrosis of the phloem (*black stained areas*)

and score the outer xylem (Fig. 22.4). Immature larvae are found primarily from late summer to early fall feeding on the xylem surface in CA (Haavik et al. 2013). Larvae rarely feed in the xylem. Mature larvae return to the outer phloem where they construct a pupal cell just under the outer bark. Mature larvae, or prepupae, constrict into a hairpin configuration in the pupal cell where they remain until the following spring. Found throughout most of the year (mid-October to mid-June) when compared to the other life stages mature larvae/prepupae can be sampled easily from trees to verify infestation or to obtain live material for laboratory studies. Pupation begins to occur during the spring to early summer in southern CA. Pupae are similar in size to adults and white in color until the cuticle begins to melanize and sclerotize.

22.6 Host Range of *Agrilus auroguttatus*

Field observations in CA have recorded that *A. auroguttatus* can attack and reproduce in coast live oak, *Q. agrifolia* Née, California black oak, *Q. kelloggii* Newb., canyon live oak, *Q. chrysolepis* Liebm, and Engelmann oak, *Q. engelmannii* Greene. Red oaks (section *Lobatae*) were killed more frequently by *A. auroguttatus* (*Q. agrifolia*: 91 % and *Q. kelloggii*: 88 %) than white oaks (*Q. engelmannii*: 0 %) in CA (Coleman et al. 2012a). *Quercus chrysolepis*, a goldencup oak, which is a taxonomically intermediate oak species (subgenus *Quercus*, section *Protobalanus*), has been injured and killed by *A. auroguttatus*, but mortality was associated less frequently with this species (60 %) than with the red oaks. We have hypothesized that red oaks are much more susceptible to injury by *A. auroguttatus* with phloem thickness, bark structure, and/or host chemistry as factors that contribute to this susceptibility (Coleman and Seybold 2011). Interior live oak, *Q. wislizenii* A.DC., and Shreve oak, *Quercus parvula* Greene var. *shrevei* (C.H. Mull.) Nixon, two red oak species that are present farther north in CA, are likely to be susceptible to *A. auroguttatus* and may experience elevated levels of tree mortality as the invaded range of *A. auroguttatus* expands. Numerous red and white scrub oak (shrub-like) species occur in the infested area of San Diego Co. and throughout CA, but injury from *A. auroguttatus* has never been recorded on these species. These scrub oak species rarely exceed 12.5 cm diameter at breast height (dbh), which is a key threshold of susceptibility for red oaks to attack by *A. auroguttatus* (see below).

In AZ, the native hosts of *A. auroguttatus* are Emory oak, *Quercus emoryi* Torrey, and silverleaf oak, *Q. hypoleucoides* A. Camus (both section *Lobatae*). The range of these species extends along the southern edge of the Mogollon Rim in central AZ, east into southern New Mexico, and south into Sonora and Chihuahua, Mexico (USDA Forest Service 2009). *Agrilus auroguttatus* prefers to colonize these red oaks more than the white oaks that grow in this region, i.e., AZ white oak, *Q. arizonica* L., and gray oak, *Q. grisea* Liebm. (subgenus *Quercus*, section *Quercus*) (Coleman and Seybold 2011; Haavik et al. 2014a). In southern Mexico, *A. coxalis* was found killing *Q. peduncularis* Née, a white oak. Only low levels of tree mortality have been associated with these sibling species of *Agrilus* in their respective native regions (Coleman et al. 2012a; 2015).

In laboratory host range tests, *A. auroguttatus* was capable of completing larval development in cut logs of *Q. agrifolia*, *Q. kelloggii*, *Q. wislizenii*, *Q. chrysolepis*, *Q. suber*, valley oak, *Q. lobata* Née, and blue oak, *Q. douglasii* Hook. & Arn. (Haavik et al. 2014b) (Fig. 22.5). Gallery construction by *A. auroguttatus* larvae was significantly greater on red oaks when compared to white oaks, to *Cerris* species (*Q. suber* only), and to goldencup species. This supports the hypothesis of greater risk for red oak species than white oak species, goldencup species, and ornamental species in the section *Cerris*. Adult no-choice feeding bioassays on foliage resulted in no statistically significant differences for female longevity, days until fecund, total fecundity, daily oviposition, proportion of eggs melanized, and proportion of eggs hatched across red, white, goldencup, and *Cerris* oak species and a non-host species, white alder, *Alnus rhombifolia* Nutt. (Haavik et al. 2014b). Chen et al. (2013) showed that adult *A.*

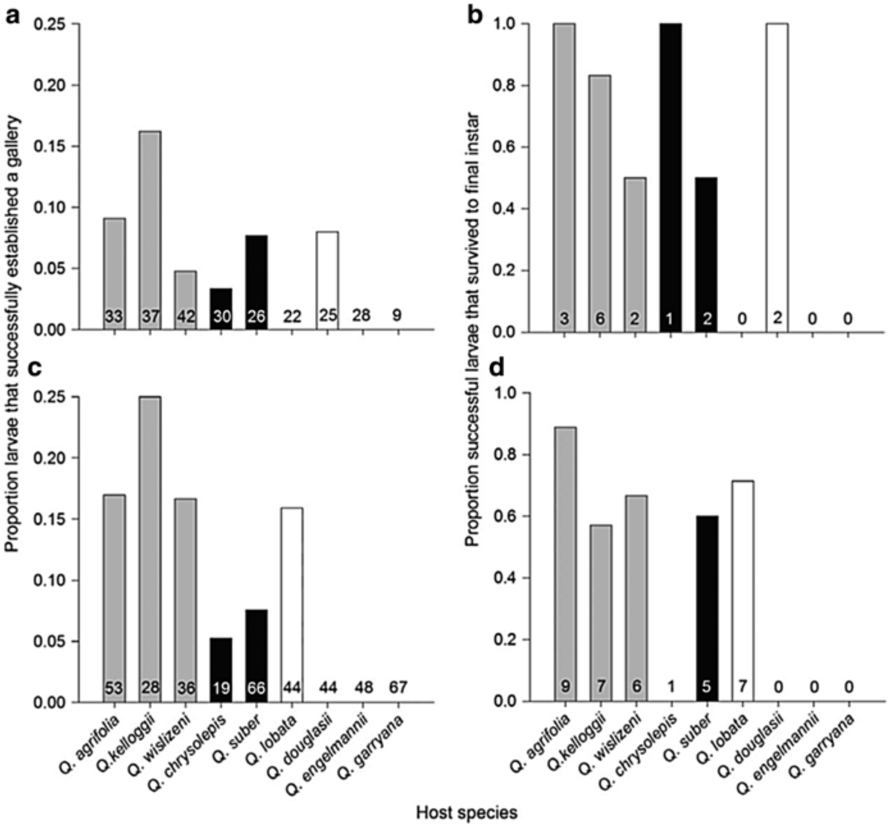

Fig. 22.5 Measurements of host suitability for *Agrilus auroguttatus* grouped by oak species from laboratory tests conducted in 2010 (**a** and **b**) and 2011 (**c** and **d**) (Reproduced from Haavik et al. 2014b). *Gray bars* represent oaks in Section *Lobatae*; *black bars* represent oaks in other sections (*Quercus chrysolepis* Section *Protobalanus*, *Q. suber* Section *Cerris*); and *white bars* represent oaks in Section *Quercus*. A–D were analyzed separately; no difference was significant. Sample sizes are indicated at the base of the bars

auroguttatus consumed more foliar weight and foliar area of *Q. kelloggii* than *Q. agrifolia*, *Q. chrysolepis*, and *Q. engelmannii* in no-choice and dual choice tests, suggesting that *A. auroguttatus* prefers foliage from this red oak species over the other three oak species. Analysis of four macronutrients (nitrogen, sulfur, phosphorus, and potassium) and two micronutrients (zinc and copper) suggests that these nutrients might be directing preferential feeding of *A. auroguttatus* (Chen et al. 2013). *Quercus suber*, holm oak, *Q. ilex* L., and southern live oak, *Q. virginiana* Mill., are frequently planted as ornamental trees in CA; however, we hypothesize these species will be at low risk to *A. auroguttatus* injury and mortality since they are not in the red oak section.

22.7 Injury Symptoms Associated with *Agrilus auroguttatus*

External symptoms of tree injury associated with *A. auroguttatus* can include premature twig dieback and thinning in the crown; D-shaped emergence holes through the bark surface of the stem and larger branches; woodpecker foraging damage to the bark surface; and bark staining or weeping and cracking (Coleman et al. 2011; Hishinuma et al. 2011). As tree injury from *A. auroguttatus* becomes more extensive, crown thinning and dieback worsen progressively, generally from the upper branches to the lower branches in the crown. In the infested areas of CA, severe crown thinning on host oak species has been associated frequently with extensive injury from *A. auroguttatus* larvae and imminent tree mortality. Adult feeding does not likely contribute to crown thinning and is rarely detectable in the field. Distinct twig and branch mortality (i.e., flagging) is not a common injury symptom of *A. auroguttatus* and is frequently associated with injury by other insects (Flint et al. 2013).

Adult emergence of *Agrilus* species leaves a characteristic D-shaped hole (4 mm wide for *A. auroguttatus*) in the outer bark. Emergence holes can be found from the root collar to the larger branches (>20.3 cm in diameter) on host oaks, but the majority of holes are found primarily along the lower main stem (Haavik et al. 2012b). *Agrilus auroguttatus* is the only *Agrilus* species that infests the main stem and larger branches of oaks in CA, making this injury symptom diagnostic for this species in CA (Coleman et al. 2011). Furthermore, no other *Agrilus* species have been reared from *A. auroguttatus*-infested host material in AZ and CA (Coleman and Seybold 2011; Coleman et al. 2012b; Jones et al. 2013). Emergence holes from *A. auroguttatus* occur randomly on the lower bole (<1.52 m) and three random samples collected in 0.09 m^2 quadrats can provide a reliable estimate of injury from this species (Haavik et al. 2012b). The density of *A. auroguttatus* emergence holes in declining oaks was significantly greater than the density of these holes from other wood borers in CA, but this was not the case in its native region of AZ (Haavik et al. 2014a). Secondary wood borers and bark beetles are frequently encountered on *A. auroguttatus*-infested trees once severe tree injury or areas of the phloem and cambium have been patch-killed. Attack from these secondary insects can be distinguished from *A. auroguttatus* by the size and shape of the entrance and emergence holes, the location of injury on the tree, and the density of attacks (Flint et al. 2013).

Bark removed by acorn woodpeckers, *Melanerpes formicivorus* (Swainson), and Nuttall's woodpeckers, *Picoides nuttallii* (Gambel) (both Piciformes: Picidae) as they forage for prepupae in the outer phloem is a frequent sign of infestation in CA (Coleman et al. 2011). Bark removal by woodpeckers foraging in search of *A. auroguttatus* larvae is shallow and penetrates only to the outer phloem. Foraging by other woodpecker species penetrates more deeply to the xylem surface where other wood-boring insect species occur. Woodpecker foraging for *A. auroguttatus* follows the larval gallery in the outer phloem to the pupal cell where the predation occurs. Exposed brick-red phloem of coast live oaks contrasts with the grey outer bark, making this injury symptom very visible at first. The red coloration of the phloem fades to a black color as time passes. The impact of predation from woodpeckers is unknown in CA, but may contribute significantly to reducing population densities of *A. auroguttatus* in nesting areas.

Bark staining or weeping can appear as black patches, wet staining, or red oozing sap on the bark exterior (Hishinuma et al. 2011; Flint et al. 2013). The size of stained bark sections can vary greatly on the bark exterior from <2.4 to 15.2 cm^2 patches. Pockets of sap may accumulate under the bark where the phloem and cambium have been killed by extensive larval feeding. Bark staining is not always present on *A. auroguttatus*-infested trees, but is observed more frequently after severe injury from the beetle has occurred. An ensemble of secondary fungi has been associated with these stained areas in and out of the *A. auroguttatus* infested area in CA (Lynch et al. 2014). The bark often cracks after extensive larval feeding has killed the phloem and cambium and the tissue desiccates under the bark. Crown thinning and bark staining are a general response to declining tree health and do not necessarily signify *A. auroguttatus* infestation in the native and introduced regions. Additional evidence of *A. auroguttatus* infestation must be found to verify injury from this phloem-boring species.

A health rating system was developed based on the external injury symptoms of *A. auroguttatus*, and was disseminated to land managers, pest specialists, and private homeowners to assist with management decisions and to quantify tree injury (Hishinuma et al. 2011) (Fig. 22.6). Crown thinning is ranked on a scale of 1–5 (1: full, healthy crown [0 % leaf loss]; 2: minor twig dieback and/or light thinning [10–25 % leaf loss]; 3: moderate thinning and twig dieback [25–50 % leaf loss]; 4: severe dieback to larger branches [>50 % leaf loss]; and 5: tree is dead); D-shaped emergence hole density is ranked on a scale of 1–3 (1: <10 emergence holes; 2: 10–25 emergence holes, 3: >25 emergence holes on the lower 2 m of the main stem); bark staining is ranked on a scale of 1–4 (1: 1–5 stained areas, 2: 6–10 stained areas, 3: >10 stained areas, and 4: bark cracking is evident on the lower 2 m of the main stem); and the presence or absence of woodpecker foraging damage is also noted. Increases in emergence hole densities were correlated with crown thinning and dieback and the change in density of emergence holes was significantly greater on trees with severe crown thinning (rating of "4," Hishinuma et al. 2011) and recently killed (<1 year) trees (Coleman et al. 2011, See Figure 5.B in Coleman et al. 2014a). Total count of D-shaped emergence holes on the main stem (<2 m) has been the most practical measure of the extent of tree injury from *A. auroguttatus*.

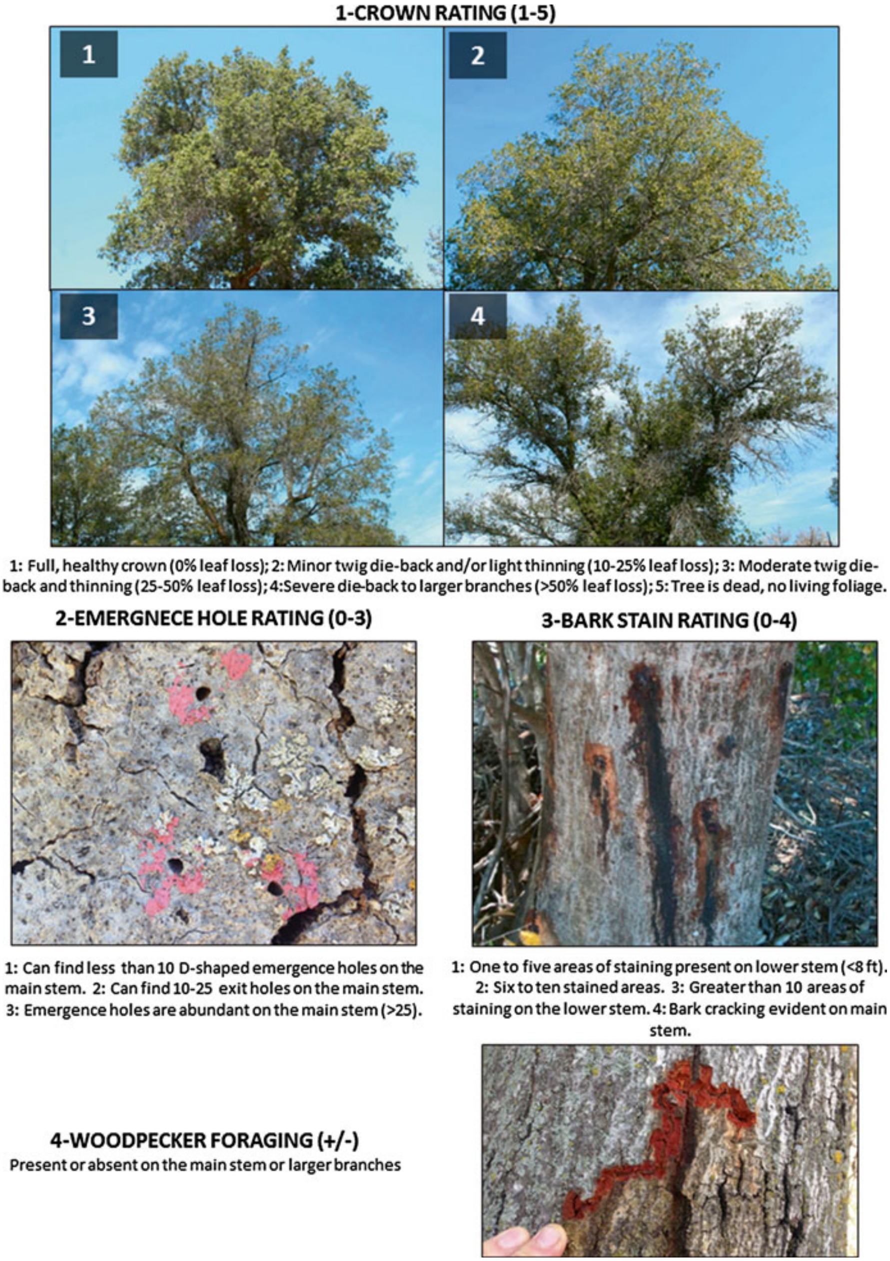

Fig. 22.6 A tree health rating system associated with goldspotted oak borer, *Agrilus auroguttatus*, injury in California. The health rating system incorporates crown thinning/dieback (rank 1–5), adult emergence hole densities (rank 1–3), bark staining/weeping (rank 1–4), and woodpecker foraging (presence/absence) (Modified from Hishinuma et al. 2011; Coleman et al. 2011, 2015)

As the number of emergence holes surpasses 120 on the main stem (<2 m) of *Q. agrifolia*, tree mortality will likely occur in a few years (Fig. 22.7).

Tree injury associated with *A. auroguttatus* is similar to other *Agrilus* species on hardwood trees, including *A. anxius*, twolined chestnut borer, *A. bilineatus* (Weber), and *A. planipennis* (Haack and Acciavatti 1992; Katovich et al. 2000; McCullough and Roberts 2002). However, injury *A. auroguttatus* the larvae does not occur in the branches of the upper crown of a tree. In contrast, larval injury from *A. auroguttatus* is concentrated on the lower bole and larger branches during all stages of infestation, allowing ground surveys to be an effective tool for monitoring these populations and for use in management decisions.

The primary internal injury symptom of *A. auroguttatus* is the dark, meandering larval galleries on the xylem surface (Fig. 22.8). The dark coloration of the galleries is believed to result from the oxidation of injured tree tissue (Coleman et al. 2011). The larval galleries are tightly packed with frass, characteristic of most Buprestidae. Galleries are approximately 4 mm wide when the larvae are mature and lightly score the outer xylem. When larval feeding is concentrated in an area, or feeding becomes very extensive, areas of the phloem and cambium can be strip or patch-killed. Tyloses have been observed in the xylem on trees injured by *A. auroguttatus* and late summer measurements of leaf water potential and cell turgor potential suggest *A. auroguttatus* infestation increases drought stress in trees (Coleman et al. 2011). Furthermore, infested old growth trees with greater *A. auroguttatus* injury exhibited the greatest decline in water use efficiency over a growing season.

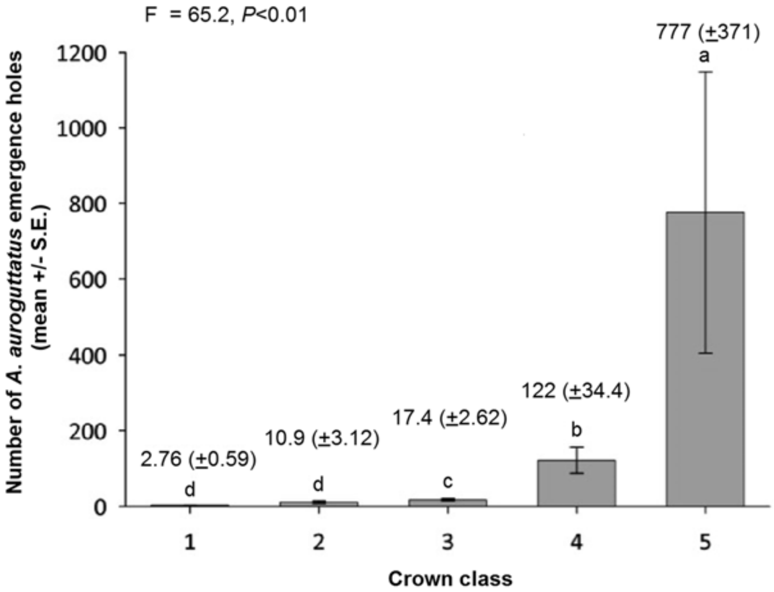

Fig. 22.7 Number of adult goldspotted oak borer, *Agrilus auroguttatus*, emergence holes [mean (± S.E.)] recorded across the five crown health classes of coast live oak, *Quercus agrifolia*, found on the Descanso Ranger District, Cleveland National Forest, San Diego Co. California. Coleman et al. (2014a) presents these data in terms of emergence hole density (See Figure 5.B therein)

Fig. 22.8 Black meandering larval galleries of the goldspotted oak borer, *Agrilus auroguttatus*, on the xylem of California black oak, *Quercus kelloggii*, on the Cleveland National Forest, San Diego County, California

In response to injury from *A. auroguttatus*, wound-induced periderm (i.e., callus) tissue has been observed on the xylem surface in association with larval galleries and in the phloem of host trees (Coleman and Seybold 2008b). Callus tissue formation can be extensive in the phloem, covering large patches of larval feeding. Feeding by *A. auroguttatus* on the callus tissue rarely occurs (Coleman, unpublished data 2013). Callus tissue has been observed on living and dead trees with *A. auroguttatus* injury, suggesting the callus tissue may slow injury by the beetle but does not prevent mortality. A callus response has been observed on *Q. agrifolia* and *Q. kelloggii*, further implying these trees are not under severe stress (Dunn et al. 1990).

22.8 Impact of *Agrilus auroguttatus* with an Emphasis on California

Agrilus auroguttatus prefers to land on, attack, and kill larger diameter oaks in AZ and CA (Coleman et al. 2012a, 2014a; Chen et al. 2015) (Fig. 22.9). In CA, *A. auroguttatus* landing rates were higher on larger (>50.8 cm dbh) than on smaller (25.4–50.8 cm dbh) diameter *Q. agrifolia* and on trees with severe crown thinning (rating of "4," Hishinuma et al. 2011; Coleman et al. 2014a) (Fig. 22.10). Diameters of infested *Q. agrifolia* and *Q. kelloggii* have ranged from 15.8 to 193 cm dbh in CA (Coleman et al. 2012a). Chen et al. (2015) reported that *Q. agrifolia* with diameters between 20 and 41 cm dbh had the greatest cumulative increase in emergence holes over a 2.5-year assessment period. Surveys of oaks killed by *A. auroguttatus* on the Descanso Ranger District of the Cleveland National Forest (San Diego Co.) revealed that 80 % of the dead trees consisted of *Q. agrifolia* that were >43.7 cm dbh and *Q. kelloggii* that were >51.6 cm dbh (Coleman, unpublished data 2013). In AZ, the mean diameters of *Q. emoryi* and *Q. hypoleucoides* infested by *A. auroguttatus* were 43.5 and 29.9 cm dbh, respectively (Coleman et al. 2012a).

The impact of *A. auroguttatus* in CA is characteristic of an invader relative to its impact recorded in AZ and relative to the impact of *A. coxalis* in Mexico (Coleman et al. 2012a). The mean infestation rate for *A. auroguttatus* in San Diego Co. was 61 %, whereas the mean infestation rate in AZ was 4 %, and for *A. coxalis* in Mexico was 3 % (Coleman et al. 2012a). Chen et al. (2015) reported that over a 2.5 year study period at two sites near the core area of the invaded range, the new infestation rates of initially uninfested coast live oaks were 50 % and 32 %. Oak woodlands that have been infested by the exotic beetle for longer than a decade have infestation rates >90 % near the presumed point of introduction of the beetle. High infestations rates were recorded in these areas because, in part, large diameter red oaks dominate the forest cover type (e.g., basal area and tree density per hectare) (Coleman et al. 2012a). The infestation is spreading radially from southeastern San Diego Co., so infestation rates decrease away from the predicted origin of the introduction near Guatay, CA (Coleman et al. 2012a) (Fig. 22.11). However, infestation and mortality levels associated with satellite infestations *via* movement of infested firewood in San Diego Co. may not follow this trend.

Crown injury ratings associated with *A. auroguttatus* and *A. coxalis* were significantly different among the infested areas of AZ, CA, and Mexico and uninfested areas in CA (Coleman et al. 2012a). Healthy crown classes (no crown thinning or dieback, Hishinuma et al. 2011) dominated (>70 %) the sites in AZ, Mexico, and uninfested sites in CA. However, oaks were distributed relatively evenly across the crown rating categories in infested stands in CA, i.e., healthy (28 %), minor thinning (24 %), moderate thinning (20 %), and dead trees (18 %) (Coleman et al. 2012a). Ten percent of the trees were rated with severe crown thinning in the CA infested sites. Newly infested outlier sites in San Diego Co. also had few severely injured trees. These "brood" trees produced 66–93 % of the *A. auroguttatus* population during one year at these newly infested outlier sites (Haavik et al. 2015).

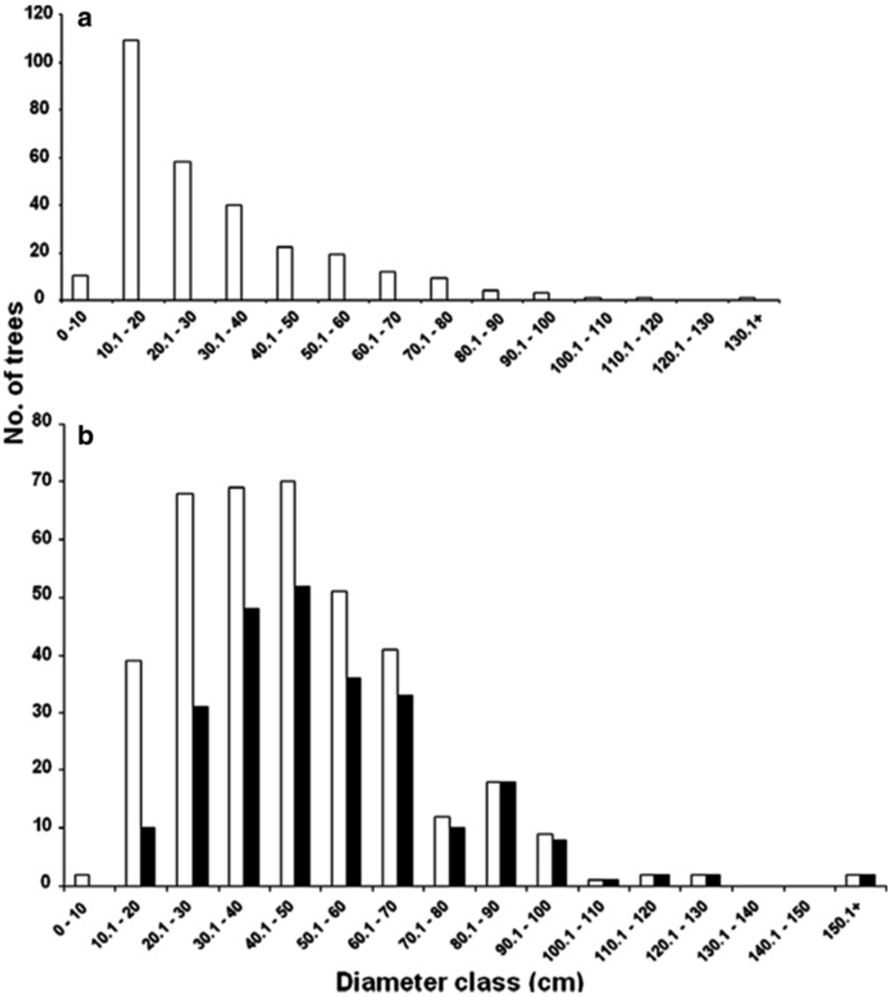

Fig. 22.9 Frequency distribution by diameter of 289 Engelmann oaks, *Quercus engelmannii* (**a**) and 386 coast live oaks, *Q. agrifolia* (**b**) from a survey of a private land parcel (Japatul Valley, California) showing all trees (*open bars*) and trees infested with goldspotted oak borer, *Agrilus auroguttatus* (*black bars*) (Reproduced from Coleman et al. 2012a). Note that none of the *Q. engelmannii* were infested (**a**) and the proportion of infested *Q. agrifolia* increased with diameter class (**b**)

Oak mortality, measured as trees ha^{-1} and basal area (m^2ha^{-1}), associated with *A. auroguttatus* was significantly greater in infested sites of San Diego Co. than uninfested sites in CA, in its native region of AZ, and in native stands of oaks within the distribution of *A. coxalis* in Mexico (Coleman et al. 2012a). The highest rates of mortality attributed to either *A. auroguttatus* or *A. coxalis* was 18 % in AZ, 8 % in Mexico, and 48 % in infested CA sites. In CA, mean oak mortality caused by *A. auroguttatus* was 3.01 (±0.63) and 1.50 (±0.56) trees ha^{-1}, representing 13 % and

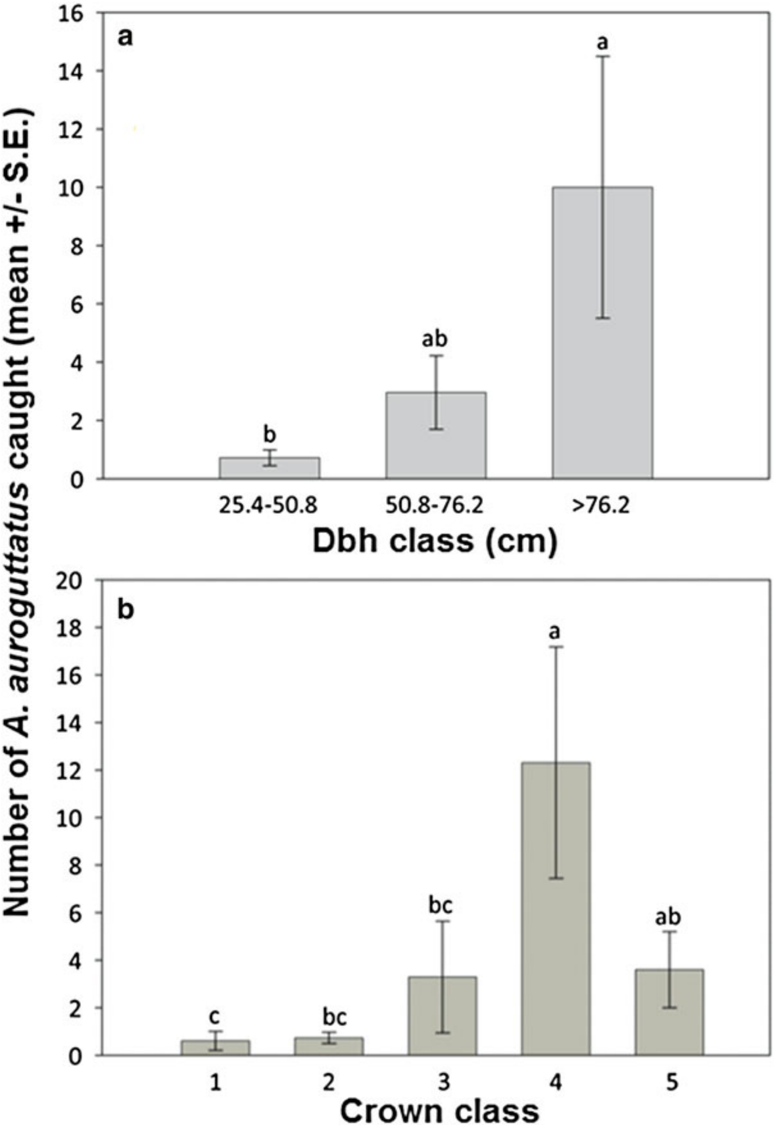

Fig. 22.10 Mean number (±SE) of adult goldspotted oak borer, *Agrilus auroguttatus*, trapped on clear stem panel traps on coast live oaks, *Quercus agrifolia*, across three size classes (**a**) and five crown classes (**b**) in 2010 and 2011, San Diego Co., California (Reproduced from Coleman et al. 2014a). Different lowercase letters above histogram bars within a figure panel indicate significant differences among means (panel **a**: $F_{2,73}=6.13$, $P=0.004$; panel **b**: $F_{4,71}=6.51$, $P=0.001$). Means in panel **a** were calculated (*left* to *right*) based on sample sizes of $N=33$, 26, and 18; means in panel B were calculated (*left* to *right*) based on sample sizes of $N=17$, 21, 21, 13, and 5

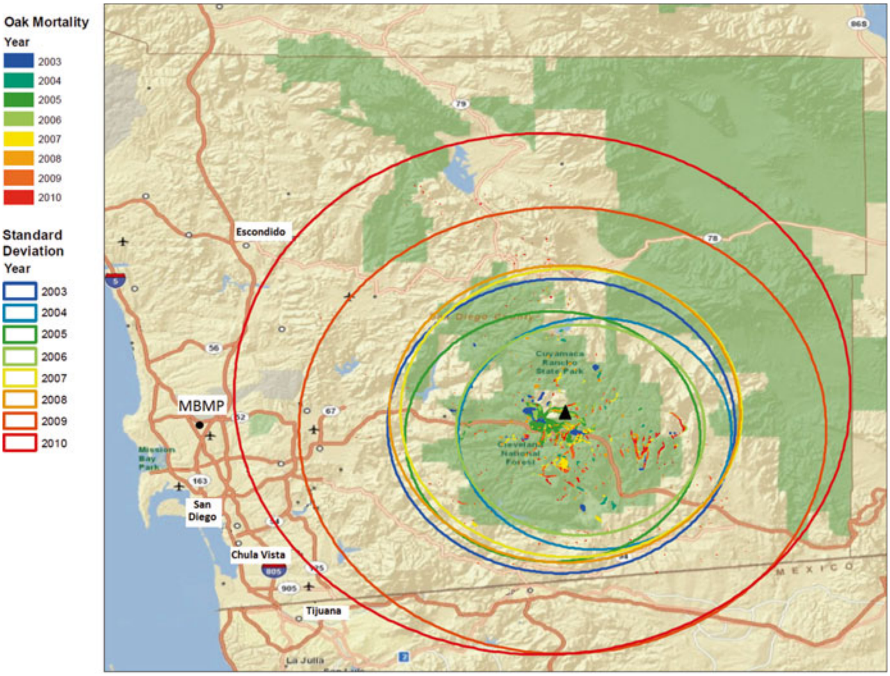

Fig. 22.11 Standard distance analysis of aerial oak mortality polygons (2003–2010) associated with *Agrilus auroguttatus* in San Diego Co., California, USA (Reproduced from Coleman et al. 2012a). The predicted center of oak mortality polygons from 2003 to 2010 is noted in the middle of the geometric means (N). The known satellite infestation in Marian Bear Memorial Park (MBMP) north of urban San Diego is also presented

7 % oak mortality in infested and uninfested sites, respectively. Other studies assessing the impact of *A. auroguttatus* on oak stands in areas where the pest has been present for greater than a decade, report that infestation rates were greater than 80 % and basal killed was greater than 70 % in *Q. agrifolia* and *Q. kelloggii* stands (Coleman, unpublished data).

Oak mortality has continued to accumulate following these initial surveys in San Diego Co. (USDA FHM 2014, Fig. 22.12). From 2012 to 2015, CA experienced a drought that caused increasing water stress to trees throughout the region. In 2014, tree mortality associated with *A. auroguttatus* increased threefold during aerial detection surveys. Oaks killed by *A. auroguttatus* persist in these savannas and woodlands for decades making management options costly due to the numerous reentries required to mitigate safety hazards and reduce fuel loads.

The loss of dominant and co-dominant oaks in savannas, woodlands, and mixed conifer stands and high-value oaks at developed sites (e.g., private residences, parks, campgrounds, trailheads, etc.) has resulted in significant economic and ecological impacts in southern CA. Public and private expenditures and losses have exceeded an estimated $10 million for direct costs and opportunity costs, dead tree mitigation, research, public education/outreach, survey and detection, and lost revenues

Fig. 22.12 Oak mortality (*red stippling*) associated with the goldspotted oak borer, *Agrilus auroguttatus*, in southern California. Satellite infestations in San Diego (San Diego County), Idyllwild (Riverside County), and Orange (Orange County), California are indicated by the names of these communities

(e.g., due to closures of parks and campgrounds for hazard tree mitigation) (GSOB Steering Committee, San Diego Co. 2014). The San Diego Resource Conservation District of Greater San Diego Co. received $3 million dollars from the USDA Forest Service to remove oaks killed by *A. auroguttatus* from private property, reducing the threat of hazard trees and wildfire in and around rural communities.

To date, the secondary ecological impacts associated with elevated tree mortality from *A. auroguttatus* have been poorly studied. These oak savannas and woodlands and mixed conifer stands are habitat for hundreds of species of wildlife, including deer, birds, salamanders, insects, and toads (Pavlik et al. 1996). Habitats of several threatened and endangered species, including the Arroyo toad, *Bufo californicus* Camp (Anura: Bufonidae), are restricted to these oak woodlands with specific requirements of canopy cover or foraging areas provided by *Q. agrifolia* or *Q. kelloggii*. The impact of the loss of the dominant canopy tree species on these wildlife species is not known. Acorns represent an abundant food source for several wildlife species and the loss of this nutritive food source on wildlife populations in these areas is also unknown. The increase of standing dead oaks (snags) may benefit some cavity-nesting birds and the increase of downed woody material may increase habitat for amphibians and rodents, but these impacts have not been studied in San Diego Co. However, the changes in fuel loading structure and composition from extensive oak mortality may influence wildfire behavior in these fire-dominated ecosystems of CA. Preliminary surveys suggest that oak snags still dominate the canopy following >10 years of oak mortality in San Diego Co. and only minimal increases of 1-, 10-, 100-, and 1000-h fuels were recorded on the forest floor (Coleman 2015). Native American tribes of CA have strong cultural ties to these oak woodlands and elevated oak mortality is threatening culturally significant sites and activities, such as pow wows and preparation of native foods. The secondary impacts of *A. auroguttatus* may remain largely understudied for several years because the majority of funding has been directed at developing an integrated pest management program for this new invasive species.

22.9 Community Ecology Centered on *Agrilus auroguttatus*

The absence of aggressive phloem- and wood-boring insects along the main stem of oaks in CA may have represented a relatively vacant *niche* that *A. auroguttatus* has exploited to establish and proliferate in the region (Table 22.1). Like many bark beetles and wood borers, *A. auroguttatus* is found frequently on previously attacked trees (Coleman et al. 2014a; Chen et al. 2015; Haavik et al. 2015), but the beetle will also attack healthy trees in CA (Coleman et al. 2011). Secondary insects are rarely associated with the initial attack of *A. auroguttatus*-infested trees (Flint et al. 2013), and these other subcortical species were found at significantly lower densities on newly killed trees in CA (Haavik et al. 2014a). As tree injury from *A. auroguttatus* has become extensive, these secondary insects have been found more frequently at a later stage of woody biodeterioration throughout the tree (Table 22.1). Western oak bark beetles, *Pseudopityophthorus* spp. Swaine (Coleoptera: Scolytidae), and lead cable borers, *Scobicia declivis* (LeConte) (Coleoptera: Bostrichidae), attack the upper branches of oaks, whereas appletree borers and related species, *Chrysobothris* spp. Eschscholtz (Coleoptera: Buprestidae); oak cordwood borer, *Xylotrechus nauticus* (Mannerheim) (Coleoptera: Cerambycidae); bark and ambrosia beetles (Coleoptera: Scolytidae) e.g., *Xyleborinus saxeseni* (Ratzeburg), *Monarthrum* spp. Kirsch, and *Gnathotrichus pilosus* Wood; and clearwing moths, *Synanthedon resplendens* (Edwards) (Lepidoptera: Sessidae), colonize the main stem (Brown and Eads 1965; Swiecki and Bernhardt 2006; Flint et al. 2013; Coleman et al. 2015). Lynch et al. (2014) report several secondary fungi on oaks in CA that are likely more prevalent on trees due to injury from *A. auroguttatus*.

Interactions of *A. auroguttatus* with native defoliators in CA, such as the western tussock moth, *Orgyia vetusta* Boisduval (Lepidopetra: Erebidae), and California oakworm, *Phryganidia californica* Packard (Lepidoptera: Notodontidae), have not been observed or documented. However, in the eastern USA, defoliation by European gypsy moth, *Lymantria dispar* L. (Lepidopetra: Erebidae) has been noted as a predisposing factor for attack on oaks by the twolined chestnut borer, *A. bilineatus* (Weber) (Haack and Acciavatti 1992), and may serve as a model for interactions between *A. auroguttatus* and the native CA defoliator complex. *Phytophthora ramorum* and *A. auroguttatus* distributions (Grünwald et al. 2012; Coleman et al.

Table 22.1 The entomological context for the goldspotted oak borer, *Agrilus auroguttatus*, invasion of California: bark and wood-boring insects associated with declining oaks and tanoaks[a]

Species	Feeding group	Significance (Early vs. late in decline cycle)
Agrilus auroguttatus[b]	Flatheaded borer, phloem and outer xylem of stem and largest branches	**Highly significant, early**
Coleoptera: Scolytidae		
Pseudopityophthorus pubipennis/ P. agrifoliae	Bark beetles, phloem of stem and branches	Moderately significant, can be early on seriously weakened trees
Monarthrum dentiger/M. scutellare	Ambrosia beetles, xylem of stem and branches	Moderately significant, late – stem breakage of SOD-infected trees
Gnathotrichus pilosus	Ambrosia beetle, xylem of stem and branches	Moderately significant, late – stem breakage of SOD-infected trees
Xyleborinus saxeseni[b]	Ambrosia beetle, xylem of stem and branches	Not significant, late, important for wood decomposition
Cyclorhipidion bodoanum[b]	Ambrosia beetle, xylem of stem and branches	Not significant, late, important for wood decomposition
Coleoptera: Buprestidae		
Chrysobothris femorata/mali /wintu	Flatheaded borers, Pacific flatheaded borer, bark and outer xylem of stem and branches	Not significant, late, important for wood decomposition
Agrilus angelicus	Flatheaded borer, Pacific oak twig girdler, xylem of small branches and twigs	Not significant, early, but attacks peripheral portions of tree
Coleoptera: Bostrichidae		
Scobicia declivis	False powderpost beetle, lead cable borer, xylem of stems and branches	Not significant, late, important for wood decomposition
Coleoptera: Cerambycidae		
Xylotrechus nauticus	Roundheaded borer, oak cordwood borer, phloem and xylem of stem and branches	Moderately significant, can be early on seriously weakened trees
Phymatodes lecontei/ decussatus	Roundheaded borers, phloem and xylem of dying branches/ stem	Moderately significant, can be early on seriously weakened trees
Neoclytus conjunctus	Roundheaded borer, phloem and xylem of dying branches/stem	Moderately significant, can be early on seriously weakened trees

[a] Brown and Eads (1965); Furniss and Carolin (1977); Swiecki and Bernhardt (2006); McPherson et al. (2008); Coleman and Seybold (2008b, 2011); Kelsey et al. (2013); and Beh et al. (2014)

[b] Invasive species

2015) currently do not overlap in CA, but the potential interaction of these two exotic species threatens native oak stands along CA's Central Coast. *Phytophthora ramorum* appears to be spreading faster in a northern direction along the moister, coastal areas of CA and Oregon (OR) than to the drier regions of southern CA (Grünwald et al. 2012; Kanaskie et al. 2013; USDA FHM 2014). The distributions of the polyphagous shot hole borer, *Euwallacea* nr. *fornicatus* (Eichhoff) (Coleoptera: Scolytidae), a new exotic ambrosia beetle to CA (Coleman et al. 2013), and *A. auroguttatus* do overlap in San Diego Co. However, preliminary surveys suggest that *E.* nr. *fornicatus* does not favor oaks and the two exotic species infrequently attack the same trees (Coleman, unpublished data 2015).

In addition to *A. auroguttatus*, *E.* nr. *fornicatus*, and *P. ramorum*, there are a few other potential exotic threats to oak ecosystems in CA. There are at least 42 species of *Agrilus* associated with oaks in North America (Nelson et al. 2008; Haack et al. 2009; Petrice and Haack 2014), but here are two species in the eastern half of the North American continent that may threaten CA. One of these is native and quite damaging (*A. bilineatus*, Haack and Acciavatti 1992), whereas the other is from Europe (*A. sulcicollis* Lacordaire, Petrice and Haack 2014). Both of these species colonize both white and red oaks; *A. sulcicollis* appears to utilize oaks that are in a more advanced state of biodeterioration and no direct oak mortality has been ascribed to this species in eastern North America (Petrice and Haack 2014). However, in Europe, *A. sulcicollis* has been considered amongst a complex of *Agrilus* sp. to have been associated with oak decline (Moraal and Hilszczański 2000; Evans et al. 2004; Hilszczański and Sierpinski 2007). Another member of this complex that may be even more damaging to CA oaks is *A. biguttatus* (Moraal and Hilszczański 2000; Vansteenkiste et al. 2004; Davis et al. 2005a; Brown et al. 2015). This species has demonstrated that it can expand its range (Pederson and Jørum 2009) and appears to have markedly increased its population density and distribution in Britain (Brown et al. 2015). The life history, habits, and impact of *A. biguttatus* in Europe seem to be quite similar to those of *A. auroguttatus* in CA (Brown et al. 2015). Other potentially invasive forest insects that may exert stress on oaks in CA include another flatheaded borer, the black-banded oak borer, Coraebus florentinus (Herbst) (Jurc et al. 2009; Sallé et al. 2014); a relatively aggressive bark beetle, Scolytus intricatus (Ratzeburg) (Jurc et al. 2009, Sallé et al. 2014); and the aforementioned *L. dispar* and related erebids (formerly lymantriids) from Eurasia (Gninenko and Gninenko 2002; Davis et al. 2005b).

22.10 Management of *Agrilus auroguttatus*

Components of an integrated pest management (IPM) program have been developed, or assessed, to prevent tree mortality from *A. auroguttatus* in CA (Coleman et al. 2009; Coleman et al. 2015; Seybold and Coleman 2015). This program includes tools for monitoring *A. auroguttatus*, managing infested wood, preventing attack through insecticide applications, and assessing options for classical or augmentative biological control. Future research should synthesize all aspects of these tools to prevent elevated levels of tree mortality at a site and to maintain management objectives.

Ground surveys are an effective means for identifying *A. auroguttatus*-infested trees as a consequence of the tendency for *A. auroguttatus* to oviposit on the lower parts of the main stem, thus allowing trees of all infestation levels to be identified (Coleman et al. 2011; Hishinuma et al. 2011). Large-diameter red oaks are the preferred host and should be the focus of ground surveys in which infested trees are ranked according to the degree of injury from *A. auroguttatus* (Hishinuma et al. 2011). However, these ground surveys are time consuming, can be limited in scope, and require trained technicians.

Monitoring techniques for *A. auroguttatus* based on flight trapping are not very sensitive. Purple and green prism flight-intercept traps (three-sided, 35.6 by 59.7 cm) developed for monitoring *A. planipennis* (Francese et al. 2008) were more effective at catching adults of *A. auroguttatus* when compared to other trap types (Coleman and Seybold 2008b). Purple and green flight-intercept prism traps were equally effective at catching *A. auroguttatus* males, but purple traps caught more females than green traps (Coleman et al. 2014a). When purple and green traps were hung at 3.0 m, significantly more adults of both sexes were caught on the purple traps. Traps hung at 4.5 m caught significantly more *A. auroguttatus* females than traps placed at 1.5 m. Males did not respond differently to prism traps hung at 1.5, 3.0, and 4.5 m. The addition of Manuka oil [i.e., the steam distillate of the manuka tree (New Zealand teatree), *Leptospermum scoparium* J.R.Forst. & G.Forst.], Phoebe oil (i.e., the steam distillate of the Brazilian walnut tree, *Ocotea porosa* (Nees & Martius) Barroso, and the green leaf volatile (3*Z*)-hexenol did increase trap catch of *A. auroguttatus* males on green and purple prism traps hung at 3.0 m (Coleman et al. 2014a). Additional laboratory (e.g., electroantennographic detection assays) and field studies have assessed the potential effectiveness of oak volatiles as an attractant for *A. auroguttatus*. Oak volatiles have been sampled from stressed and uninfested and *A. auroguttatus*-infested *Q. agrifolia*, but none have been effective for monitoring *A. auroguttatus* populations. Clear sticky coated panel traps (37.5 × 25 cm, Tanglefoot Company, Grand Rapids, MI, USA) affixed to the main stem of oaks at breast height were effective for monitoring the landing rates of *A. auroguttatus* (Coleman et al. 2014a). Clear sticky panel traps may be useful for monitoring *A. auroguttatus* populations in management actions at high-value sites.

Adult flight for *A. auroguttatus* detected with purple prism traps or clear sticky panel traps hung on the bole of infested trees began in late May and ended by early September over a several year period (reviewed in Coleman et al. 2014a). Coleman and Seybold (2008b) and Haavik et al. (2013) recorded seasonal flight patterns for *A. auroguttatus* and found activity as late as early November and October, respectively. Peak adult flight for *A. auroguttatus* across a range of elevations in southern CA occurs primarily from late June to early July (Coleman et al. 2014a). Emergence data from infested firewood-sized pieces of *Q. agrifolia* in the field support these general seasonal trends in flight activity for *A. auroguttatus* (Jones et al. 2013).

Research on monitoring *A. auroguttatus* with flight trapping has led so far to the use of the unbaited purple prism flight-intercept trap as the primary tool. These traps (hung at 3 m) have been used to delimit the distribution of *A. auroguttatus* in native oak woodlands and at high-value sites in CA (Coleman et al. 2014a). Traps are typically installed in late May and monitored until early September to coincide with our knowledge of adult flight activity. The traps are recommended solely as a monitoring tool and are not effective for preventing or suppressing infestations. As has been demonstrated for other species of buprestids, additional research on responses to host volatiles (Silk et al. 2011; Fürstenau et al. 2012), and to visual (Domingue et al. 2011, 2013a, b) and/or olfactory (Crook and Mastro 2010; Silk et al. 2009, 2011; Fürstenau et al. 2012; Ryall et al. 2012, 2013) signals from conspecifics may be merited with *A. auroguttatus*.

Movement of infested wood was likely the pathway for the introduction of *A. auroguttatus* into CA and was responsible for the establishment of the Orange, Riverside, and Los Angeles Cos. satellite infestations in southern CA, as well as several major range expansions in San Diego Co. (Marion Bear and Heise Parks). Education and outreach programs have sought to limit the movement of infested wood since no quarantines or restrictions were established for *A. auroguttatus* in CA. Grinding infested wood to a particle size of <7.62 cm was effective at killing *A. auroguttatus* in trials (Jones et al. 2013, Fig. 22.13); however, this management option is often restricted to large-scale management operations due to the cost of the specialized equipment required. Solarizing infested wood with clear plastic sheeting did not prevent emergence of *A. auroguttatus*, but did restrict the dispersal of the adults that may eventually cause tree mortality (Jones et al. 2013). Removing the bark and phloem from infested wood pieces (=debarking) can separate *A. auroguttatus* from the wood, but the bark and phloem can still harbor viable populations (Jones et al. 2013). Debarking is restricted to small quantities of wood because this option is very labor intensive. However, this technique does preserve the integrity of the firewood pieces for sale or use.

Application of contact insecticides to the main stem and larger branches (20.3 cm in diameter) of high-value red oaks may prevent tree mortality from this exotic species. Carbaryl (carbamate), bifenthrin, lambda-cyhalothrin, and permethrin (all pyrethroids) have killed *A. auroguttatus* adults and reduced adult feeding in laboratory no-choice leaf-feeding bioassays 1 and 12 months post-application (Coleman et al. 2015). Contact treatments should be applied once a year in May and applied only to uninfested trees or trees with only low levels of injury from *A. auroguttatus*. Insecticides should not be applied to GSOB-infested oaks with a crown injury ranking of "3" or greater and an emergence hole ranking of "3" (>25 emergence holes) (Hishinuma et al. 2011) because they have already experienced high levels of injury and are not likely to recover.

Systemic insecticides applied as a trunk injection have been the most promising treatment for preventing attack and mortality from *A. auroguttatus*. Applications of emamectin benzoate or imidacloprid have been made experimentally from December to February in southern CA (when precipitation is most likely) (Chen et al. 2015; Coleman et al. 2015). In no-choice leaf-feeding bioassays with *Q. agrifolia* and *Q. kelloggii*, emamectin benzoate and imidacloprid significantly reduced adult *A. auroguttatus* feeding and survival (Coleman et al. 2015). Residues of imidacloprid were detected at high levels (17 μg/g) in foliage 2 years post-application. Chen et al. (2015) reported that emamectin benzoate-injected trees had reduced annual increases in the appearance of *A. auroguttatus* emergence holes when compared to untreated

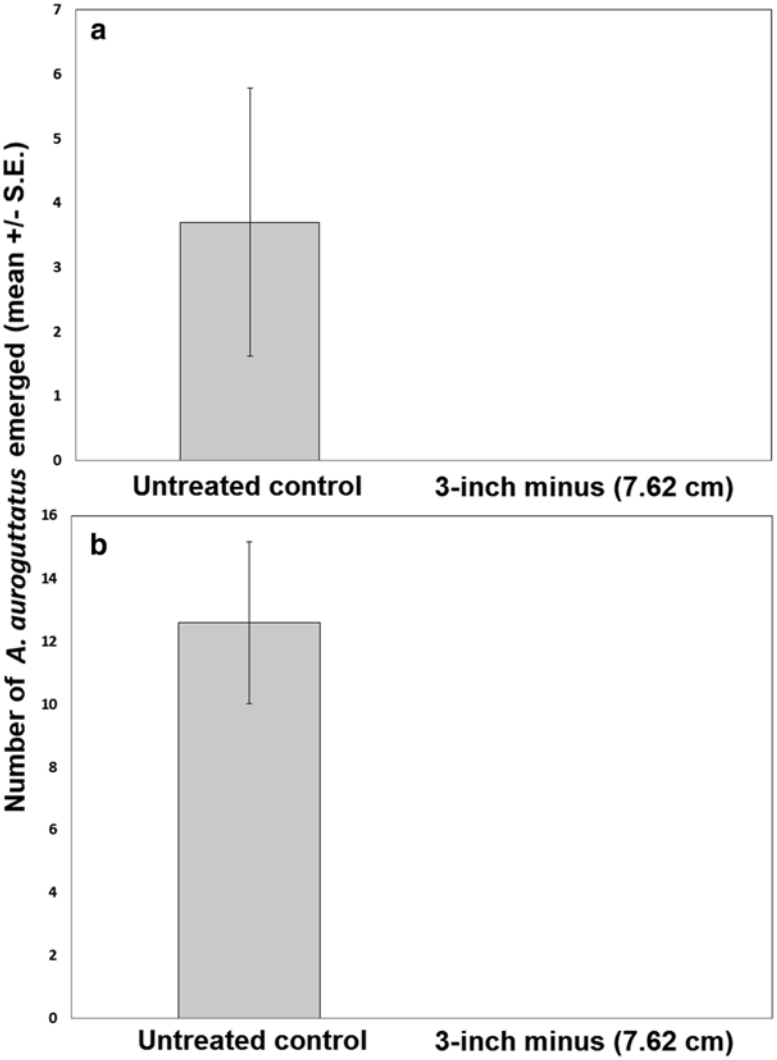

Fig. 22.13 Mean (±S.E.) emergence of adult goldspotted oak borer, *Agrilus auroguttatus*, following grinding infested coast live oak, *Quercus agrifolia*, firewood to a 3 inch-minus (7.62 cm) piece size in 2010 (panel **a**: $F1,12 = 22.2$, $P < 0.001$) and 2011 (panel **b**: $F1,12 = 103$, $P < 0.001$) in southern California (Reproduced from Jones et al. 2013)

trees. This suggests that larvae of *A. auroguttatus* may be impacted by the treatment. In the same study, imidacloprid-injected trees had significantly lower annual increases in emergence holes 1.5 and 2.5 years after the treatment (Chen et al. 2015). Stem injections of emamectin benzoate and imidacloprid should be reapplied during the dormant months once every 2 years until additional data is collected. Applications of dinotefuran (a neonicotinoid) did not reduce beetle feeding or survival in no-choice leaf-feeding bioassays, but residues were highest (3 μg/g) 2 weeks following application in the foliage when bioassays were conducted (Coleman et al. 2015). However, residues of dinotefuran declined drastically 5 months post-application and should be reapplied to trees every year at the first of June to coincide with the peak adult flight period.

Large diameter moderately- and severely-infested trees (i.e., "brood" trees) are unlikely to be saved by insecticide treatment and will likely die in a few years. At newly infested sites, these trees may contain 66–93 % of the *A. auroguttatus* population density in an oak woodland (Haavik et al. 2015). As a result, these brood trees should be felled and the wood handled and processed properly to potentially reduce the local population. This management option (e.g., removal of large diameter moderately- and severely-infested trees) has been assessed at several satellite infestations in high-value settings in CA, but no data are currently available to support recommendation of this approach.

Natural enemies may contribute to controlling populations in its native region, but other biotic factors may also be involved (e.g., host resistance). *Calosota elongata* Gibson (Hymenoptera: Eupelmidae), a newly described ectoparasitoid wasp (Gibson 2010), was discovered killing *A. auroguttatus* prepuae in AZ (Coleman and Seybold 2011; Coleman et al. 2012b, Fig. 22.14). The parasitoid has never been found attacking other species, but little is known about this new species of wasp. *Calosota elongata* was later found in the *A. auroguttatus*-infested areas of CA, and was likely introduced with the original population of *A. auroguttatus* (Haavik et al. 2012a). A *Trichogramma* sp. wasp (Hymenoptera: Trichogrammatidae) was found parasitizing GSOB eggs in AZ, but it is believed to be a generalist parasitoid (Lopez and Hoddle 2013). Other generalist predators and parasitoids, including the straw itch mite, *Pyemotes tritici* Lagrèze-Fossat and Montané (Acari: Pyemotidae), *Atanycolus simplex* (Hymenoptera: Braconidae), snakeflies (Raphidioptera), and bark-gnawing beetles (Trogossitidae), have been associated with *A. auroguttatus* in its native or introduced regions (Coleman and Seybold 2011; Coleman et al. 2014b, 2015). The impact of these parasitoid and predators on *A. auroguttatus* populations is unknown in AZ and CA. Classical and augmentative biological control will likely not be effective for *A. auroguttatus* in CA despite the discovery of several parasitoids and predators in AZ, CA, and Mexico (Lopez et al. 2014a; Coleman et al. 2015). Hurdles encountered when rearing *A. auroguttatus* on cut logs and the difficulty of rearing high densities in a laboratory setting make biological control infeasible at this time.

22.11 Risk of *Agrilus auroguttatus* in the United States of America and Potential for Introduction to Other Forest Ecosystems

A risk assessment model was developed for *A. auroguttatus* primarily in the USA and based on climate suitability and various biological factors: mean temperature during the warmest quarter; total rainfall during the driest month; cold tolerance

Fig. 22.14 Larvae of *Calosota elongata* (Hymenoptera: Eupelmidae) feeding on a larva of the goldspotted oak borer, *Agrilus auroguttatus*, in the phloem of Emory oak, *Quercus emoryi*. Specimens were photographed on the Coronado National Forest in southeastern Arizona

(e.g., supercooling point for mature prepupae); host range; and adult flight distance (Venette et al. 2015, Fig. 22.15). The highest risk of establishment for *A. auroguttatus* was predicted throughout CA along the Coastal Mountain Range and the foothills of the Sierra Nevada Mountain Range and into southwestern Oregon. Additional risk was predicted in its native region of southeastern AZ and southwestern New Mexico and in Baja California Norte, Mexico. The risk model was based on natural dispersal and in 2022 its northern distribution is predicted to be along the Transverse Mountain Ranges in southern CA. The model did not account for spread and punctuated discontinuities in the invaded range *via* the movement of infested firewood, which was likely responsible for several satellite infestations in San Diego and introductions into Riverside (2012), Orange (2014), and Los Angeles (2015) Cos. The introduction of *A. auroguttatus* in Orange Co. (discovered in December 2014) and Los Angeles Co. (discovered in August 2015) surpasses the 2016 predicted range in the model; again, suggesting that human-assisted dispersal may have been the source for the original introduction to CA. No risk of establishment was predicted for *A. auroguttatus* in the eastern USA using these parameters. It is also unknown how *A. auroguttatus* may interact with *L. dispar*, *A. bilineatus*, other wood-boring species, and their associated natural enemies in this eastern region. The model describes no risk of *A. auroguttatus* for this region.

A lumber market does not exist for oaks killed by *A. auroguttatus* in CA; most dead or dying oaks are converted to wood for heating. The revenue gained for selling oak firewood far exceeds the cost benefits for utilizing and processing this wood for other means (e.g., mulch, biofilters for water treatment facilities, high-end lumber markets).

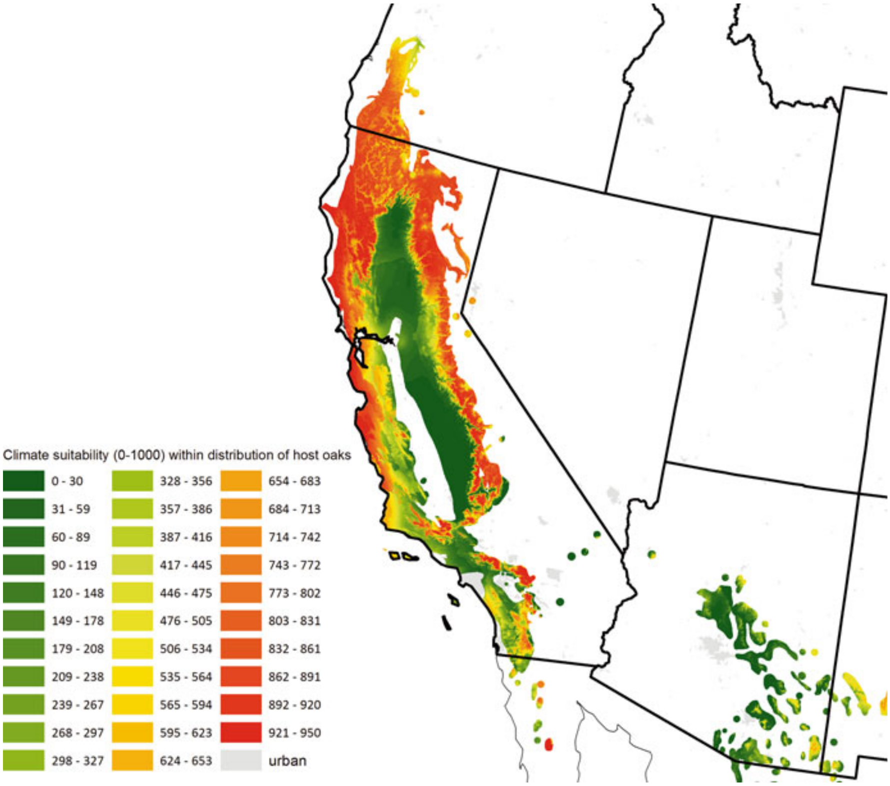

Fig. 22.15 Risk to oak resources from the goldspotted oak borer, *Agrilus auroguttatus*, in the western USA and Baja California Norte, Mexico. The risk map is based on the host distributions and climate suitability for *A. auroguttatus* as determined by laboratory host range tests and the distribution of historical collection records in southeastern Arizona and the invaded range in southern California (Reproduced from Venette et al. 2015)

However, the cost of moving large quantities of firewood is not cost effective over long distances. Satellite introductions in CA have likely resulted from small quantities of wood (e.g., a pick-up truck load). *Agrilus auroguttatus* does not frequently attack smaller diameter oaks (<12.5 cm dbh), so the risk of moving this species *via* nursery stock is not likely. Thus, the spread of *A. auroguttatus* to other Mediterranean countries is not likely either *via* the movement of lumber products, infested firewood, or ornamental trees.

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References

Aukema JE, McCullough DG, Von Holle B et al (2010) Historical accumulation of nonindigenous forest pests in the continental United States. BioScience 60:886–897

Baranchikov Y, Akulov E, Astapenko S (2010) Bark beetle *Polygraphus proximus*: a new aggressive far Eastern invader on *Abies* species in Siberia and European Russia. In: McManus KA, Gottschalk KW (eds) Proceedings, 21st U.S. Department of Agriculture interagency research forum on invasive species 2010, January 12–15, 2010. General technical report NRS-P-75. USDA Forest Service, Northern Research Station, Newtown Square, PA, pp 64–65

Basham JP, Waayers RJ, Westcott RL (2015) Discovery of Chrysobothris costifrons costifrons Waterhouse, 1887 (Coleoptera: Buprestidae) in southern California, U.S.A. Pan Pac Entomol 91:200–202

Beh MM, Metz MR, Seybold SJ et al (2014) The novel interaction between *Phytophthora ramorum* and wildfire elicits elevated ambrosia beetle landing rates on tanoak, *Notholithocarpus densiflorus*. For Ecol Manag 318:21–33

Billings RF, Pase HA III (2008) Mexican soapberry borer, *Agrilus prionurus* (Coleoptera: Buprestidae) an exotic pest recently detected in Texas. Texas Forest Service. http://tfsweb.tamu.edu/main/popup.aspx?id=5316. Accessed 31 Jan 2015

Brasier CM (1996) *Phytophthora cinnamomi* and oak decline in Southern Europe. Environmental constraints including climate change. Ann Sci For 53:347–358

Brasier CM, Scott JK (1994) European oak declines and global warming: a theoretical assessment with special reference to the activity of *Phytophthora cinnamomi*. Bull OEPP 24:221–232

Brasier CM, Roberdo F, Ferraz JFP (1993) Evidence for *Phytophthora cinnamomi* involvement in Iberian oak decline. Plant Pathol 42:140–145

Bright DE Jr (2014) A catalog of Scolytidae and Platypodidae (Coleoptera), Supplement 3 (1999–2010), with notes on subfamily and tribal reclassification. Insecta Mundi 0356:1–336

Brockerhoff EG, Liebhold AM, Jactel H (2006) The ecology of forest insect invasions and advances in their management. Can J For Res 36:263–268

Brown L, Eads CO (1965) A technical study of the insects affecting the oak tree in Southern California. Calif Agric Exp Station Bull 810:106

Brown N, Inward DJG, Jeger M, Denman S (2015) A review of *Agrilus biguttatus* in UK forests and its relationship with acute oak decline. Forestry 88:53–63

Carlos WJ, Johnson WS, Skelley J et al (2002) The bronze birch borer, Cooperative Extension Fact Sheet 02–38, University of Nevada, Reno, NV, 4 pp

Carlson RW, Knight FB (1969) Biology, taxonomy, and evolution of four sympatric *Agrilus* beetles (Coleoptera: Buprestidae). Con Am Entmol Inst 4:1–105

Coleman TW (2015) Influence of the invasive goldspotted oak borer on fuel loading in Southern California. In: Standiford RB, Purcell KL (tech. coords.) Proceedings of the seventh California oak symposium: managing oak woodlands in a dynamic world, 3–6 Nov 2014. USDA Forest Service General Technical Report, PSW-GTR-251, Visalia, pp 339–343, 579 pp

Chen Y, Coleman TW, Jones MI et al (2013) Foliar nutrients explain goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), adult feeding preference among four California oak species. Entomol Exp Appl 149:57–66

Chen Y, Flint ML, Coleman TW et al (2015) Impact of the goldspotted oak borer, *Agrilus auroguttatus*, on the health of coast live oak before and after treatment with two systemic insecticides. Pest Manag Sci 71:1540–1552. doi:10.1002/ps.3959

Cibrian TC, Mendez MJT, Campos BR et al (1995) Forest insects of Mexico, North American forestry commission publication no. 6. Universidad Autónoma Chapingo, Chapingo, 453 pp

Coleman TW (2015) Influence of the invasive goldspotted oak borer on fuel loading in Southern California. In: Standiford RB, Purcell KL (tech coords) Proceedings of the seventh California oak symposium: managing oak woodlands in a dynamic world. General technical report, PSW-GTR-251. USDA Forest Service, Visalia, 3–6 Nov 2014 pp 339–343, 579 pp

Coleman TW, Seybold SJ (2008a) New pest in California: the goldspotted oak borer, *Agrilus coxalis* Waterhouse. USDA Forest Service, Pest Alert, R5-RP-022, 28 Oct, 2008, 4 pp

Coleman TW, Seybold SJ (2008b) Previously unrecorded damage to oak, *Quercus* spp., in Southern California by the goldspotted oak borer, *Agrilus coxalis* Waterhouse (Coleoptera: Buprestidae). Pan Pac Entomol 84:288–300

Coleman TW, Seybold SJ (2010) Verification of a useful character for separating the sexes of the goldspotted oak borer, *Agrilus coxalis auroguttatus* (Coleoptera: Buprestidae). Pan Pac Entomol 86:58–62

Coleman TW, Seybold SJ (2011) Collection history and comparison of the interactions of the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), with host oaks in Southern California and Southeastern Arizona. Coleopt Bull 65:93–108

Coleman TW, Flint ML, Seybold SJ (2009) Managing the invasive goldspotted oak borer in the California wildland-urban interface: outlines of an IPM program. In: The Sixth International IPM Symposium, 24–26 Mar 2009, Portland, OR, Abstract P159, p 132

Coleman TW, Grulke NE, Daly M et al (2011) Coast live oak, *Quercus agrifolia*, susceptibility and response to goldspotted oak borer, *Agrilus auroguttatus*, injury in Southern California. For Ecol Manag 261:1852–1865

Coleman TW, Graves AD, Hoddle MS et al (2012a) Forest stand composition and impacts associated with *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) and *Agrilus coxalis* Waterhouse in oak woodlands. For Ecol Manag 276:104–117

Coleman TW, Lopez V, Rugman-Jones PF et al (2012b) Can the destruction of California's oak woodlands be prevented? Potential for biological control of the goldspotted oak borer, *Agrilus auroguttatus*. BioControl 57:211–225

Coleman TW, Eskalen A, Stouthamer R (2013) New pest complex in California: the polyphagous shot hole borer, *Euwallacea* sp., and Fusarium Dieback, *Fusarium euwallaceae*. USDA Forest Service, Pest Alert, R5-PR-032, 4 Nov 2013, 5 pp

Coleman TW, Graves AD, Chen Y et al (2014a) Developing monitoring techniques for the invasive *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) in California. Environ Entomol 43:729–743

Coleman TW, Jones MI, Hoddle MS et al (2014b) *Pyemotes tritici*: a parasitoid of *Agrilus auroguttatus* and *Agrilus coxalis* in the southwestern U.S. and southern Mexico. Can Entomol 147:244–248. doi:10.4039/tce.2014.38

Coleman TW, Jones MI, Smith SL et al (2015) Goldspotted oak borer, *Agrilus auroguttatus*, Forest Insect and Disease Leaflet, No. 183. USDA Forest Service, Portland, OR, 16 pp.

Crook DJ, Mastro VC (2010) Chemical ecology of the emerald ash borer, *Agrilus planipennis*. J Chem Ecol 36:101–112

Davis EE, French S, Venette RC (2005a) Mini risk-assessment: metallic beetle: *Agrilus biguttatus* Fabricius [Coleoptera: Buprestidae]. USDA: CAPS PRA. http://extension.entm.purdue.edu/CAPS/pdf/datasheets/OakSplendourBeetle.pdf. Accessed 17 Feb 2015

Davis EE, French S, Venette RC (2005b) Mini risk-assessment: Pink Gypsy Moth, *Lymantria mathura* Moore [Lepidoptera: Lymantriidae]. USDA: CAPS PRA, 31 pp. http://extension.entm.purdue.edu/CAPS/pdf/datasheets/RussianGypsyMoth.pdf. Accessed 17 Feb 2015

Dodds KJ, Gilmore DW, Seybold SJ (2010) Assessing the threat posed by indigenous exotics: a case study of two North American bark beetle species. Ann Entomol Soc Am 103:39–49

Domingue MJ, Csoka G, Toth M et al (2011) Field observations of visual attraction of three European oak buprestid beetles toward conspecific and heterospecific models. Entomol Exp Appl 140:112–121

Domingue MJ, Imrei Z, Lelito JP et al (2013a) Trapping of European buprestid beetles in oak forests using visual and olfactory cues. Entomol Exp Appl 14:116–129

Domingue MJ, Lelito JP, Fraser I et al (2013b) Visual and chemical cues affecting the detection rate of the emerald ash borer in sticky traps. J Appl Entomol 137:77–87

Dunn J, Potter D, Kimmerer T (1990) Carbohydrate reserves, radial growth and mechanisms of resistance of oak trees to phloem-boring insects. Oecologia 83:458–468

Evans HF, Moraal LG, Pajares JA (2004) Biology, ecology and economic importance of Buprestidae and Cerambycidae. In: Lieutier F, Day KR, Battisti A, Grégoire J-C, Evans HF (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Springer, Dordrecht, pp 447–474

Flint ML, Jones MI, Coleman TW et al (2013) Goldspotted oak borer. University of California Statewide Integrated Pest Management Program, Agriculture and Natural Resources Pest notes, publication 74163, Oakland, CA, Jan 2013, 7 pp, http://www.ipm.ucdavis.edu/PMG/PESTNOTES/pn74163.html. Accessed 19 Dec 2013

Francese JA, Oliver JB, Fraser I et al (2008) Influence of trap placement and design on capture of the emerald ash borer (Coleoptera: Buprestidae). J Econ Entomol 101:1831–1837

Fuhrer E (1998) Oak decline in Central Europe: a synopsis of hypotheses. In: McManus, ML, Liebhold AM (eds) Proceedings: population dynamics impacts, and integrated management of forest defoliating insects. USDA Forest Service General technical report NE-247, pp 7–24

Furniss RL, Carolin VM (1977) Western forest insects. US Department of Agriculture, Forest Service, Miscellaneous publication no. 1339, 655 pp

Fürstenau B, Rosell G, Guerrero C et al (2012) Electrophysiological and behavioral responses of the black-banded oak borer, *Corebus florentinus*, to conspecific and host-plant volatiles. J Chem Ecol 38:378–388

Galford JR (1984) The locust borer, No. 71, Forest Insect and Disease Leaflet. U.S. Department of Agriculture Forest Service. Northeastern Forest Experiment Station, Delaware, OH, 6 pp

Gibbs JN, Greig JW (1997) Biotic and abiotic factors affecting the dying back of pedunculate oak *Quercus robur* L. Forestry 70:399–406

Gibson GAP (2010) *Calosota* Curtis (Hymenoptera, Chalcidoidea, Eupelmidae) – review of the New World and European fauna including revision of species from the West Indies and Central and North America. ZooKeys 55:1–75

Gninenko YI, Gninenko MY (2002) Little known lymantriids of the Russian far East – potential for movement to other countries of the Pacific region. Bull OEPP/EPPO Bull 32:477–480

Goldspotted Oak Borer (GSOB) Steering Committee, San Diego County (2014) Goldspotted oak borer (GSOB) situation, Oct 2014. http://ucanr.edu/sites/gsobinfo/files/199780.pdf. Accessed 11 Dec 2014

Grünwald NJ, Goss EM, Press CM (2008) Phytophthora ramorum: a pathogen with a remarkably wide host range causing sudden oak death on oaks and ramorum blight on woody ornamentals. Mol Plant Pathol 9:729–740. doi:10.1111/J.1364-3703.2008.00500.X

Grünwald NJ, Garbelotto M, Goss EM et al (2012) Emergence of the sudden oak death pathogen Phytophthora ramorum. Trends Microbiol 20:131–138. doi:10.1016/j.tim.2011.12.006

Haack RA (2006) Exotic bark-and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can J For Res 36:269–288

Haack RA, Acciavatti RE (1992) Twolined chestnut borer, No. 168, Forest Insect and Disease Leaflet. USDA Forest Service, State and Private Forestry, Northeastern Area, Newtown Square, 10 pp

Haack RA, Petrice TR, Zablotny JE (2009) The first report of the European oak borer, *Agrilus sulcicollis* (Coleoptera: Buprestidae), in the United States. Great Lakes Entomol 42:1–7

Haack RA, Petrice TR, Wiedenhoeft AC (2010) Incidence of bark and wood-boring insects in firewood: a survey at Michigan's Mackinac Bridge. J Econ Entomol 103:1682–1692

Haavik LJ, Coleman TW, Chen Y et al (2012a) First occurrence of the goldspotted oak borer parasitoid, *Calosota elongata* (Hymenoptera: Eupelmidae), in California. Pan Pac Entomol 88:374–376

Haavik LJ, Coleman TW, Flint ML et al (2012b) *Agrilus auroguttatus* exit hole distributions on *Quercus agrifolia* boles and a sampling method to estimate their density on individual trees. Can Entomol 144:1–12

Haavik LJ, Coleman TW, Flint ML et al (2013) *Agrilus auroguttatus* (Coleoptera: Buprestidae) seasonal development within *Quercus agrifolia* (Fagales: Fagaceae) in southern California. Ann Entomol Soc Am 106:189–197

Haavik LJ, Coleman TW, Flint ML et al (2014a) Densities of *Agrilus auroguttatus* and other borers in California and Arizona oaks. Insects 4:287–300. doi:10.3390/insects40x000x

Haavik LJ, Graves AD, Coleman TW et al (2014b) Suitability of native and ornamental oak species in California for *Agrilus auroguttatus*. Entomol Exp Appl 150:86–97

Haavik LJ, Flint ML, Coleman TW et al (2015) Goldspotted oak borer effects on tree health and colonization patterns at six newly-established sites. Agric For Entomol 17:146–157. doi:10.1111/afe.12090

Hespenheide HA (1979) Nomenclature notes on the Agrilinae (Buprestidae). IV. Coleopt Bull 33:105–120

Hespenheide HA, Bellamy CL (2009) New species, taxonomic notes, and records for *Agrilus* Curtis (Coleoptera: Buprestidae) of México and the United States. Zootaxa 2084:50–68

Hespenheide HA, Westcott RL, Bellamy CL (2011) *Agrilus* Curtis (Coleoptera: Buprestidae) of the Baja California peninsula, México. Zootaxa 2805:36–56

Hilszczański J, Sierpinski A (2007) *Agrilus* spp. The main factor of oak decline in Poland. In: Hoyer-Tomiczek U, Knížek M, Forster B, Grodzki W (eds) IUFRO working party 7.03.10, Proceedings of the 7th workshop on methodology of forest insect and disease survey in Central Europe, 11–14 Sept 2006, Gmunden, pp 121–125. Published on CD-Rom, BFW, Vienna or http://bfw.ac.at/400/iufro_workshop/proceedings/121-125_B5_Jacek%20Hilszczanski_Andrzej%20Sierpinski_paper.pdf. Accessed 19 Dec 2013

Hishinuma S, Coleman TW, Flint ML et al (2011) Goldspotted oak borer: field identification guide, University of California Agriculture and Natural Resources, Statewide Integrated Pest Management Program, 6 pp, 13 Jan 2011. http://www.ipm.ucdavis.edu/PDF/MISC/GSOB_field-identification-guide.pdf. Accessed 19 Dec 2013

Jones MI, Coleman TW, Graves AD et al (2013) Sanitation options for managing oak wood infested with the invasive goldspotted oak borer (Coleoptera: Buprestidae) in southern California. J Econ Entomol 106:235–246

Jurc M, Bojović S, Komjanc B et al (2009) Xylophagous entomofauna in branches of oaks (*Quercus* spp.) and its significance for oak health in the Karst region of Slovenia. Biologia 64:130–138

Kanaskie A, Hansen E, Goheen EM et al (2013) Detection and eradication of Phytophthora ramorum from Oregon forests, 2001–2011. In: Proceedings of the sudden oak death fifth science symposium. General Technical Report PSW-GTR-243. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 3–13. http://www.fs.fed.us/psw/publications/documents/psw_gtr243/psw_gtr243_003.pdf

Katovich SA, Munson AS, Ball J et al (2000) Bronze birch borer, No. 111, Forest Insect and Disease Leaflet. U.S. Department of Agriculture Forest Service, State and Private Forestry, Northeastern Area, Newtown Square, PA, 8 pp

Kelsey RG, Beh MM, Shaw DC et al (2013) Ethanol attracts scolytid beetles to *Phytophthora ramorum* cankers on coast live oak. J Chem Ecol 39:494–506

Klepzig KD, Poland TM, Gillette NG et al (2010) Forest service R&D – invasive insects: visions for the future. In: Dix ME, Britton K (eds) A dynamic invasive species research vision: opportunities and priorities 2009–29. USDA Forest Service General technical report WO-79, Washington, DC, May 2010, pp 13–21

Langor DW, DeHaas LJ, Foottit RG (2009) Diversity of non-native terrestrial arthropods on woody plants in Canada. Biol Invasions 11:5–19

Lelito JP, Fraser I, Mastro VC et al (2007) Visually mediated 'paratrooper copulations' in the mating behavior of *Agrilus planipennis* (Coleoptera: Buprestidae), a highly destructive invasive pest of North American ash trees. J Insect Behav 20:537–552

Liebhold AM, MacDonald WL, Bergdahl D et al (1995) Invasion by exotic forest pests: a threat to forest ecosystems. Forensic Sci 41:a0001–z0001

Lopez VM, Hoddle MS (2013) Mortality factors affecting *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae) eggs in the native and invaded ranges. Biol Contol 67:143–148

Lopez VM, Hoddle MS (2014) Effects of body size, diet, and mating on the fecundity and longevity of the goldspotted oak borer (Coleoptera: Buprestidae). Ann Entomol Soc Am 107:539–548

Lopez VM, Coleman TW, Seybold SJ et al (2014a) Goldspotted oak borer (*Agrilus auroguttatus* Schaeffer) (Coleoptera: Buprestidae) In: Van Driesche R, Reardon RC (eds) The use of classical biological control to preserve forests in North America. USDA Forest Service, Forest Health Technology Enterprise Team, Morgantown, WV, pp 211–219

Lopez VM, McClanahan MN, Graham L et al (2014b) Assessing the flight capabilities of the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae), with computerized flight mills. J Econ Entomol 107:1127–1135

Lopez V, Rugman-Jones PF, Coleman TW et al (2014c) Population genetics of the goldspotted oak borer, *Agrilus auroguttatus* Schaeffer (Coleoptera: Buprestidae): investigating the origin of an invasive pest of native oaks in California. Biol Invasions 16:2393–2402

Lynch SC, Zambino PJ, Scott TA et al (2014) Occurrence, incidence and associations among fungal pathogens and *Agrilus auroguttatus*, and their roles in *Quercus agrifolia* decline in California. For Pathol 44:62–74

Manos PS, Doyle JJ, Nixon KC (1999) Phylogeny, biogeography, and processes of molecular differentiation in *Quercus* subgenus *Quercus* (Fagaceae). Mol Phylogenet Evol 12:333–349

Mayr E (1963) Animal species and evolution. Harvard University Press, Cambridge, MA

McCullough D, Roberts D (2002) Pest alert – Emerald ash borer, USDA Forest Service, Northeastern Area State and Private Forestry, NA-PR-07-02, Washington, DC, 2 pp

McPherson BA, Erbilgin N, Wood DL et al (2008) Attraction of ambrosia and bark beetles to coast live oaks infected by *Phytophthora ramorum*. Agric For Entomol 10:315–321

Moraal LG, Hilszczański J (2000) The oak buprestid beetle, *Agrilus biguttatus* (F.) (Col., Buprestidae), a recent factor in oak decline in Europe. J Pest Sci 73:134–138

Nelson GH, Walters GC Jr, Haines RD et al (2008) A catalog and bibliography of the Buprestoidea of America north of Mexico. Coleop Soc, Special Publication 4:1–274

Nixon KC (1993) Infrageneric classification of *Quercus* (Fagaceae) and typification of sectional names. Ann For Sci 50:25s–34s

Pavlik BM, Muick P, Johnson S et al (1996) Oaks of California. Cachuma Press, Los Olivos

Pederson H, Jørum P (2009) The jewel beetle *Agrilus biguttatus* (Fabricius, 1777) found in Denmark (Coleoptera, Buprestidae). Entomologiske Meddelelser 77:19–26

Petrice TR, Haack RA (2014) Biology of the European oak borer in Michigan, United States of America, with comparisons to the native twolined chestnut borer. Can Entomol 146:36–51

Rizzo DM, Garbelotto M (2003) Sudden oak death: endangering California and Oregon forest ecosystems. Front Ecol Environ 1:197–204

Rodriguez-Saona CR, Miller JR, Poland TM et al (2007) Behaviors of adult *Agrilus planipennis* (Coleoptera: Buprestidae). Great Lakes Entomol 40:1–16

Ryall KL, Silk PJ, Mayo P et al (2012) Attraction of *Agrilus planipennis* (Coleoptera: Buprestidae) to a volatile pheromone: effects of release rate, host volatile, and trap placement. Environ Entomol 41:648–656. doi:10.1603/EN11312

Ryall KL, Fidgen JG, Silk PJ et al (2013) Efficacy of the pheromone (3*Z*)-lactone and the host kairomone (3*Z*)-hexenol at detecting early infestation of the emerald ash borer, *Agrilus planipennis*. Entomol Exp Appl 147:126–131. doi:10.1111/eea.12052

Sallé A, Nageleisen L-M, Lieutier F (2014) Bark and wood boring insects involved in oak declines in Europe: current knowledge and future prospects in a context of climate change. For Ecol Manag 328:79–93

Schaeffer C (1905) Some additional new genera and species of Coleoptera found within the limit of the United States, vol 1. Science Bulletin of the Museum of the Brooklyn Institute of Arts and Sciences, New York, pp 141–179

Service, Northeastern Area State and Private Forestry Pest Alert, NA-PR-02-10, originally published May 2010, reprinted Aug 2010, Oct 2011, and Feb 2013, 2 pp. http://www.na.fs.fed.us/pubs/detail.cfm?id=5225. Accessed 31 Jan 2015

Seybold SJ, Coleman TW (2015) The goldspotted oak borer: revisiting the status of an invasive pest six years after its discovery. In: Standiford RB, Purcell KL (tech. coords.) Proceedings of the seventh California oak symposium: managing oak woodlands in a dynamic world, 3–6 Nov 2014. USDA Forest Service General Technical Report, PSW-GTR-251, Visalia, pp 285–305, 579 pp

Seybold SJ, Haugen D, O'Brien J et al (2013) Thousand cankers disease. USDA Forest Service, Northeastern Area State and Private Forestry Pest Alert, NA-PR-02-10, Feb 2013, 2 pp, http://www.na.fs.fed.us/pubs/detail.cfm?id=5225

Shreve F, Wiggins I (1964) Vegetation and flora of the Sonoran Desert. Stanford University Press, Palo Alto, CA

Silk PJ, Ryall K, Lyons DB et al (2009) A contact sex pheromone component of the emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae). Naturwissenschaften 96:601–608. doi:10.1007/s00114-009-0513-1

Silk PJ, Ryall K, Mayo P et al (2011) Evidence for a volatile pheromone in *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) that increases attraction to a host foliar volatile. J Chem Ecol 40:904–916

Smith GA, Hurley JE (2005) First records in Atlantic Canada of *Spondylis upiformis* Mannerheim and *Xylotrechus sagittus sagittus* (Germar) (Coleoptera: Cerambycidae). Coleopt Bull 59:488

Solomon JD (1995) Guide to insect borers in North America broadleaf trees and shrubs, vol 706, Agricultural handbook. USDA Forest Service, Washington, DC, 735 pp

Swiecki TJ, Bernhardt EA (2006) A field guide to insects and diseases of California oaks, General technical report PSW-GTR-197. U.S. Department of Agriculture Forest Service Pacific Southwest Research Station, Albany, CA, 151 pp

Thomas FM, Blank R, Hartmann G (2002) Abiotic and biotic factors and their interactions as causes of oak decline in Central Europe. For Pathol 32:277–307

USDA Forest Service (2009) Forest Inventory Analysis (FIA), Region 3, Arizona

USDA Forest Service, Forest Health Monitoring (FHM) (2014) Aerial survey Region 5 database. http://www.fs.usda.gov/detail/r5/forest-grasslandhealth/?cid=fsbdev3_046696. Accessed 31 Jan 2015

Vansteenkiste D, Tirry L, VanAcker J, Stevens M (2004) Predispositions and symptoms of *Agrilus* borer attack in declining oak trees. Ann For Sci 61:815–823

Venette RC, Kriticos DJ, Magarey RD et al (2010) Pest risk maps for invasive alien species: a roadmap for improvement. Bioscience 60:349–362

Venette RC, Coleman TW, Seybold SJ (2015) Assessing the risks posed by goldspotted oak borer to California and beyond. In: Standiford RB, Purcell KL (tech. coords.) Proceedings of the seventh California oak symposium: managing oak woodlands in a dynamic world, 3–6 Nov 2014. USDA Forest Service General Technical Report, PSW-GTR-251, Visalia, pp 317–329, 579 pp

Westcott RL (2005) A new species of *Chrysobothris* Eschscholtz from Oregon and Washington, with notes on other Buprestidae (Coleoptera) occurring in the United States and Canada. Zootaxa 1044:1–15

Westcott RL, Haines RD, Hishinuma SM et al (2015) Chrysobothris analis LeConte, 1860 (Coleoptera: Buprestidae) discovered in California with notes on Chrysobothris wintu Wellso & Manley, 2007. Pan Pac Entomol (in press)

Wood DL, Stark RW (1968) The life history of *Ips calligraphus* (Coleoptera: Scolytidae) with notes on its biology in California. Can Entomol 100:145–151

Yates HO, Overgaard NA, Koerber TW (1981) Nantucket pine tip moth, No. 70, Forest Insect and disease Leaflet. USDA Forest Service, Washington, DC, 8 pp

Chapter 23
Pitch Canker in California Mediterranean Conifer Systems

T.R. Gordon

Abstract *Fusarium circinatum,* the cause of pitch canker in pines, is a recent introduction to California, most likely on seeds from the southeastern United States. The most common symptom of pitch canker is branch dieback that results from a lesion, usually within one or two whorls of a branch tip, that girdles and kills the affected branch distal to the point of infection. The success of *F. circinatum* as a pathogen of pines in coastal California can be attributed to: (1) an abundance of highly susceptible host trees, (2) a climate that provides conditions suitable for infection throughout much of the year, and (3) a relationship between the pathogen and native insects that can transport the fungus and create infection courts. Systemic induced resistance (SIR) to pitch canker has been documented in *P. radiata*. Trees in areas where pitch canker was well established were significantly less susceptible to the disease than trees in areas where pitch canker was a more recent occurrence. SIR may be an important part of the explanation for stabilization of pitch canker in Monterey pine forests and can help to explain, how long-lived perennials have survived infection by parasitic microbes that have generation times orders of magnitude shorter than their host plant.

23.1 Introduction

The geographic origin of the pitch canker pathosystem is not known but some evidence points to Mesoamerica (southern Mexico and Central America) as the aboriginal home of the disease (Gordon et al. 2001). In Mexico, pitch canker, caused by *Fusarium circinatum*, is reported to affect a number of pine species (Guerra-Santos 1999) but it appears to cause relatively little damage in native forests, suggesting the host and pathogen may have co-evolved over an extended period of time in that part of the world. In addition, the Mexican population of *F. circinatum* is, by some measures, more diverse than populations in other locations (Wikler and Gordon 2000), consistent with Mexico being the center of origin of the pathogen. Further support for this hypothesis derives from interfertility of *F. circinatum* with *F. temperatum*, a

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commensal associate of a grass species (*Zea mays* ssp. *mexicana*) that co-occurs with pines in Mexico and Central America (Desjardins et al. 2000; Friel et al. 2007). Other close relatives of *F. circinatum* are also associated with grasses. Thus, the ability of *F. circinatum* to colonize corn (Swett and Gordon 2015) and other members of the grass family (Swett and Gordon 2012; Swett et al. 2014) may be seen as retention of ancestral characteristics, following a host jump from grasses to pines.

Although a relationship between *F. circinatum* and pines may have originated in Mexico, a conspicuous impact on the host tree was first reported in the southeastern U.S., where pitch canker was identified as a disease of southern pines in 1945 (Hepting and Roth 1946). Thereafter, the disease became more widespread regionally and was a cause of significant damage to many plantation-grown pine species (Dwinell et al. 1985). In 1986, pitch canker was discovered in California (McCain et al. 1987), where it was associated with extensive mortality of landscape plantings of *Pinus radiata* (Monterey pine). In 1992, pitch canker was confirmed to occur in the native *P. radiata* population on the Monterey Peninsula, and shortly thereafter in the other two native populations of this species in California: Cambria and Año Nuevo. All three populations are within the range of 35° 31′–37° 17′ N latitude on the central coast, and collectively represent the entirety of the native range of *P. radiata*, save for two small island populations off the coast of Mexico. The incidence and severity of pitch canker increased in native stands of *P. radiata* over the next several years and eventually spread to two other pine species native to coastal California: *P. muricata* (bishop pine) and *P. attenuata* (knobcone pine). Significant damage to trees in native stands was at variance with what was known about pitch canker in the SE U.S., where the disease was seen to be problematic only in managed plantings (Dwinell et al. 1985). In fact, although pitch canker now occurs in many locations across the globe, it is only in California that native species are under threat from the disease.

23.2 Disease Symptoms

A typical symptom of pitch canker is branch dieback that results from a lesion, usually within one or two whorls of a branch tip, that girdles and kills the affected branch distal to the point of infection. Axial growth of the pathogen usually does not progress past the nodes distal and proximal to the infection site (Barrows-Broaddus and Dwinell 1983), probably because of the accumulation of host-produced resin. Although resin does not prevent growth of *F. circinatum* (Slinski et al. 2015), it will restrict the flow of water, which results in desiccation of the infected tissue and the pathogen. Pitch canker intensifies through multiple infections on the same tree. Infections can occur at any point along a branch, though the pathogen appears to grow more rapidly in succulent, current year growth than in older, more lignified tissue. Large-diameter branches can also be girdled and this may be caused by the coalescence of multiple lesions. Top kill is often seen in severely diseased trees, resulting from girdling of the main stem and/or attack by engraver beetles (*Ips* spp.), which are attracted to weakened trees. Girdling cankers lower on the trunk can cause death of the entire tree. A diagnostic feature of branches killed by pitch canker is a mass of resin at the junction of living and symptomatic tissue, which corresponds to the site of infection.

23.3 Origin and Establishment of the California Infestation

Genetic evidence implicates the southeastern U.S. as the proximate source of the pathogen that was introduced to California (Wikler and Gordon 2000), most likely on seed. *Fusarium circinatum* is well known to be seedborne (Storer et al. 1998a), and sowing infested seed can allow the fungus to become established in soil in seedling nurseries. When grown in infested soil, *P. radiata* can sustain root infections. Whereas some infected seedlings will be killed, others can remain symptomless (Swett et al. 2015). Trees with latent root infections were moved from nurseries to Christmas trees farms and from there to residences, which brought the fungus in contact with susceptible trees in landscapes (Gordon et al. 2001). Further distribution resulted from movement of logs cut from dead and dying trees, with insects emerging from infested logs carrying the pathogen to nearby trees (Fox et al. 1991). The success of *F. circinatum* as a pathogen of pines in California can be attributed to: (1) an abundance of highly susceptible host trees, (2) a climate that provides conditions suitable for infection throughout much of the year, and (3) a relationship between the pathogen and native insects that can transport the fungus and create infection courts.

The susceptibility of *P. radiata* to pitch canker was reported by Hepting (1961), who inoculated trees in a greenhouse. Thus, the risk to this species of limited distribution was known and the introduction of a damaging pathogen might have been prevented had there been regulatory restrictions on importation of pine seed. For whatever reason, no such restrictions were enacted, and once *F. circinatum* was established in California, development of pitch canker was greatly facilitated by the susceptibility of *P. radiata*, which during the 1980s was a popular landscape tree, particularly near the coast. *Pinus radiata* on freeway rights-of-way and in state parks provided a green bridge for movement of *F. circinatum* from planted stands into native populations of this species. On the Monterey Peninsula, which is home to the largest remaining population of *P. radiata*, an isolated stand of *P. muricata* was also affected, and this species proved to be as susceptible to pitch canker as *P. radiata* (Schmale and Gordon 2003). In proximity to the Año Nuevo population of *P. radiata*, pitch canker spread to native *P. attenuata*, which also proved to be highly susceptible to the disease (Gordon et al. 2001). *Pinus contorta* ssp. *contorta* (shore pine) is susceptible as well, but as yet there is no evidence of significant damage to native populations of this species. *Pseudotsuga menziesii* (Douglas-fir) has been shown to be susceptible to pitch canker, and it represents the only known host to this disease outside the pine genus. Although very few naturally infected trees have been observed, provenance studies show significant variation in susceptibility of *P. men-*

ziesii (Gordon et al. 2006), so there may be a more significant impact of pitch canker on this species at some point in the future.

Native *P. radiata* on the Monterey Peninsula may have been more vulnerable to incursion by an exotic pathogen because of residential and commercial development that displaced some native stands and left much of what remains on or near an urban interface. Monitoring development of pitch canker over a three period, from 1996 to 1999, showed disease to be more severe in small, isolated stands (including trees in "open spaces" within residential areas and native trees integrated into managed landscapes) than in large contiguous stands of *P. radiata*. Managed stands were fragmented to varying degrees, so more trees occupied edges, which may render them more prone to stress and may also enhance their exposure to inoculum.

Development of pitch canker on the Monterey Peninsula was also affected by location, with disease being more severe near the coast than farther inland (Wikler et al. 2003). This geographic effect has remained apparent through 2013 (Gordon, unpublished results) suggesting that differential development of pitch canker by location is not an artifact of where the pathogen initially became established. More rapid development of pitch canker near the coast might reflect differences in the activity of insect vectors or wounding agents. For example, the spittlebug, *Aphrophora canadensis*, which creates wounds that can serve as infection courts (Storer et al. 1998b), appears to be more common in coastal areas than farther inland and therefore may contribute to a geographic effect on disease severity. In addition, longer periods of free moisture on host surfaces owing to frequent intervals of fog in the coastal zone could increase the efficiency of the infection process relative to drier inland locations. This concept is supported by studies under controlled conditions that document a significant effect of ambient humidity on the frequency of infections mediated by twig beetles (*Pityophthorus* spp.) (Sakamoto et al. 2007).

23.4 The Role of Insects

The association of the pitch canker pathogen with twig beetles and other insects such as engraver beetles (*Ips* spp.) has greatly facilitated expansion of the pitch canker infestation in California. Insects were recognized as wounding agents in the SE U.S. but were regarded as less important than wounds caused by weather or silvicultural practices (Dwinell et al. 1985). In California forests, insects appear to play a more important role. In the initial report of pitch canker in California, McCain et al. (1987) described recovery of *F. circinatum* from larvae of *Pityophthorus* spp. found beneath the bark on diseased branches. These insects were well known as colonizers of dead and declining branches, and branches affected by pitch canker proved to be an additional resource for them. Subsequent work showed a significant association of *Pityophthorus* spp. with symptomatic branches, and most of the emerging beetles carried propagules of the pitch canker pathogen (McNee et al. 2002). However, because emerging adults immediately seek weakened host material in which to breed, it was not clear why *Pityophthorus* spp. would visit a healthy branch, as would be required to establish an infection. In contrast, the vector of Dutch elm disease, *Scolytus multistriatus*, must feed on a healthy tree before establishing a gallery in a declining (and possibly diseased) tree (Webber 1990), so vectoring is a natural consequence of the insect's life history. Twig beetles appear to meet the requirements for vectoring *F. circinatum* in a more circuitous manner, reflecting limitations on their ability to locate a substrate in which to breed.

Trapping studies conducted in a Monterey pine forest showed that *Pityophthorus* spp. could not locate branches that were suitable for colonization prior to landing (Bonello et al. 2001a). This suggests that *Pityophthorus* spp. will occasionally land on healthy branches before finding one in which a gallery can be established. Assessing the acceptability of a branch may require exploratory feeding. To determine if this activity results in wounds that serve as infection courts, twig beetles (*P. setosus*) were allowed to move freely over the surface of trees to which spores of *F. circinatum* had been applied. Subsequent examination revealed a high frequency of pitch canker infections on trees explored by *P. setosus*, whereas control trees not visited by insects had no infections (Sakamoto et al. 2007). Similar results were obtained using *P. carmeli* (Sakamoto et al. 2007). These findings indicate that two native associates of *P. radiata* are capable of transporting the fungus and creating infection courts on healthy branches. That this actually occurs under natural conditions is supported by the results of field studies showing that trees baited with pheromones attractive to *Pityophthorus* spp. sustained significantly higher infection rates than trees that were not baited (Storer et al. 2004).

Wounds created by *Pityophthorus* spp. engaged in exploratory feeding would not be deep enough to reach moisture within living host tissue and hence there is a need for high ambient humidity or free moisture (most likely from condensation associated with fog) in order for spores to germinate. Shallow wounds heal quickly and so impose a narrow temporal window within which infection can occur. Studies conducted under field conditions showed that over 90 % of wounds inoculated immediately became infected, whereas the infection rate dropped to 20 % when inoculation was delayed for 2 days (Inman et al. 2008). For spore germination and growth to proceed quickly enough for the pathogen to establish an infection while the wound remains susceptible requires moist conditions coinciding with moderate temperatures (Inman et al. 2008).

23.5 Ecological Limits on the Range of Pitch Canker in California

Environmental limitations on the infection process appear to have defined the range of pitch canker in California. On the central coast, conditions that are conducive to infection occur throughout much of the year, and within this region few stands of susceptible pine species remain unaffected by pitch canker. However, even within the coastal zone, microclimatic variation can influence development of pitch canker.

As noted above, such an effect was evident on the Monterey Peninsula, where proximity to the coast was associated with greater severity of pitch canker.

Pitch canker affects native and planted pines as far north as 39°N latitude (approximately 160 km north of San Francisco) but has failed to become established in stands of susceptible species (native shore pine and bishop pine, and planted Monterey pine) farther north. The absence of pitch canker in this area presumably reflects the fact that temperatures tend to be relatively low during periods when moisture is available, limiting the frequency and duration of intervals suitable for infection. The same limitations apply to more inland locations, though perhaps not to the same degree. In 2003, pitch canker was discovered in the Sierra Nevada, approximately 110 km east of what had been the most inland location where the disease was known to occur (Vogler et al. 2004). The pathogen was isolated from symptomatic *P. menziesii* in a breeding orchard and was also recovered from branch washings of nearby symptomless trees. These findings confirmed that *F. circinatum* can survive and infect trees at an elevation of approximately 1000 M in the Sierra Nevada foothills. As such the disease may pose a threat not only to *P. menziesii* but also to native pines such as *P. lambertiana* (sugar pine), *P. coulteri* (coulter pine) and *P. ponderosa* (ponderosa pine), all of which are known to be susceptible to pitch canker based on greenhouse tests (Gordon et al. 2001). Conditions that are conducive for infection would be expected to occur at times in the Sierra Nevada during spring and fall. Whether or not these infection windows will prove to be sufficient for pitch canker to become established in this area remains to be seen. Presently it appears that eradication efforts were successful, as there have been no reports of the disease in the Sierra Nevada since affected trees were burned shortly after pitch canker was identified.

23.6 Host Susceptibility to Pitch Canker

Early studies of disease progression in California showed most Monterey pines to be susceptible to pitch canker, with only 2 % of trees remaining free of disease over a 4-year monitoring period (Storer et al. 2002). Disease progress was quite rapid in plots with mean disease ratings of moderate or severe, but the increase was more gradual in plots with lower severity ratings. Thus, in first few years following establishment in a stand of *P. radiata*, many trees became infected before the disease intensified in infected trees. This pattern would be consistent with random branch selection by insects vectoring the pathogen, such that when disease incidence is low, new infections are more likely to occur on previously uninfected trees than on trees already infected. As the incidence of pitch canker increases, random selection by insects is more likely to result in infection of branches on trees that have already sustained infections, rather than on the few remaining trees that are free of disease (Storer et al. 2002). Hence, disease incidence increases more rapidly than disease severity.

In the early years of the epidemic in California, pitch canker was a cause of widespread damage to both planted and native stands of *P. radiata*, consistent with the impact of an exotic pathogen on a naïve host population devoid of resistance. The progressive nature of the disease as it affected *P. radiata* contrasted with the manifestation of pitch canker in the southeastern United States, where trees were commonly observed to recover from the disease (Dwinell et al. 1985). This distinction appeared to be consistent with greater inherent (i.e., genetically determined) susceptibility of *P. radiata* as compared to southern pines such as *P. taeda* (loblolly pine). However, over time it became apparent that the inherent susceptibility of an individual tree was not the sole determinant of the impact of pitch canker on that tree.

As the range of pitch canker expanded in California, clear distinctions became apparent between stands in areas where the disease was of recent occurrence and severity increased rapidly, and stands in areas where pitch canker was of longer residence and the visual impact had diminished. To better understand the basis for this change, plots originally established in 1992 (Storer et al. 2002) were re-surveyed in 1999. This assessment revealed that many trees observed to be severely diseased in 1996 were disease-free 3 years later (Gordon et al. 2001). This phenomenon of "disease remission" required both that existing infections became inactive and that new infections either did not occur or failed to become symptomatic. The first requirement is satisfied by the fact that individual infections do limited damage and growth of branches subtending the affected node will eventually mask a killed branch, provided the tree has not become too debilitated by disease or other forms of stress. The absence of new infections could have many causes, including the possibility that a tree has become less susceptible to pitch canker.

Studies conducted under controlled conditions demonstrated that resistance to pitch canker can be elevated in trees as a result of prior exposure to the pathogen (Bonello et al. 2001b). To determine if this phenomenon could explain disease remission in *P. radiata*, symptomless trees that had been severely diseased were inoculated to obtain a direct measure of susceptibility. The results showed 89 % of trees in remission to be resistant to pitch canker, based on the length of the lesion that developed at the site of inoculation (Gordon et al. 2011), providing evidence for systemic induced resistance (SIR) to pitch canker in *P. radiata*. Further support for the operation of SIR in natural populations of *P. radiata* derives from the fact that trees in areas where pitch canker was well established were significantly less susceptible to the disease than trees in areas where pitch canker was a more recent occurrence. This is consistent with elevated resistance in trees with a longer period of exposure to the pitch canker pathogen (Gordon et al. 2011).

It seems likely that SIR is an important part of the explanation for stabilization of pitch canker in Monterey pine forests, where disease severity has not increased since 1999 (Gordon, unpublished data). The low rate of mortality observed in native stands of *P. radiata* contrasts with a much more dramatic impact of pitch canker on landscape plantings of this species. Extensive mortality occurred in stands that were located outside the native range of *P. radiata*, and most tree deaths occurred during a protracted drought between 1987 and 1991. Thus, the impact of pitch canker was likely aggravated by stress, and hence native populations may also suffer high mortality where and when drought stress occurs in stands affected by pitch canker.

Disease development in a native population of *P. muricata* appears to be consistent with this expectation. At Pt. Reyes National Seashore on the California coast north of San Francisco, a stand replacement fire occurred in 1995. Thereafter, abundant regeneration resulted in dense stands of *P. muricata* that far exceeded historic stocking levels. Consequently, trees were likely subjected to drought stress, and this may have facilitated the rapid development of pitch canker that was observed between 2007 and 2009. Since that time disease severity has continued to increase. Based on plots that were established at the periphery of infection centers, mean disease severity (as a percent of maximum) rose from 2 % in 2011 to 6 % in 2012, 11 % in 2013, and 17 % in 2014 (Gordon, unpublished data).

23.7 Management

A principal focus of management of pitch canker in native populations should be on limiting opportunities for expansion of the infestation. To this end, branches removed from infected trees should be disposed of locally either by burning or chipping and composting. Chipping has the benefit of reducing insect emergence, but *F. circinatum* can survive in chipped wood for one year or more (McNee et al. 2002). For this reason, further treatment may be desirable. Agustí-Brisach et al. (2012) reported that *F. circinatum* was killed by temperatures above 50 °C under controlled conditions. Consistent with that result, exposure to moist heat (50 °C or higher) for 10 days was found to eliminate the pathogen in branches taken from infected trees (Gordon, unpublished data). Based on these findings, proper composting should be sufficient to eliminate *F. circinatum* from infested material. *Fusarium circinatum* can survive in logs cut from diseased trees for up to 18 months. To prevent dissemination of the pathogen, logs can be heated to reach a minimum continuous core temperature of 70 °C for more than 4 h, or fumigated with an effective material such as sulfuryl fluoride.

In stands affected by pitch canker, management should aim to promote regeneration and to achieve stocking densities that reduce the likelihood of water stress. Intraspecific variation in susceptibility to pitch canker is common in pines, and progeny that are relatively resistant to the disease should be favored by natural selection. Maximizing opportunities for regeneration should minimize the time required for populations to adapt to the presence of pitch canker. Where mortality is extensive, it may be necessary to suppress the growth of invasive plant species, which might otherwise cover open ground to the exclusion of pine seedlings.

Although pitch canker is now found throughout the world, susceptible species are grown in many locations where the disease does not yet occur. Consequently, quarantine restrictions remain important. Such restrictions should focus on preventing importation of infected or infested plant material, of which seed is of particular concern. Seed can carry the pathogen both externally and internally, and seems likely to have been the vehicle for movement of *F. circinatum* to many of the countries where pitch canker is now problematic (Wingfield et al. 2008). Spores of *F. circinatum* may be found on seeds collected from healthy trees, if neighboring trees are infected.

Seedlings that emerge from infested seed may die quickly, but some sustain root infections that do no damage and hence will not be detectable by visual surveys (Storer et al. 1998a). In fact, it is now apparent that *F. circinatum* can establish a biotrophic relationship with pine seedlings, growing within roots that show no symptoms (Swett et al. 2015). Under controlled conditions, above-ground symptoms were observed to precede visible damage to the root system, suggesting that root decay was not the cause of seedling death but rather was a secondary consequence of girdling of the root collar (Swett et al. 2015). If so, root symptoms are not an early indication of disease and would not serve as a useful means of detecting seedlings infected by *F. circinatum*.

Given that even rigorous procedures may fail to detect *F. circinatum* in seedlings before it has induced symptoms, by the time an infestation is recognized it may be too widespread to contain. For this reason, in countries where pitch canker is regarded as a threat to indigenous species or to exotic plantations, a ban on importation of pine seed may be advisable. Although seed is of primary concern, other forms of plant material require attention as well. This is well documented by the detection of *F. circinatum* in Douglas-fir cuttings in quarantine in New Zealand (Vogler et al. 2004), which prevented introduction of the pitch canker pathogen into a country where extensive plantations of *P. radiata* would be at risk.

23.8 Conclusions

The saga of pitch canker in California shows how a pathogen already present in the continental U.S. can display characteristics of an invasive species when moved beyond its established range, underscoring the risks inherent in moving plant materials. Although enough was known about pitch canker to have anticipated the risk to *P. radiata*, nothing in the history of this disease suggested that it would be a threat to trees in native forests. Likewise the importance of relationships that were established between *F. circinatum* and insect associates of native California pines could not have been anticipated. Although some of the insects that vector *F. circinatum* can be damaging to trees independently of the pathogen, twig beetles were regarded as benign colonizers of branches that were dead or suppressed to the point that they were no longer productive. By chance, the life history of twig beetles allows species in this genus to serve as vectors of the pitch canker pathogen, and the present association might represent an initial step toward a more enduring symbiotic relationship. Lastly, pitch canker in California has revealed a form of physiological plasticity (SIR) in *P. radiata* that appears to have allowed genetically susceptible trees to adapt to an exotic pathogen. If operative in other species, SIR, can help to explain, how long-lived perennials have survived the ravages of parasitic microbes that have generation times orders of magnitude shorter than their host plant.

References

Agusti-Brisach C, Pérez-Sierra J, Armengol J et al (2012) Efficacy of hot water treatment to reduce the incidence of *Fusarium circinatum* on *Pinus radiata* seeds. Forestry 85:629–635

Barrows-Broaddus J, Dwinell LD (1983) Histopathology of *Fusarium moniliforme* var. *subglutinans* in four species of southern pines. Phytopathology 73:882–889

Bonello P, McNee WR, Storer AJ et al (2001a) The role of olfactory stimuli in the location of weakened hosts by twig-infesting *Pityophthorus* spp. Ecol Entomol 26:8–15

Bonello P, Gordon TR, Storer AJ (2001b) Systemic induced resistance in Monterey pine. For Pathol 31:99–106

Desjardins AE, Plattner RD, Gordon TR (2000) *Gibberella fujikuroi* mating population A and *Fusarium subglutinans* from teosinte species and maize from Mexico and Central America. Mycol Res 104:865–872

Dwinell LD, Barrows-Broaddus JB, Kuhlman EG (1985) Pitch canker: a disease complex of southern pines. Plan Dis 69:270–276

Fox JW, Wood DL, Koehler CS et al (1991) Engraver beetles (Scolytidae: *Ips* species) as vectors of the pitch canker fungus, *Fusarium subglutinans*. Can Entomol 123:1355–1367

Friel CJ, Desjardins AE, Kirkpatrick SC et al (2007) Evidence for recombination and segregation of virulence to pine in a hybrid cross between *Gibberella circinata* and *G. subglutinans*. Mycol Res 111:827–831

Gordon TR, Storer AJ, Wood DL (2001) The pitch canker epidemic in California. Plant Dis 85:1128–1139

Gordon TR, Kirkpatrick SC, Aegerter BJ et al (2006) Susceptibility of Douglas fir (*Pseudotsuga menziesii*) to pitch canker, caused by *Gibberella circinata* (anamorph = *Fusarium circinatum*). Plant Pathol 55:231–237

Gordon TR, Kirkpatrick SC, Aegerter BJ et al (2011) Evidence for the occurrence of induced resistance to pitch canker, caused by *Gibberella circinata* (anamorph *Fusarium circinatum*), in populations of *Pinus radiata*. For Pathol 41:227–232

Guerra-Santos JJ (1999) Pitch canker in Monterey pine in Mexico. In: Devey M, Matheson C, Gordon T (eds) Current and potential impacts of Pitch Canker in Radiata Pine. Proceedings of IMPACT Monterey workshop, Monterey. CSIRO, Australia, pp 58–61

Hepting GH (1961) *Pinus radiata* susceptible to pitch canker. Plant Dis Rep 45:889–890

Hepting GH, Roth ER (1946) Pitch canker, a new disease of some southern pines. J For 44:742–744

Inman AR, Gordon TR, Kirkpatrick SC et al (2008) Limiting effects of low temperature on growth and spore germination in *Gibberella circinata*, the cause of pitch canker in pine species. Plant Dis 92:542–545

McCain AH, Koehler CS, Tjosvold SA (1987) Pitch canker threatens California pines. Calif Agric 41:22–23

McNee WR, Wood DL, Storer AJ et al (2002) Incidence of the pitch canker pathogen and associated insects in intact and chipped Monterey pine branches. Can Entomol 134:47–58

Sakamoto JM, Gordon TR, Storer AJ et al (2007) The role of *Pityophthorus* spp. as vectors of pitch canker affecting *Pinus radiata*. Can Entomol 139:864–871

Schmale DG, Gordon TR (2003) Variation in susceptibility to pitch canker disease, caused by *Fusarium circinatum*, in native stands of *Pinus muricata*. Plant Pathol 52:720–725

Slinski SL, Zakharov F, Gordon TR (2015) The effect of resin and monoterpenes on spore germination and growth in *Fusarium circinatum*. Phytopathology 105:119–125

Storer AJ, Gordon TR, Clark SL (1998a) Association of the pitch canker fungus, *Fusarium subglutinans* f. sp. *pini* with Monterey pine seeds and seedlings in California. Plant Pathol 47:649–656

Storer AJ, Wood DL, Wikler KR et al (1998b) Association between a native spittlebug (Homoptera: Cercopidae) on Monterey pine and an introduced tree pathogen which causes pitch canker disease. Can Entomol 130:783–792

Storer AJ, Wood DL, Gordon TR (2002) The epidemiology of pitch canker of Monterey pine in California. For Sci 48:694–700

Storer AJ, Wood DL, Gordon TR (2004) Twig beetles, *Pityophthorus* spp. (Coleoptera: Scolytidae), as vectors of the pitch canker pathogen in California. Can Entomol 136:685–693

Swett CL, Gordon TR (2012) First report of grass species (Poaceae) as naturally occurring hosts of the pine pathogen *Gibberella circinata*. Plant Dis 96:908–908

Swett CL, Gordon TR (2015) Endophytic association of the pine pathogen *Fusarium circinatum* with corn (*Zea mays*). Fungal Ecol 13:120–129

Swett CL, Porter B, Fourie G et al (2014) Association of the pitch canker pathogen *Fusarium circinatum* with grass hosts in commercial pine production areas of South Africa. Southern For 76:161–166

Swett CL, Kirkpatrick SC, Gordon TR (2015) Evidence for a hemibiotrophic association of the pitch canker pathogen, *Fusarium circinatum*, with *Pinus radiata*. Plant Dis (in press)

Vogler DR, Gordon TR, Aegerter BJ et al (2004) First report of the pitch canker fungus (*Fusarium circinatum*) in the Sierra Nevada of California. Plant Dis 88:772–772

Webber JF (1990) Relative effectiveness of *Scolytus scolytus*, *Scolytusmultistriatus* and *Scolytus kirschi* as vectors of Dutch elm disease. Eur J For Pathol 20:184–192

Wikler K, Gordon TR (2000) An initial assessment of genetic relationships among populations of *Fusarium circinatum* in different parts of the world. Can J Bot 78:709–717

Wikler KR, Storer AJ, Newman W et al (2003) The dynamics of an introduced pathogen in a native Monterey pine (*Pinus radiata*) forest. For Ecol Manage 179:209–221

Wingfield MJ, Hammerbacher A, Ganley RJ et al (2008) Pitch canker caused by *Fusarium circinatum*: a growing threat to pine plantations and forests worldwide. Australas Plant Pathol 37:319–334

Chapter 24
Insects Colonizing Eucalypts in California

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Abstract The Mediterranean climate zone in North America is restricted to the states of California in the USA and parts of Baha California Norte in Mexico. As described in other chapters in this volume, the climate is characterized by cool wet winters and hot dry summer conditions. The greatest amount of precipitation falls in the late fall and winter months. The remainder of the year is dry. Eucalypts were introduced from Australia as seed in the mid nineteenth century and have been widely planted in California. Although there have been a few rare reports of occasional host use, no native insect species have undergone a host shift onto the trees. Until the mid 1980s there were only two exotic insects that feed on eucalypts introduced from Australia to California. In a 20 year period beginning in 1984, 16 exotic insects from four feeding guilds established in the state. Three of these insects are under complete biological control [the blue gum psyllid (*Ctenerytinae eucalypti* (Maskell)), the eucalyptys longhorned borer (*Phoracantha semipunctata* F), and the eucalyptus snout weevil (*Gonipterus scutellatus* Gyll.)] are under complete biological control. Several more [the red gum lerp psyllid (*Glycaspsis brimblecombei* Moore), the lemon gum psyllid (*Cryptoneossa triangular* Taylor), the spotted gum psyllid (*Eucalytolyma maideni* Froggatt), and, possibly, a second longhorned borer (*Phoracantha recurva* Newman)] are under partial biological control. The introductions have continued since 2004, but at a much slower pace than the previous 20 years. Although there have been differences in the patterns of introductions of insects that feed on eucalypts in different Mediterranean climates zones, the community of insects is becoming homogenized as movement of people and goods continues to spread the insects into new areas. The management approaches developed in one part of the Mediterranean world will find broader applications in other parts of that world as the movement of invasive arthropods continues.

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24.1 Eucalyptus in California

Eucalypts, species in the genera *Angophora*, *Corymbia*, *and Eucalyptus*, are such common sights throughout the state that many visitors to California accept the trees as native. However, the trees were introduced into the states in the mid nineteenth century and were planted from seed. There are approximately 90 species that have been planted in the state (Doughty 2000); some are planted as individual specimen trees in botanic gardens and approximately ten species that are widely planted. The trees were highly valued for their rapid and vigorous growth, tolerance of drought and poor soils, and their horticultural characteristics (e.g., Ingham 1908). Although initially planted for use as railroad ties and mine timbers, they were also widely planted for use as wind breaks, fuel wood, shade, and ornamental trees (Doughty 2000). Small plantations have been established in some parts of the state for the commercial production of ornamental foliage for use in flower arrangements and decoration (Dahlsten et al. 1998b; Bethke 2007).

There have been a number of attempts to grow commercial plantations of eucalypts for biomass production for cogeneration electrical power plants or as a local supply of fuel-wood. The popularity of these efforts rises as the cost of oil rises and falls and the price of water for irrigation increases. These plantations often receive little care once established. Unlike other parts of the world, including other regions with Mediterranean climates, there has been little interest in growing eucalypts for cellulose. There has been only one recent attempt to grow plantations of eucalypts for cellulose specifically for the paper industry. The plantation was established in a region of the state with poor soils, cold winter temperatures, and limited rainfall. Irrigation was provided initially to get the trees established, but discontinued after a few years. Unfortunately the enterprise did not meet the commercial expectations and was abandoned.

24.2 Native Insect Species on Eucalypts

Because the trees were initially brought as seed, no insect herbivores were introduced with them, and very few native insects expanded their host ranges to include eucalypts as host plants. The Myrtaceae are most commonly native to the Southern Hemisphere and the Neotropics; there are no native species of myrtaceous plants in California (Munz 1959). Consequently, there is not a native insect community that would make an easy host shift between members of the same plant family. These shifts in host range have been commonly observed in South America and in South Africa as insects move from native myrtaceous plants to the introduced eucalypts (Paine et al. 2011). There are occasional reports in California of generalist herbivores feeding on eucalypt foliage (e.g., grasshoppers) or on plant fluids (e.g., cicadas). The cerambycid, *Xylotrechus nauticus* (Mannerheim), known as either the nautical borer or the oak cordwood borer, is a native insect that colonizes a wide range of hardwood species (Brown and Eads 1965). Females of this borer will oviposit on dead and dying eucalypts and the larvae can complete their development on these trees. However, it has not been reported from living trees.

There has been a unique example of a generalist exotic insect that utilizes eucalypts in addition to a side range of other host trees. The glassy-winged sharpshooter, *Homaladisca vitripennis* (Germar) (Hemiptera, Ciccadellidae) was introduced into California from southeastern North America (Varela et al. 2007). It is of particular concern because it is an important vector of a bacterial plant pathogen that can kill important agricultural crops, including grapes. The nymphs and adults need on nutritionally poor xylem fluids, so they process large volumes of fluids through their bodies. They are also active throughout the year. The eucalypts retain their foliage throughout the year and can be used by the sharpshooter when deciduous potential hosts have lost their leaves. Consequently, they can serve as a reservoir for the insect during winter and a source of populations moving into agricultural crops in the spring.

24.3 First Introductions of Exotic Eucalypt Herbivores into California

The first two exotic eucalypt-feeding insects were introduced into California in the middle of the last century. The seed galling eulophid wasp, *Quadrastichodella nova* Girault, was reported by Timberlake (1957) but could have arrived much earlier in shipments of seeds. The acacia psyllid, *Acizzia uncatoides* (Ferris & Klyver), was introduced in 1954 (Ulyshen and Miller 2007). Although occasionally reported colonizing eucalypts, the trees are not the normal host for the psyllid. Other than these two early introductions of eucalyptus feeding insects from Australia, there were no further introductions of significant pests of eucalypts into California until the latter part of the twentieth century. Between 1984 and 2008, however, 16 Australian species distributed across four different feeding guilds (two species of coleopteran wood borers, three species of coleopteran defoliators, eight species of fluid feeding psyllids, and three species of hymenopteran gallers) were introduced into California (Paine et al. 2010).

24.4 Coleopteran Borers

The first invasive wood borer, the eucalyptus longhorned borer, *Phorcantha semipunctata* F., was introduced into California in 1984 was (Gill 1998) (Fig. 24.1). Detected first in southern California, the beetle quickly spread around the state and killed large numbers of trees (Hanks et al. 1993a). Adults are attracted to volatile chemicals emanating from stressed, dying, recently killed, or damaged eucalyptus

Fig. 24.1 *Phoracantha semipunctata* adult feeding on pollen and nectar

trees (Hanks et al. 1996a, 1998a), and beetles can fly long distances to locate suitable resources (Hanks et al. 1998a). Females oviposit on the bark surface, typically under exfoliating bark or in bark cracks and crevices. Neonate larvae penetrate through the outer bark and initiate feeding at the interface of the cambium and xylem. Larval feeding can effectively girdle and kill living trees (Hanks et al. 1993a) (Fig. 24.2).

Differences in host tree species susceptibility to infestation and suitability for larval development may affect beetle population dynamics (Hanks et al. 1991, 1993b, 1995a). In studies conducted in California, *E. trabutii* Vilmorin and *E. camaldulensis* were more attractive to ovipositing females than *E. cladocalyx* F., *E. grandis* Hill ex Maiden, or *E. tereticornis* Small, but very high infestation densities in the most attractive species in the field resulted in lower beetle survival due to competition among larvae (Hanks et al. 1993b). Larval survival can be reduced by cannibalism when larval density is high and adult fitness may also be reduced if larvae feed on low quality food resources (Hanks et al. 1993b; Paine et al. 2001; Powell 1978, 1982). Larvae developing in poor quality resources often take longer to develop and are smaller as adults than are individuals from high quality resources (Hanks et al. 1995a). The extent of drying of the host tissue is a significant factor in nutritional quality for developing beetle larvae; the suitability of *Eucalyptus* for neonate larval survival is a direct function of bark moisture content (Hanks et al.

Fig. 24.2 *P. semipunctata* egg galleries resulting from a single egg mass oviposited on the bark surface

1991, 1995c, 1999). Newly-eclosed larvae are unable to reach the cambium if bark moisture content is too high, larval survival is greatly improved if bark moisture is below 55 %, and survival declines as the bark becomes progressively drier.

Interactions between the beetle, host tree susceptibility, and host tree suitability, as well as intraspecific competitive interactions, are important in population regulation of the *P. semipunctata* in California. The beetles, however, are also subject to mortality from natural enemies (Paine et al. 1997). Egg and larval parasitoids have been released for biological control. The larval parasitoids (Joyce et al. 2002, 2011; Millar et al. 2002; Paine et al. 2011) have not successfully established. The egg parasitoid *Avetianella longoi* Siscaro (Fig. 24.3) has been introduced into California from Australia and has achieved complete biological control of the beetle (Hanks et al. 1995b, 1996b).

Unfortunately, a second species, *Phoracantha recurva* Newman, was detected in southern California in 1995 (Hanks et al. 1998b) and has replaced *P. semipunctata* (Fig. 24.4). The more recently introduced borer species appears to have very similar

Fig. 24.3 The egg parasitoid *Avetianella longoi*

Fig. 24.4 *Phoracantha recurva* is shown on the left and *P. semipunctata* on the right

ecological requirements to *P. semipunctata*, but it does not have an obligatory diapause observed in *P. semipunctata*, so it is active longer in the year (Bybee et al. 2004a, b). When colonizing the same host materials, there were differences in survival between the two species, but there does not appear to be interspecific competition (Eatough-Jones et al. 2015).

Replacement of one species of borer by the congener appears to have been a result of biological control. Although parasitized by *A. longoi*, eggs of *P. recurva* were not preferred by host-seeking wasps and they were much less a suitable for wasp development as those of *P. semipunctata* (Luhring et al. 2000, 2004). In fact, eggs of *P. recurva* were capable of encapsulating and killing the parasitoid eggs (Reed et al. 2007). A second strain of *A. longoi* was collected specifically from *P. recurva* eggs in Australia (Wang et al. 2008). The two borers were in sympatry in the part of Australia where the collections were made, as were the two strains of parasitoids. The strains of parasitoids are indistinguishable from one another using either morphological or genetic characters, so the only way to ensure that a *P. recurva* strain was collected was to make sure that only *P. recurva* eggs were available. Ovipositing *P. recurva* females were caged on suitable eucalypt logs in a way that allowed parasitoids to have access to the eggs laid on the logs, but also exclude any other species of beetles from laying eggs. The egg parasitoids were returned to quarantine in California for processing and rearing before finally being released for biological control of *P. recurva*. Parasitized eggs have been recovered from release sites (TDP pers. obs.) so it appears to have established successfully. To date, however, it has been difficult to fully evaluate the effectiveness of the introduction of the second *Avetianella* strain.

24.5 Coleopteran Defoliators

The eucalyptus snout beetle, *Gonipterus scutellatus* Gyll. (Coleoptera: Curculionidae) (Fig. 24.5), was discovered defoliating eucalyptus in California in 1994 (Cowles and Downer 1995). This insect has been introduced into several eucalyptus-growing regions around the world from Australia early in the twentieth century and has caused extensive damage wherever it has become established. In California, the initial infestations were in blue gums grown as windbreaks between agricultural fields. The trees were stripped of the leaves very quickly by the feeding larvae. The young larvae trench the leaves but the older larvae consume the entire leaf (Fig. 24.6). The very egg parasitoid, *Anaphes nitens* (Girault) (Fig. 24.7), had been collected from Australia and successfully established in many parts of the world, providing effective biological control. The parasitoid was obtained from South African collaborators, processed through the necessary quarantine and regulatory requirements, and introduced into the infested regions of southern California in 1996. In a remarkably short time, densities of beetle larvae had dropped to barely detectable levels by 1997 (Hanks et al. 2000). To date, that control has been maintained. Fortunately, other members of the group of cryptic sibling species (Mapondera et al. 2012) that have been introduced into other parts of the world with Mediterranean climates (Reis et al. 2012) have not been detected in the state.

Two chrysomelid leaf beetles have been introduced in the last two decades. The eucalyptus tortoise beetle, *Trachymela sloanei* (Blackburn) (Fig. 24.8), was first collected in southern California in March of 1998 (Gill 1998). All life stages of the

Fig. 24.5 Adult eucalyptus snout weevil, *Gonipterus scutellatus*

Fig. 24.6 Larvae of *G. scutellatus* trench the leaves in the early instars but consume the entire leaves during the late instars

Fig. 24.7 The egg parasitoid, *Anaphes nitens*, has established complete biological control of the eucalyptus snout weevil in California

Fig. 24.8 Adults of the chrysomelid, *Trachymela sloanei*, feed on foliage at night and hide under loose bark during the day

Fig. 24.9 *T. sloanei* larvae are nocturnal foliage feeders and hide under loose bark during the day

insect are cryptically colored, blending in with the bark of eucalyptus trees where they typically remain hidden during the day (Fig. 24.9). Adults and larvae feed on leaves and young stems, but of particular importance, adults will clip off young, tender leaf shoots as the tree attempts to refoliate. Unfortunately, the preferred hosts are members of the red gum species group. During the period following the initial introduction of the leaf beetle, the trees were often simultaneously infested by both the red gum lerp psyllid (see below) and the beetle. The trees would suffer significant defoliation as a result of heavy psyllid infestations, and as they attempted to refoliate, those young leaves would either be food for beetle larvae or the leaf shoots would be clipped by adults. Consequently, the trees were under very significant growth stress. In an effort to establish biological control, large numbers of the egg parasitoid *Enoggera reticulata* Naumann were released in California. This parasitoid was originally recovered from eggs of *Trachymela tinticollis* (Blackburn) in Australia, rather than *T. sloanei*. It was hoped that the parasitoid would successfully shift onto the congener. Unfortunately, there was no evidence of establishment (Millar et al. 2009), and it is unclear if that was a result of species incompatibility or a failure to adapt to the new environment.

The second chrysomelid beetle, *Chrysophtharta m-fuscum* (Boheman), was introduced into southern California in 2005 (von Ellenreider 2003). Unlike *T. sloanei*, the adults and larvae of this species are not cryptic (Fig. 24.10) and actively feed during the day, preferentially on blue-gums (Bethke 2007). The combined feeding effects of the leaf beetle and the shoot psyllids can cause significant damage to commercial eucalyptus foliage production. As part of normal cultural practices for this industry, the trees are cut back to main scaffold branches each year to keep the trees short in stature and to stimulate the epicormic buds. The epicormic shoots are produced in response to the severe pruning treatment and these young shoots are

Fig. 24.10 The adults and larvae of *Chrysophtharta m-fuscum* are conspicuous during the day

harvested for sale. Damage to the leaves caused by feeding beetles and distortion caused by the psyllids greatly reduces the value of the foliage. Control is maintained solely through the use of insecticides (Bethke 2007).

24.6 Hemipteran Fluid Feeders

At least eight Australian psyllid species have been introduced into North America (*Ctenerytinae eucalypti* (Maskell), *Glycaspsis brimblecombei* Moore, *Eucalytolyma maideni* Froggatt, *Blastopsylla occidentalis* Taylor, *Ctenarytaina longicauda* Taylor, *Ctenarytaina spatulata* Taylor, *Acizzia uncatoides* (Ferris & Klyver), and *Cryptoneossa triangular* Taylor) (Paine et al. 2010). As noted previously, the acacia psyllid, *A. uncatoides*, was introduced in the decade of the 1950s and only occasionally shifts onto eucalypts as a host plant. The free-living psyllids, *B. occidentalis*, *C. longicauda*, and *C. spatulata*, were introduced more than 30 years after *A. uncatoides*. Although they may colonize a variety of eucalyptus hosts, they rarely cause significant damage (Brennan et al 2001; Brennan and Weinbaum 2001). However, the lerp-forming psyllids that have been introduced have caused critical problems with eucalypts.

The blue gum psyllid, *C. eucalypti*, was discovered in California in 1991 (Gill 1998). Nymphal feeding on the young terminals and leaves causes serious damage to the foliage of members of the blue gum species group, including several species used for ornamental foliage production. In addition to leaf distortion the psyllid feeding caused a type of injury peculiar to this industry. Young shoots are harvested and either transported fresh to the foliage markets for use in flower displays or processed for use in dry arrangements. The cut ends of the shoots are placed in buckets containing a glycerol dye solution that is taken up by the transpiring foliage. The dyed shoots are then hug in ventilated spaces to dry before being offered for sale. Areas on the leaves where psyllids had fed took up the dyes unevenly compared to foliage that had been free of psyllids. The resulting product had an unappealing mottled appearance that was not suitable for the markets. However, release of the parasitoid, *Psyllaphagus pilosus* Noyes resulted in complete biological control (Dahlsten et al. 1998a, b) throughout the state.

The red gum lerp psyllid, *G. brimblecombei*, has killed thousands of host trees in California (Brennan et al. 1999). The feeding nymphs produce a conical cover, a lerp, of sugar and wax and feed under its protection (Fig. 24.11). Heavy infestations

Fig. 24.11 The nymphs of *Glycaspis brimblecombei* feed beneath sugary lerps they form from excrement and wax

Fig. 24.12 Redgum lerp psyllds can cause extensive defoliation resulting in a significant increase in fuel-loading and risk of urban wild fire

caused extensive defoliation of the trees. There were high levels of tree mortality following successive defoliation. Although mortality was a primary concern in urban forests, the defoliation itself resulted in large amounts of leaf litter building up under stands of red gums (Fig. 24.12). This accumulation of fuel in urban environments was of very great concern to urban foresters and fire protection agencies who feared the increased of urban wild fires. Much of the mortality was associated with sites that lacked any supplementary irrigation. In fact, high levels of supplemental water applied in the dry Mediterranean summer conditions makes the trees more resistant to psyllid infestations (Paine and Hanlon 2010). Although there are effective insecticides that can control psyllid populations (Paine and Hanlon 2010), the abundance of the hosts, the widespread nature of the infestations, and the cost of applications made this tactic difficult to implement. Consequently a permanent solution using biological control was undertaken.

An encyrtid parasitoid, *Psyllaephagus bliteus* Riek, has established good biological control of the red gum lerp psyllid in many parts of California (Daane et al. 2005; Dahlsten et al. 2005) and reports of psyllid-caused tree mortality are now rare. However, the effective biological control is not uniform across the state. The parasitoid is not as effective in regions of the state with high summer temperatures compared to more coastal regions (Daane et al. 2012). In addition, inconsistency in the biological control could also be a result of infection of the psyllid with an endosymbiotic bacterium that appears to confer some resistance in the psyllid to parasitism (Hansen et al. 2007).

Fig. 24.13 The spotted gum lerp psyllid nymphs construct linear open lerps on the leaf surface

The spotted gum lerp psyllid, *E. maideni*, colonizes leaves of spotted gum *Corymbia* (*Eucalyptus*) *maculata* (Hook) Hill & Johnson and lemon-scented gum *Corymbia* (*Eucalyptus*) *citriodora* (Hook) Hill & Johnson. It was first discovered in California in 2000 (Garrison and von Ellenreider 2003). Like other lerp-forming psyllids, this species produces a shelter on the leaf surface constructed primarily of sugars. The lerp is a flat feather shape, with many lateral ribs forming a narrowed tubular space, closed end at its inception and a larger, opened end that becomes broader as the lerp increases in size (Fig. 24.13). Occupied or abandoned lerps may be colonized by the free-living lemon gum psyllid, *C. triangular*. The lemon gum psyllid appeared in California in 1995 (Gill 1998). Lemon gum psyllid does not construct a lerp itself, but uses the lerps of spotted gum psyllid for shelter. Consequently, it may be living as a commensal organism within an occupied lerp. As such, lemon gum psyllid can occur in high numbers when spotted gum psyllid is present. Although infestations can be severe and honeydew production can be heavy, no tree mortality has been reported as a result of infestation by these psyllids. However, high levels of infestation of both the red gum lerp psyllid and the spotted gum psyllid resulted in changes in the arthropod community in leaf litter below the trees suggesting that there were significant community changes as a result of the introduction of these psyllids (Eatough Jones and Paine 2012).

A biological control program was initiated against the lerp forming, *E. maiden* with the expectation that reduction in the populations of this psyllid would also have consequences for populations of the commensal *C. triangula*. The nymphal parasitoid *Psyllaephagus parvus* Riek (Hymenoptera: Encyrtidae) was collected from Australia and established in a quarantine facility. In anticipation of the parasitoid release, a pre-release sampling program was conducted for 2 years in areas where releases were expected to be made. However, just weeks prior to the first release, the parasitoids were discovered in the field monitoring sites, apparently introduced by other means. In addition, *Psyllaephagus perplexans* Cockerell (Hymenoptera: Encyrtidae) was collected from lemon gum psyllid nymphs and from monitoring traps (Eatough Jones et al. 2011).

The populations of the two psyllids were greatly reduced following establishment of the natural enemies and did not return to the levels that had observed prior to the discovery of the parasitoids. The biological control of the two psyllids has been less than complete due, in part, to the presence of a hyperparasitoid that appears to reduce effectiveness of the primary natural enemies (Eatough Jones et al. 2011). Of all the herbivores that have been introduced into California, this insect herbivore/ natural enemy system is the first example where natural enemies have either accompanied the introduction of the herbivore or have been subsequently introduced unintentionally (Paine et al. 2010).

24.7 Hymenopteran Gallers

Five species of gall-forming eulophid wasps have been introduced into California (*Aprostocetus* sp. Westwood, *Epichrysocharis burwelli* Schauff, *Quadrastichodella nova* Girault, *Selitrichodes globulus* La Salle & Gates, and *Ophelimus maskelli* (Ashmead)) (Paine et al. 2010). *Quadrastichodella nova* is a seed-galling wasp and was introduced, probably with seed from Australia, in the mid-twentieth century (Timberlake 1957). Introduced in 1995, *Epichrysocharis burwelli* produces small, dark, pustule-like galls on the leaves of lemon-scented gums (Fig. 24.14) in California (Schauff and Garrison 2000). A more recent introduction, *S. globulus* produces galls on the small stems, petioles, and mid-rib of blue gums (LaSalle et al. 2009).

California was initially colonized by many species of psyllids while Europe was initially colonized by many species of gall wasps (Paine et al. 2011). However, these insects continue to colonize new portions of the world. The eulophid *Ophelimus maskelli* (Ashmead), introduced into Europe in 2000, was just recently discovered in California (Burks et al. 2015a). This gall wasp introduction has some similarity to the introductions of the spotted gum psyllid and the lemon gum psyllid, but also differed from all prior introductions, because it was accompanied by the introduction of at least one of its natural enemies (Burks et al. 2015b).

It is likely highly probable that other hymenopteran galling insects will be introduced into California. As a specific example, *Leptocybe invasa* produces galls that swell stems, petioles, and leaf midribs (Mendel et al. 2004) has moved rapidly from Israel around the Mediterranean basin in a very short amount of time. It was recently reported from Florida in North America (Wiley and Skelley 2008), but it is not yet in California. However, if the pattern of movement of the insect is similar to what was observed throughout other eucalyptus growing regions of the world with Mediterranean climates then its arrival in California is not unexpected.

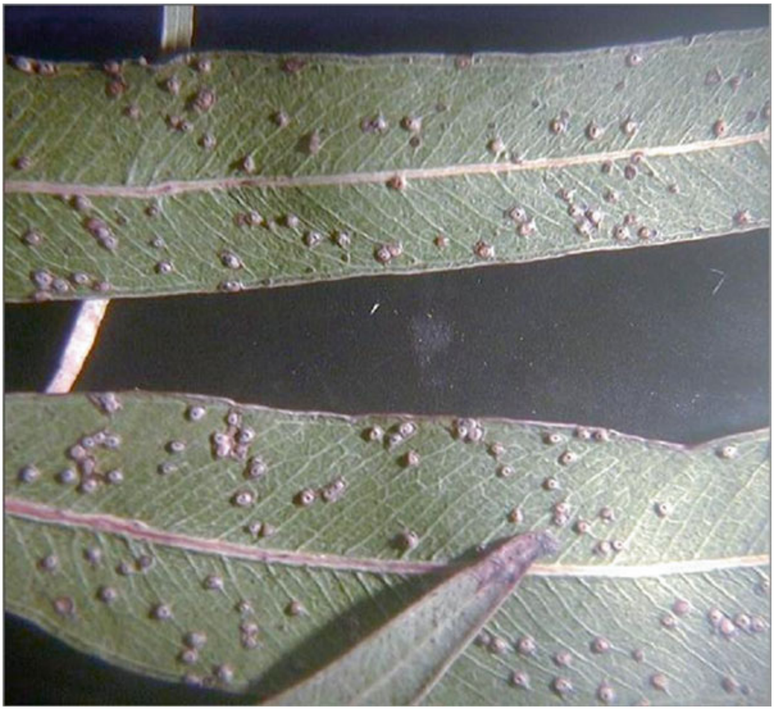

Fig. 24.14 *Epichrysocharis burwelli* pustule-like galls on the leaves of *Corymbia citriodora*

24.8 Conclusions

The Mediterranean climate zones in North America are confined to California on the south west coast of the United States and the northern portion of the state of Baja California Norte in Mexico. Eucalypts were first planted in the region in the middle of the nineteenth century and are now established broadly across this region. Although pest free for a century, the number of introductions exploded, at least 14 insect herbivores, in the two decades between 1985 and 2005. There were two introductions before that 20 year period and there have been two introductions since that time. There have been a number of hypotheses proposed to explain the dramatic pulse of introductions including increased movement of goods, increased movement of people, larger global distributions of the pest species, changes in the environment that would permit establishment, or intentional introductions (Paine et al. 2010). It is extremely doubtful that there is a single fundamental cause. However, one thing is undisputable; introductions will continue. These introductions will require a fundamental understanding of the interactions between the trees (including species specific interactions) and the herbivores, how cultural practices (e.g., irrigation) affect the community of insects colonizing the host trees, how management tactics directed against single members of the herbivore community affect other members of the community, and how introduction of natural enemies can be fostered. This is not a trivial issue in this system. Eucalypts have very strong supporters in the community, but they also engender very strong negative emotional reactions (Paine et al. 2010). This dichotomous response has been observed in other Mediterranean regions on all continents. In many ways, that may be the critical issue to maintain support for solving problems of introduced insects and diseases of these trees. The herbivore community presents a number of very interesting and complex challenges. However, these challenges can be addressed with both research and effective outreach. The difficulties lie not with the technical or economic issues, but with the social and political challenges of convincing affected parties that there is a large public and private benefit in devoting time and energy in the attempt.

There is no consequential eucalyptus industry in Mediterranean North America. Somewhat ironically, there appears to be a burgeoning interest in genetically modified eucalypts for cellulose production in the southeastern United States. It is still nascent, but there are efforts in place to obtain permission to plant genetically modified *Eucalyptus* sp. trees in experimental plantations. It is unclear how strong or how long this interest will be manifest. However, if it does continue, these commercial plantations will likely have to deal with the community of insect that have already been introduced. In California, the average eucalypt street tree has a value in excess of slightly under $6000 (Paine et al. 2015). The value of a tree in a cellulose plantation is substantially less, but the numbers are much greater. It is clear that the eucalypts represent an important economic value that merits protection. They also have critical aesthetic and ecosystem services value (McPherson et al. submitted). Fortunately, there is a large world-wide research community in place to help solve the problems. In addition, they are well poised through continued research efforts to solve the problems that will continue to arise as the community of insect herbivores becomes homogenized around the world.

References

Bethke JA (2007) *Chrysophtharta* control. CAPCA Advisor. June 2007. 10:20

Brennan EB, Weinbaum SA (2001) Effect of epicuticular wax on adhesion of psyllids to glaucous juvenile and glossy adult leaves of *Eucalyptus globulus* Labillardière. Aust J Entomol 40:270–277

Brennan EB, Gill RJ, Hrusa GF et al (1999) First record of *Glycaspis brimblecombei* (Moore) (Homoptera: Psyllidae) in North America: initial observations and predator associations of a potentially serious new pest of eucalyptus in California. Pan Pac Entomol 75:55–57

Brennan EB, Weinbaum SA, Rosenheim JA et al (2001) Heteroblasty in *Eucalyptus globulus* (Myricales: Myricaceae) affects ovipositional and settling preferences of *Ctenarytaina eucalypti* and *C. spatulata* (Homoptera: Psyllidae). Environ Entomol 30:1144–1149

Brown LR, Eads CO (1965) A technical study of insects affecting the oak tree in southern California. Calif Agricul Exp Stat Bulletin 810. Div Agricul Sci. Univ Calif, Berkeley, 105 pp

Burks RA, Mottern JL, Waterworth R et al (2015a) First report of the eucalyptus gall wasp, *Ophelimus maskelli* (Hymenoptera: Eulophidae), an invasive pest on *Eucalyptus*, from the United States. Zootaxa 3926:448–450

Burks RA, Mottern JL, Pownall NG et al (2015b) First record of *Closteroceruc chamaeleon*, a parasitoid of the eucalyptus gall wasp *Ohpelimus maskelli* (Hymenoptera, Chalcidoidea, Eulophidae), in the new world. ZooKeys 504:448–450

Bybee LF, Millar JG, Paine TD et al (2004a) Seasonal development of *Phoracantha recurva* and *P. semipunctata* (Coleoptera: Cerambycidae) in Southern California. Environ Entomol 33:1232–1241

Bybee LF, Millar JG, Paine TD et al (2004b) Effects of temperature on fecundity and longevity of *Phoracantha recurva* and *P. semipunctata* (Coleoptera: Cerambycidae). Environ Entomol 33:138–146

Cowles RS, Downer JA (1995) Eucalyptus snout beetle detected in California. Calif Agric 49:38–40

Daane KM, Sime KR, Dahlsten DL et al (2005) The biology of *Psyllaephagus bliteus* Riek (Hymenoptera: Encyrtidae), a parasitoid of the red gum lerp psyllid (Hemiptera: Psylloidea). Biol Control 32:228–235

Daane KM, Sime KR, Paine TD (2012) Climate and effectiveness of *Psyllaephagus bliteus* as a parasitoid of the red gum lerp psyllid. Biocon Sci Technol 22:1305–1320

Dahlsten DL, Hansen EP, Zuparko RL et al (1998a) Biological control of the blue gum psyllid proves economically beneficial. Calif Agric 52:35–40

Dahlsten DL, Rowney DL, Copper WA et al (1998b) Parasitoid wasp controls blue gum psyllid. Calif Agric 52:31–34

Dahlsten DL, Daane KM, Paine TD et al (2005) Imported parasitic wasp helps control red gum lerp psyllid. Calif Agric 59:229–234

Doughty RW (2000) The eucalyptus: a natural and commercial history of the gum tree. The Johns Hopkins University Press, Baltimore, 237 pp

Eatough Jones M, Paine TD (2012) Associations between invasive eucalyptus psyllids and arthropod litter communities under tree canopies in southern California. Entomol Exp Appl 43:280–291

Eatough Jones M, Daane KM, Paine TD (2011) Establishment of *Psyllaephagous parvus* and *P. perplexans* as serendipitous biological control agents of eucalyptus psyllids in southern California. BioControl 56:737–744

Eatough Jones M, Hanlon CC, Paine TD (2015) Potential for interspecific competition between congeneric longhorned beetle species in an adventive environment. Environ Entomol 44:960–965

Garrison RW, von Ellenreider N (2003) Spotted gum lerp psyllid (*Eucalyptolyma maideni*) Calif. Depart. Agricul. Pest sheets. CDFA, Sacramento, 4 pp

Gill RJ (1998) Recently introduced pests of *Eucalyptus*. Calif Plant Pest Disease Rep 17:21–24

Hanks LM, Paine TD, Millar JG (1991) Mechanisms of resistance in eucalyptus against the larvae of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) in California. Environ Entomol 20:1583–1588

Hanks LM, McElfresh JS, Millar JG et al (1993a) *Phoracantha semipunctata* (Coleoptera: Cerambycidae), a serious pest of *Eucalyptus* in California: biology and laboratory rearing procedures. Ann Entomol Soc Am 86:96–102

Hanks LM, Paine TD, Millar JG (1993b) Host species preference and larval performance in the wood-boring beetle *Phoracantha semipunctata* F. Oecologia 95:22–29

Hanks LM, Paine TD, Millar JG et al (1995a) Variation among eucalyptus species in resistance to eucalyptus longhorned borer in southern California. Entomol Exp Appl 74:185–194

Hanks LM, Gould JR, Paine TD et al (1995b) Biology and host relations of *Avetianella longoi*, an egg parasitoid of the eucalyptus longhorned borer. Ann Entomol Soc Am 88:666–671

Hanks LM, Millar JG, Paine TD (1995c) Biological constraints on host-range expansion by the wood-boring beetle *Phoracantha semipunctata* (Coleoptera: Cerambycidae). Ann Entomol Soc Am 88:183–188

Hanks LM, Millar JG, Paine TD (1996a) Mating behavior of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) and the adaptive significance of long “horns”. J Insect Behav 9:383–393

Hanks LM, Paine TD, Millar JG (1996b) A tiny wasp comes to the aid of California's eucalyptus trees. Calif Agric 50:14–16

Hanks LM, Millar JG, Paine TD (1998a) Dispersal of the eucalyptus longhorned borer (Coleoptera: Cerambycidae) in urban landscapes. Environ Entomol 27:1418–1424

Hanks LM, Paine TD, Millar JG et al (1998b) Another tree-killing pest of eucalyptus invades California. Calif Plant Pest Dis Rep 16:19–21

Hanks LM, Paine TD, Millar JG et al (1999) Water relations of host trees and resistance to the phloem-boring beetle *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). Oecologia 119:400–407

Hanks LM, Millar JG, Paine TD et al (2000) Classical biological control of the Australian weevil *Gonipterus scutellatus* (Coleoptera: Curculionidae) in California. Environ Entomol 29:369–375

Hansen AK, Jeong G, Paine TD et al (2007) Frequency of secondary symbiont infection in an invasive psyllid relates to parasitism pressure on a geographic scale in California. Appl Environ Microbiol 73:7531–7535

Ingham ND (1908) Eucalyptus in California. Univ Calif Agric Exp Stn Bull 196:25–112

Joyce AL, Millar JG, Paine TD (2002) The effect of host size on the sex ratio of *Syngaster lepidus*, a parasitoid of eucalyptus longhorned borers (*Phoracantha* spp.). Biol Control 24:207–213

Joyce AL, Millar JG, Gill JS et al (2011) Do acoustic cues mediate host finding by *Syngaster lepidus* Brullé (Hymenoptera: Braconidae)? BioControl 56:145–153

La Salle J, Arakelian G, Garrison RW et al (2009) A new species of invasive gall wasp Hymenoptera: Eulophidae: Tetrastichinae) on blue gum (*Eucalyptus globulus*) in California. Zootaxa 2121:35–43

Luhring KA, Paine TD, Millar JG et al (2000) Suitability of the eggs of two species of eucalyptus longhorned borers (*Phoracantha recurva* and *P. semipunctata*) as hosts for the parasitoid *Avetianella longoi* Siscaro. Biol Control 19:95–104

Luhring KA, Millar JG, Paine TD et al (2004) Oviposition preferences and progeny development of the egg parasitoid *Avetianella longoi*: factors mediating replacement of one species by a congener in a shared habitat. Biol Control 30:382–391

Mapondera TS, Burgess T, Matsuki M et al (2012) Identification and molecular phylogenetics of the cryptic species of the *Gonipterus scutellatus* complex (Coleoptera: Curculionidae: Gonipterini). Aust J Entomol 51:175–188

McPherson EG, van Doom N, De Goede J. Structure, function and value of street trees in California, USA. Arboricul. Urban Forest, 37 pp (Submitted)

Mendel Z, Protasov A, Fisher N et al (2004) The taxonomy and natural history of *Leptocybe invasa* (Hymenoptera: Eulophidae) gen. & sp. nov., an invasive gall inducer on *Eucalyptus*. Aust J Entomol 43:101–113

Millar JG, Paine TD, Campbell KA et al (2002) Methods for rearing *Syngaster lepidus* and *Jarra phoracantha* (Hymenoptera : Braconidae), larval parasitoids of the phloem-colonizing longhorned beetles *Phoracantha semipunctata* and *P. recurva* (Coleoptera: Cerambycidae). Bull Entomol Res 92:141–146

Millar JG, Paine TD, Bethke JA et al (2009) Eucalyptus tortoise beetles. Pest notes 74104. Univ. Calif. Agricul. Nat. Res. Statewide UC Integ. Pest Manage. Prog., 5 pp

Munz PA (1959) A California flora. University of California Press, Berkeley, 1681 pp

Paine TD, Hanlon CC (2010) Integration of tactics for management of *Eucalyptus* herbivores: influence of moisture and nitrogen fertilization on red gum lerp psyllid colonization. Entomol Exp Appl 137:290–295

Paine TD, Millar JG, Bellows TS et al (1997) Enlisting an under-appreciated clientele: public participation in distribution and evaluation of natural enemies in urban landscapes. Am Entomol 43:163–172

Paine TD, Millar JG, Paine EO et al (2001) Influence of host log age and refuge from natural enemies on colonization and survival of *Phoracantha semipunctata*. Entomol Exp Appl 98:157–163

Paine TD, Millar JG, Daane KM (2010) Accumulation of pest insects on eucalyptus in California: random process or smoking gun. J Econ Entomol 103:1943–1949

Paine TD, Steinbauer MJ, Lawson SA (2011) Native and exotic pests of eucalyptus: a worldwide perspective. Annu Rev Entomol 56:181–201

Paine TD, Millar JG, Hanks LM et al (2015) Cost-benefit analysis for biological control programs that targeted insect pests of eucalypts in urban landscapes of California. J Econ Entomol (In Press). doi:10.01093/jee/tov224

Powell W (1978) Colonization of twelve species of Eucalyptus by *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae) in Malawi. Bull Entomol Res 68:621–626

Powell W (1982) Age-specific life table data for the Eucalyptus boring beetle, *Phoracantha semipunctata* (F.) (Coleoptera: Cerambycidae) in Malawi. Bull Entomol Res 72:645–653

Reed DA, Luhring KA, Stafford CA et al (2007) Host defensive response against an egg parasitoid involves cellular encapsulation and melanization. Biol Control 41:214–222

Reis AR, Ferreira L, Tome M et al (2012) Efficiency of biological control of *Gonipterus platensis* (Coleoptera: Curculionidae) by *Anaphes nitens* (Hymenoptera: Mymaridae) in cold areas of the Iberian Peninsula: Implications for defoliation and wood production in *Eucalyptus globulus*. For Ecol Manage 270:216–222

Schauff ME, Garrison RW (2000) An introduced species of *Epichrysocharis* (Hymenoptera: Eulophidae) producing galls on *Eucalyptus* in California with notes on the described species and placement of the genus. J Hymenopt Res 9:176–181

Timberlake PH (1957) A new entedontine chalcid-fly from seed capsules of eucaplyptus in California (Hymenoptera: Eulophidae). Pan Pac Entomol 33:110

Ulyshen MD, Miller D (2007) First record of *Acizzia jamatonica* (Hemiptera: Psyllidae) in North America: friend or foe? Fla Entomol 90:573

Varela LG, Hashim-Buckey JM, Wilen CA et al (2007) Pest notes: glassy-winged sharpshooter. Univ. Cali. Div. Agric. Nat. Res. UC Statewide IPM Program. Publication 7492, 4 pp

von Ellenreider N (2003) Eucalyptus leaf beetle (*Chrysophtharta m-fuscum*) Calif. Dept. Agricul. Pest sheets. CDFA, Sacramento, 1 p

Wang Q, Millar JG, Reed DA et al (2008) Development of a strategy for selective collection of a parasitoid attacking one member of a large herbivore guild. J Econ Entomol 101:1771–1778

Wiley J, Skelley P (2008) A eucalyptus pest, Leptocybe invasa Fisher and LaSalle (Hymenoptera: Eulophidae), genus and species new to Florida and North America. Pest alerts. Fl. Depart. Agricul. Consumer Serv., 1 p

Chapter 25
Sudden Oak Death in California

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Abstract *Phytophthora ramorum* was first observed in 1993 as an undescribed species that caused shoot blighting of rhododendron in European nurseries. A genetically distinct lineage of *P. ramorum* was introduced into northern California nurseries in the same period. By 1995, *P. ramorum* had moved from infected nursery stock in the wildland interface into adjacent native coastal forests, where, it causes sudden oak death (SOD), a lethal trunk canker disease of several important hardwood trees in the Fagaceae. SOD has since become the single most important cause of mortality in these species. Tanoak (*Notholithocarpus densiflorus*) is the most severely impacted host because the entire *P. ramorum* disease cycle can be completed on this species and all age classes are susceptible. In contrast, susceptible oak (*Quercus*) species are infected and killed by inoculum produced on a separate foliar host, California bay (*Umbellularia californica*). Because SOD risk in oak stands depends on the density and distribution of California bay, disease risk can be greatly reduced or eliminated if bay canopy can be removed near oaks.

25.1 Introduction

The introduced pathogen *Phytophthora ramorum* Werres, de Cock & Man in't Veld causes a lethal trunk-canker disease known as sudden oak death (SOD) (Svihra 2001; Garbelotto et al. 2001; Rizzo et al. 2002). In California, only a few members of the family Fagaceae are known to develop lethal trunk cankers. Tanoak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H.Oh), coast live oak (*Quercus agrifolia* Née), Shreve oak (*Q. parvula* Greene var. *shrevei* (C.H. Mull.) Nixon), California black oak (*Q. kelloggii* Newberry), and canyon live oak (*Q. chrysolepis* Liebm.) are native California trees that are killed by SOD. In areas invaded by *P. ramorum*, SOD has quickly become the most common cause of mortality of these trees (Swiecki and Bernhardt 2010). Mortality rates are greater than 50 % in some areas and continue to increase (Maloney et al. 2005; Swiecki and Bernhardt 2008a, 2010).

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Fig. 25.1 Classic progression of sudden oak death in coast live oak. Bleeding cankers and ambrosia beetle boring dust first appeared in fall 2007 (*upper left*). Dark bordered cankers are visible in the phloem where the outer bark has been removed (*upper right*). This tree was dead 1 year later (*bottom*)

Oaks known to be susceptible to *P. ramorum* trunk cankers (Fig. 25.1) are in the red or black oak and intermediate oak subgroups. Oaks in the white oak and other subgroups are not known to be susceptible to trunk cankers under natural conditions. The ability of *Phytophthora ramorum* to kill trees is not restricted to Mediterranean climates or to Fagaceae, as it has recently been shown to be causing widespread mortality of Japanese larch (*Larix kaempferi)* in Great Britain (Webber et al. 2010).

In addition to causing trunk cankers on the trees listed above, *P. ramorum* causes nonlethal lesions on leaves, twigs, and small stems of many California native species, including tanoak, California bay (*Umbellularia californica* (Hook. & Arn.) Nutt.), Pacific madrone (*Arbutus menziesii* Pursh), California huckleberry (*Vaccinium ovatum* Pursh), manzanita (*Arctostaphylos* spp.), toyon (*Heteromeles arbutifolia* (Lindl.) M. Roem.), poison oak (*Toxicodendron diversilobum* (Torr. & A. Gray) Greene), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), and coast redwood (*Sequoia sempervirens* (Lamb. ex D. Don) Endl.). In addition, *P. ramorum* causes foliar and stem diseases in a wide variety of non-native plants, including many ornamentals (Garbelotto et al. 2003). These diseases are referred to as ramorum blight. *Phytophthora ramorum* causes only minor damage on most of these foliar hosts.

As research on *P. ramorum* has continued, the list of plants known to be susceptible has expanded (USDA APHIS 2012). This wide host range contributes to the ability of *P. ramorum* to invade and become established in new areas. In this chapter, we give a brief overview of the history, epidemiology, and management of SOD in California.

25.2 History

25.2.1 Origin and Distribution of Phytophthora ramorum *in California*

Phytophthora ramorum was first detected in Europe in 1993, causing twig blight of rhododendron in Germany and the Netherlands (Werres et al. 2001). It was found to kill rhododendron in both nursery and horticultural settings. Although recognized as a distinct and new *Phytophthora* species, its description and a name were not published at that time. Beginning in 1998, it was found on diseased *Viburnum* and recovered from water in recirculation systems of nurseries (Werres et al. 2001).

Sudden oak death (SOD) was first widely recognized in California in 1995, when large numbers of tanoaks (*Notholithocarpus densiflorus)* began dying in coastal Marin, Santa Cruz, and Monterey Counties (Svihra 2001). Symptoms included oozing from bark cankers, ambrosia or bark beetle colonization (including *Monarthrum* and *Pseudopityophthorus* spp.), and development of hemispherical fruiting bodies of *Annulohypoxylon thouarsianum,* an opportunistic sapwood decay fungus (Figs. 25.1 and 25.2). It was initially unclear why oaks and tanoaks were being killed in unprecedented numbers by opportunistic secondary invaders such as beetles and/or *A. thouarsianum.* However, in 2000, a new and undescribed species of *Phytophthora* was isolated from the margins of bleeding cankers (Rizzo et al. 2002). Shortly after it was isolated, visiting *Phytophthora* expert Dr. Clive Brasier observed the culture and was able to help show that the *Phytophthora* isolated from California oaks was the same species affecting rhododendrons in European nurseries (Kliejunas 2010). This early observation helped researchers identify nursery stock as the ave-

Fig. 25.2 A bleeding *P. ramorum* canker (*left*) developed on this coast live oak near the base of one scaffold in 2006, following two successive years of abundant spring rainfall. A dark bordered canker was visible in the phloem when the outer bark was cut away. Two years later (*right*) the canker had expanded to encompass most of the lower trunk and sporulation by *Annulohypoxylon thouarsianum* (black stromata) and ambrosia beetle boring dust were extensive. This tree died within 3 years of initial symptom expression

nue for introduction of *P. ramorum* to California (Kliejunas 2010). Ornamental *Rhododendron* species in particular are highly susceptible, produce large numbers of spores (Moralejo et al. 2007), and are commonly planted in affected counties.

Genetic analyses and other data suggest that *P. ramorum* moved via infested nursery stock to multiple locations in several counties, including Santa Cruz and Marin, and then moved into the adjacent forests. Eventually, the forest infestations expanded and served as sources for continued spread of the pathogen to other counties (Mascheretti et al. 2008; Croucher et al. 2013).

Phytophthora ramorum is currently found in coastal California forests from Humboldt to Monterey Counties, and in Curry County in southern Oregon. It is also found in the counties bordering San Francisco Bay. Its range continues to expand. All counties with confirmed *P. ramorum* in natural settings are under state and federal quarantine. Quarantined counties are subject to regulations regarding the movement and use of susceptible plants.

Phytophthora ramorum has also been found in nursery, horticultural, and wild settings in many European countries since its original discovery in the 1990s. Of particular interest is the fact that the strain of *P. ramorum* originally found in Europe (designated EU1), is different from the strain originally introduced into California (strain NA1) (Ivors et al. 2006; Grünwald et al. 2009). Another unique strain of *P. ramorum* was initially known only from nurseries in Washington state and is designated as NA2 (Ivors et al. 2006; Grünwald et al. 2009). This strain was subsequently found in California and nurseries in British Columbia. A second European strain (EU2, Van Poucke et al. 2012) is present on Japanese larch (*Larix kaempferi* (Lam.)

Carrière) in the United Kingdom (including Northern Ireland, southwest England, Wales, and southwest Scotland). The distribution of these four strains and other genetic data indicate that *P. ramorum* is an introduced pathogen in both North America and Europe. The native range of *P. ramorum* is unknown at this time.

The early association of *P. ramorum* with nursery-grown container plants led to quarantines by states and countries limiting the importation of nursery stock, soil, and wood products of known hosts (Frankel 2008). The original quarantine efforts targeted the infested counties, but in 2004, *P. ramorum* was detected in two large southern California nurseries and one in Oregon, well outside of the known infested counties. Millions of potentially infected plants were shipped to over 1200 nurseries in 39 states. These finds prompted some states and USDA APHIS to impose new quarantines and inspections (Frankel 2008). USDA APHIS regulations associated with *P. ramorum* in nurseries in the regulated and quarantined areas of California, Oregon, and Washington nurseries continue to evolve and are posted at the USDA APHIS *P. ramorum* web page (http://www.aphis.usda.gov/wps/portal/aphis/home/).

In addition to the regulatory response, a federal program of competitive grants for research and education was funded through the USDA Forest Service. This program has provided funding for studies on ecology, modeling of disease risk, epidemiology, nursery transmission, chemical control, disease resistance, and other related topics. Results from these studies have been published in multiple scientific journals and shared via a series of symposium that have been held at regular intervals (Frankel et al. 2006, 2008, 2010, 2013). Multiple review articles covering various aspects of *P. ramorum* have been written. The Sudden Oak Death website (suddenoakdeath.org), run by the California Oak Mortality Task Force, serves as a distribution center for up-to date information about SOD. Maps of *P. ramorum* distribution are available from the SODMAP (University of California–Berkeley 2012) and OakMapper (Kelly et al. 2012) web sites.

25.3 Pathogen Biology

Phytophthora ramorum and other *Phytophthora* species are members of the Oomycota, or water molds. The Oomycota are not true fungi. They are placed in the kingdom Stramenopila, which also includes diatoms and kelp. Most *Phytophthora* species attack living plants, and many are serious plant pathogens affecting forests, agricultural crops, and horticultural plants worldwide. Like true fungi, *Phytophthora* species grow as a network of microscopic filaments referred to as hyphae (collectively, mycelium). As *P. ramorum* hyphae penetrate and grow into a host plant, they secrete chemicals that kill and degrade plant tissues. The hyphae absorb nutrients released from dead and dying host cells to fuel their continued growth.

Phytophthora ramorum is disseminated via several spore types that are produced by the hyphae. During periods of rainy weather, especially when temperatures are relatively warm, sporangia are produced on the surfaces of infected leaves and twigs of some hosts. Large numbers of sporangia are produced on only a few of the many hosts that can be infected. The sporangia detach readily and can be dispersed via splashing water and wind-blown droplets. These deciduous sporangia allow *P. ramorum* to function as a foliar pathogen, similar to the potato late blight pathogen *Phytophthora infestans*.

Sporangia can germinate directly, producing hyphae that can penetrate the host. Alternatively, sporangia in water and in water films on plant surfaces can release multiple zoospores, about 30 zoospores from each sporangium (Widmer 2009). Zoospores are motile and can swim small distances, 3 cm or more flooded soil, using their threadlike flagella (Duniway 1976; Erwin and Ribiero 1996). They can be carried large distances by flowing water, at least tens of meters to kilometers, depending on the type of watercourse. Zoospores actively swim toward certain chemicals released by host plants, which helps them aggregate on the host. Upon reaching the host, each zoospore transforms into a nonmobile cyst that germinates by producing a single hypha that can penetrate and infect the plant. If zoospores aggregate before they encyst, host tissue may be attacked by many hyphae in a small area. This mass attack increases zoospores' ability to overwhelm host defenses.

Zoospores are short-lived, typically swimming for a few hours. Zoospore cysts persist a short while longer, but do not tolerate drying. Sporangia can persist for days, but are relatively thin-walled and do not survive dry conditions. *Phytophthora ramorum* also produces thick-walled, long-lived spores (chlamydospores) within and on various infected plant tissues. Chlamydospores are relatively resistant to environmental degradation and help *Phytophthora* species persist through periods unfavorable for growth.

Sporangia, zoospores, and chlamydospores are asexual spores. When these spores germinate, they give rise to new clones (genetically identical copies of the individual that produced the spores). *Phytophthora* species also can reproduce sexually by forming oospores. Oospores give rise to individuals that are genetically distinct from the parental strains. Oospores are thick-walled and can persist in the environment for extended periods. *Phytophthora ramorum* can only form oospores when strains of opposite mating types come in contact with each other (Werres et al. 2001). Only a single mating type of the pathogen, designated A2, is currently widespread in California, and at this time, sexual reproduction is not known to occur in California forests (Chandelier et al. 2014).

25.4 Symptom Development

In SOD-susceptible oaks and tanoak, cankers develop when *P. ramorum* infects and kills phloem in the bark of the lower trunk (Figs. 25.1 and 25.2). The pathogen may also kill the vascular cambium and invade the outer xylem (Fig. 25.3) (Parke et al. 2007; Rizzo et al. 2002). Cankers typically have a distinct edge, often delimited by a dark line (Figs. 25.1, 25.2 and 25.3).

External bleeding from cankers may develop in the spring or summer after infection occurs, but external symptoms may not appear until 1 or 2 years after infection.

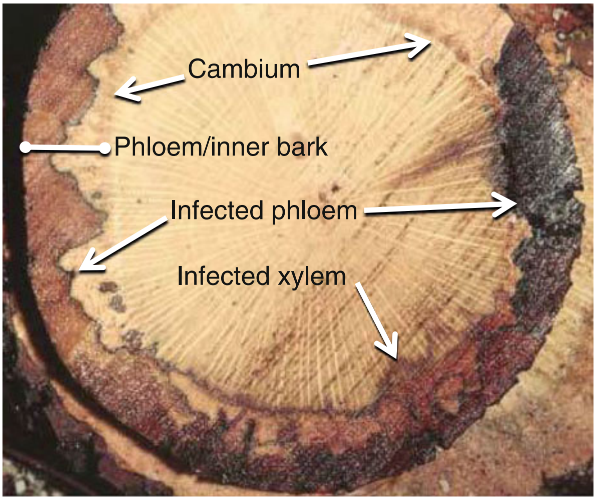

Fig. 25.3 Cross section through the trunk of a coast live oak with a *Phytophthora ramorum* canker. Discolored areas in phloem and xylem are infected tissues

Bleeding can be lacking or cryptic in some canker hosts, including tanoak and canyon live oak (Aram et al. 2011; Swiecki and Bernhardt 2013). When colonization by secondary agents (beetles, decay fungi) is the first evidence of the disease, confirming that the tree was initially infected by *P. ramorum* can be difficult or impossible.

Highly susceptible trees can be girdled by cankers within 1–2 years. In oaks, nonstressed, large diameter trees with dominant canopy exposure are most susceptible to SOD (Swiecki and Bernhardt 2004, 2005, 2013). Disruption of water transport in the trunk sapwood due to direct effects of *P. ramorum* and damage caused by secondary agents (Parke et al. 2007; Swiecki and Bernhardt 2013) eventually induces severe water stress in the tree canopy, which can turn from green to brown within a few weeks under hot, dry conditions. Trees with moderate to large cankers that do not completely girdle the trunk may decline slowly over many years (Fig. 25.4). Alternatively, the canopy may remain in good condition, but trees are killed by trunk failure (see Sect. 25.4.1). Some trees develop only small cankers that become callused over, leading to complete symptom remission (see Sect. 25.8.4).

25.4.1 Branch and Trunk Failure

Because SOD cankers typically affect the lower trunk, decay associated with SOD cankers often leads to trunk failure (Swiecki and Bernhardt 2003). Oaks infected by *P. ramorum* often die as the result of large scaffold or trunk failures before SOD cankers actually cause death of the top (Fig. 25.4). Trees with *P. ramorum* cankers that have been colonized by *A. thouarsianum* and ambrosia beetles have an increased risk of failure (breakage) compared to healthy, noninfected trees or those with

Fig. 25.4 Gradual decline in a SOD-infected coast live oak. This tree was almost entirely girdled by *Phytophthora ramorum* cankers in 2000, but had a narrow strip of callus tissue (*white arrows*, *top left*) that connected the canopy to the root system. Images from 2004 (*left top* and *center*) and 2009 (*right top* and *center*) show progressive canopy thinning and dieback. The canopy was still green when the trunk failed in September 2010 (*bottom*)

bleeding cankers that have not been invaded by secondary invaders (Swiecki et al. 2006; Swiecki and Bernhardt 2013).

Annulohypoxylon thouarsianum causes extensive white rot of the sapwood in SOD-affected trees. Cankered areas and killed branches are typically affected first. Other decay fungi, including *Phellinus gilvus*, may cause similar decay. Wood boring ambrosia and bark beetles are also attracted to SOD cankers in large numbers (McPherson et al. 2008). Flat-headed borers (Buprestidae) also attack both old trunk cankers and the branches of dead and dying trees. In small-diameter trees (less than about 30 cm), sapwood destruction caused by these secondary agents can be extensive enough to cause trunk failure, typically one to several years after the top has died (Swiecki and Bernhardt 2013). If trunk failure does not occur first, branches and scaffolds begin to fail within 1–2 years after a tree is killed by SOD (Swiecki and Bernhardt 2013).

In large trees, trunk failure commonly results from a combination of SOD-related sapwood decay and preexisting heartwood decay (Swiecki and Bernhardt 2013). Many large oaks have extensive internal decay associated with canker rot fungi (especially *Inonotus andersonii, I. dryophilus*, and *Phellinus robustus*) or other aggressive wood decay fungi such as *Laetiporus gilbertsonii*. Trunk and scaffold failures of living SOD-infected trees commonly develop where SOD-related sapwood decay approaches or merges with existing heartwood decay. Large-diameter oaks that are extensively girdled or killed by SOD but lack preexisting heartwood decay may stand for 5–10 years or more before the trunk fails (Fig. 25.4).

25.5 Diagnosis

The pathogen can be recovered from the margins of active cankers by culturing on *Phytophthora*-selective media, but it is difficult or impossible to recover *P. ramorum* from older cankers that have become inactive or been colonized by decay fungi. Isolation efficiency from various hosts also varies seasonally (Vettraino et al. 2010). *Phytophthora ramorum* can be isolated from twig cankers on tanoak and other hosts and lesions on the leaves of California bay and other foliar hosts. The pathogen can be recovered from water and soil using baits, such as rhododendron leaves or green pears. Compared with many other *Phytophthora* species, *P. ramorum* is very distinctive in culture, which has greatly simplified studies on this species. PCR-based molecular assays can detect the pathogen in infected host material when it is difficult to culture (Vettraino et al. 2010).

25.6 Epidemiology

The epidemiology of SOD differs between oak and tanoak forests because the source of *P. ramorum* inoculum differs for these hosts. Although the entire *P. ramorum* disease cycle can be completed on tanoak, *P. ramorum* infections on oak depend on inoculum produced in foliar infections on a nearby host of a different species.

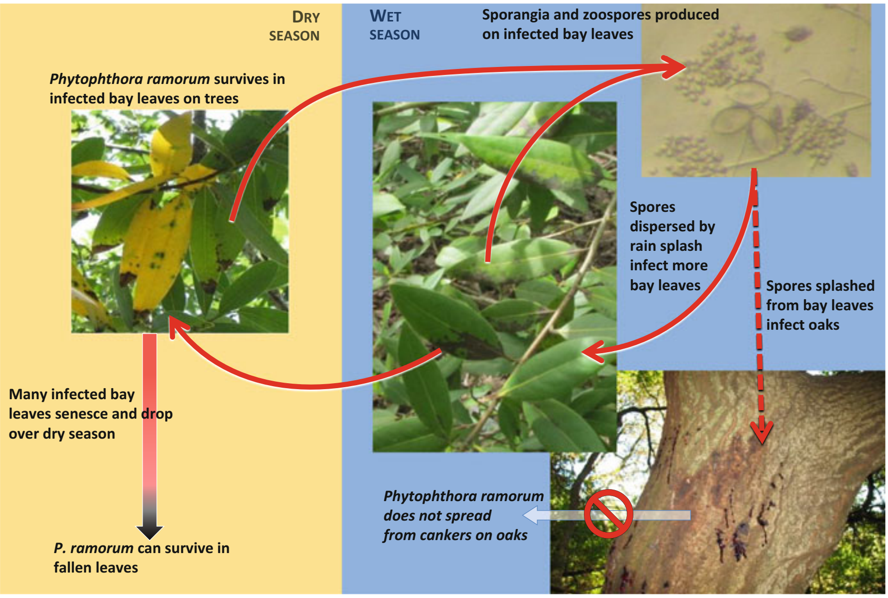

Fig. 25.5 Sudden oak death disease cycle in oak-California bay forests. *Phytophthora ramorum* survives over the dry season primarily in infected California bay leaves on trees. Sporulation occurs on bay leaves during the wet season. Rain-splashed spores initiate additional leaf infections on nearby California bay foliage. Under prolonged wet conditions, spores from California bay canopies are splashed onto nearby oaks (*dashed arrow*). Cankers develop on infected oak trunks but *P. ramorum* does not sporulate on trunk cankers

25.6.1 Disease Cycle in Susceptible Oak Forests

The *P. ramorum* spores that infect susceptible oak species are produced on the leaves of California bay (Fig. 25.5) (Davidson et al. 2002, 2005, 2008, 2011). In essence, SOD in susceptible oaks is largely a byproduct of the *P. ramorum* foliar disease cycle on California bay. California bay commonly occurs in mixed stands with oaks and tanoaks in coastal forests, where it ranges in size from small shrubby understory seedlings to codominant or dominant overstory trees. A plot-based case-control study (Swiecki and Bernhardt 2002) established California bay presence as a predictor of disease in SOD-susceptible oaks. A subsequent remote sensing GIS analysis showed that SOD in oaks was correlated with bay canopy cover at a landscape scale (Kelly and Meentenmeyer 2002).

Typically, the number of infected California bay leaves remaining in the canopy after the summer is relatively low, so few spores are produced during the first rains of the rainy season in the fall and early winter (Davidson et al. 2011). However, even small numbers of spores can initiate new leaf infections on California bay. As the rainy season progresses, spores produced on infected leaves are splashed to other leaves where they start new infections. In laboratory tests, California *P. ramorum* isolates formed sporangia at temperatures between 10 °C and 30 °C, with peak production occurring at temperatures between 16 °C and 22 °C (Davidson et al. 2005; Englander et al. 2006). *Phytophthora ramorum* requires 6–12 h of continuously wet conditions to infect California bay leaves (Garbelotto et al. 2003). Under laboratory conditions, wet California bay leaves were much less likely to become infected at 12 °C than at 18 °C. If rainfall is frequent and temperatures are moderate, the number of foliar infections on California bay can increase explosively (Davidson et al. 2005, 2008; Swiecki and Bernhardt 2008b), producing large quantities of sporangia and chlamydospores.

In spring rainstorms, large numbers of sporangia are dislodged and splashed and blown onto nearby oaks. Water running down oak stems concentrates spores in the lower trunk area, where *P. ramorum* cankers typically develop. The lower trunk also tends to dry more slowly after rain. This provides an extended period of moisture, which favors *P. ramorum* spore germination and infection.

Infection of oaks and tanoaks is greatest in years with frequent late spring rains, and disease potential may be especially severe when these conditions occur two or more years in a row (Swiecki and Bernhardt 2008a). In contrast, new infections are uncommon after a dry spring, especially in inland areas (Swiecki and Bernhardt 2008a). In coastal areas, fog can keep California bay foliage wet for extended periods, so new infections can develop even in years with low rainfall.

Sudden oak death is not known to spread from infected oaks to healthy oaks. *Phytophthora ramorum* does not produce sporangia on infected oak trunks (Davidson et al. 2005). Leaf infections caused by *P. ramorum* rarely develop on SOD susceptible oaks. Oak foliar infections are only seen in trees exposed to high spore loads from nearby infected California bay foliage (Vettraino et al. 2008). Consequently, infected oak leaves appear to have little or no role in pathogen spread.

25.6.2 California Bay–Oak Distance and Disease Risk

Sudden oak death incidence, severity, and mortality rates increase as the distance from a susceptible oak trunk to California bay foliage decreases (Fig. 25.6) (Swiecki and Bernhardt 2007, 2008b, 2013). Oaks with California bay foliage directly over or within 1.5 m of the trunk have the highest risk of infection and mortality. Disease risk also increases as the total amount of California bay cover within 2.5–5 m of the oak trunk increases.

Proximity of California bay to oaks strongly influences disease risk because few *P. ramorum* spores travel more than 5 m horizontally via rain splash (Davidson et al. 2005). Spores in water drops splashing from leaves higher in the canopy are more influenced by wind and may travel greater horizontal distances. Spores present on the soil surface and in low foliage (less than about 0.5 m above the ground) are only dispersed about 1 m by rain splash alone (Tjosvold et al. 2006).

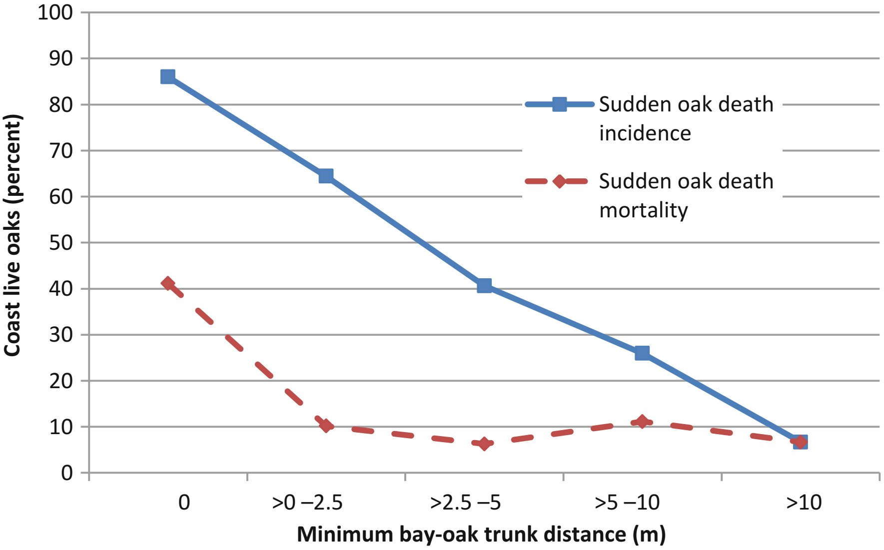

Fig. 25.6 Sudden oak death incidence and mortality in coast live oak decrease as the minimum distance between the oak trunk and California bay foliage increases. Minimum California bay-oak trunk distance is the shortest distance between the main stem of an oak and a vertical line dropped from the nearest California bay foliage. Data shown were collected in 2004 from coast live oaks in Marin and Napa Counties (Swiecki and Bernhardt 2007, 2008b)

25.6.3 Other Foliar Hosts

Limited data suggest that poison oak (*Toxicodendron diversilobum*) can serve as a source of *P. ramorum* spores. Oaks that are relatively far from infected California bay (>10 m) have an elevated SOD infection risk if poison oak is climbing in their canopies. Climbing poison oak is not associated with SOD unless infected California bay is present in the area. Poison oak that occurs as a small shrub or ground cover is not associated with SOD risk in oaks (Swiecki and Bernhardt 2005, 2007, 2008b).

Other than California bay, tanoak, and possibly poison oak, none of the other known native *P. ramorum* foliar hosts have been associated with disease risk in oaks or tanoak in California forests. Infections on many of these other foliar hosts typically develop only under very wet conditions when inoculum levels from California bay and tanoak sources are already very high, so additional inoculum produced on these species is not epidemiologically important.

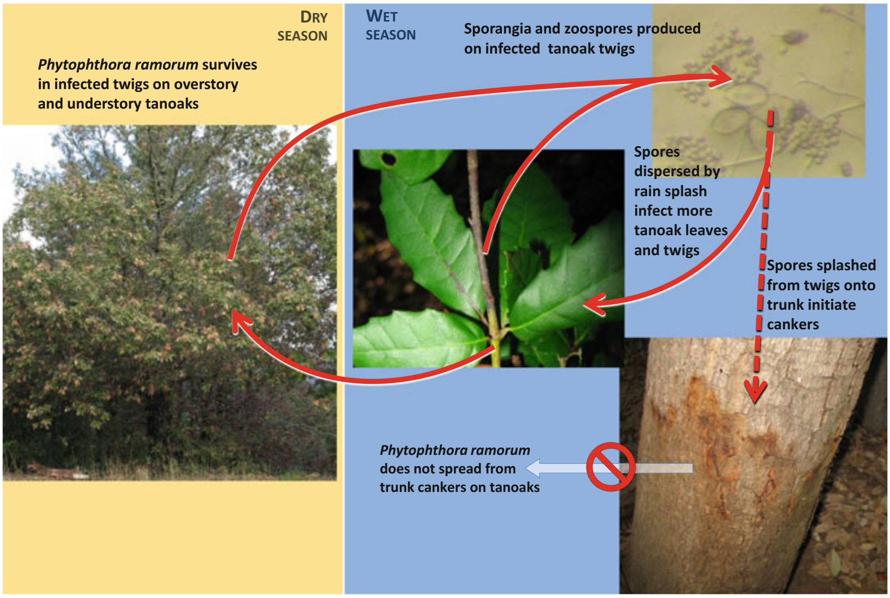

Fig. 25.7 Sudden oak death disease cycle in tanoak stands. *Phytophthora ramorum* survives over the dry season primarily in tanoak twig infections. Sporulation occurs during the wet season primarily on infected twigs. Rain-splashed spores initiate new leaf and twig infections within the trees and on nearby tanoaks. Under prolonged wet conditions, high numbers of spores produced in the canopy are splashed onto trunks and initiate trunk cankers (*dashed arrows*)

25.6.4 Disease Cycle in Tanoak Forests

Unlike the situation in SOD-susceptible oaks, *Phytophthora ramorum* commonly causes twig dieback on both mature tanoaks and understory seedlings and saplings (Fig. 25.7). *Phytophthora ramorum* sporangia form readily on tanoak twig cankers (Davidson et al. 2008). They can be dispersed by splashing rain to other parts of the canopy, initiating additional leaf and twig infections. Spores can also be splashed from infected tanoak twigs to canopies of adjacent tanoaks, so *P. ramorum* can readily spread between trees in a tanoak stand.

Under wet conditions, as more twig cankers form in tanoak canopies, increasingly large numbers of *P. ramorum* spores are produced and dispersed. These spores splash onto tanoak trunks and can also move down the trunk in the rainwater that flows along the stems. The spores can initiate trunk cankers that can kill infected trees. Cankers on the trunk commonly form within 1–2 m of the ground but may occur higher on the trunk or on branches. Tanoak trunk cankers do not produce *P. ramorum* spores.

Phytophthora ramorum sporangia are produced in much greater quantities in California bay canopies than in tanoak canopies (Davidson et al. 2008). When *P. ramorum* initially spreads into tanoak stands, trees located near California bay are among the first to develop lethal trunk cankers. Disease incidence around California bay trees is also higher than in pure tanoak stands. However, unlike the situation in affected oak forests, SOD can cause widespread and heavy mortality in tanoak in the absence of California bay.

25.6.5 Inoculum in Soil and Water

Phytophthora ramorum spores can be washed by rain into soil and surface water. Bay leaves in watercourses are readily colonized by *P. ramorum* and remain infective for months (Aram and Rizzo 2014). California bay or tanoak foliage on seedlings and low hanging branches may be infected by splashing of inoculum from streams or soil (Fichtner et al. 2009). Flooding of *P. ramorum*-infested streams has also been associated with the development of foliar infections on inundated hosts (Chastagner et al. 2010). Heavily infested soil or water that is directly deposited on oak trunks by human or animal vectors could initiate trunk infections, especially if the inoculum is introduced into bark wounds. This infection pathway may account for some of the uncommon trunk cankers seen in oaks without nearby California bay trees. However, unlike soil-borne *Phytophthora* species, *P. ramorum* does not survive well in soil and the number of detectable propagules in soil decreases to zero over the course of the summer dry season (Fichtner et al. 2009).

25.6.6 Long-Range Pathogen Dispersal

Long-distance dispersal may occur via spores that enter streams or via turbulent airflow that may transport sporangia aerially up to several kilometers (Hansen 2008). Short-range local dispersal of *P. ramorum* spores by rain splash delivers spores from infected California bay foliage or tanoak twigs in sufficient quantities to initiate trunk infections on susceptible oaks and tanoak. In contrast, long-distance transport methods can deliver only low numbers of spores to a target host, normally too few to initiate trunk cankers, but enough to initiate foliar infections. If long-range dispersal is followed by a prolonged period of favorably wet weather, new disease foci can develop kilometers away from existing infestations (Kanaskie et al. 2013).

25.7 Stand-Level Sudden Oak Death Impacts

Mortality rates have increased greatly among SOD canker hosts since *P. ramorum* was introduced into California forests. Between 2000 and 2012, mortality caused by SOD among coast live oaks (1.15 % per year) was 50 % higher than mortality

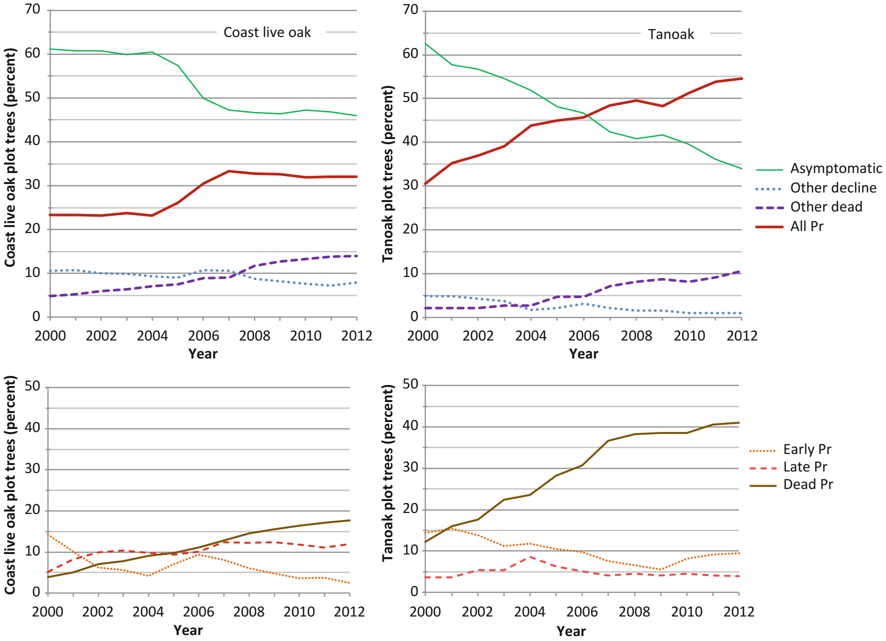

Fig. 25.8 Changes in disease status of coast live oak (*left*) and tanoak (*right*) from September 2000 through September 2012 in 150 permanent plots in Marin, Sonoma, and Napa Counties, California. *Top* graphs: *Asymptomatic* no evident symptoms of *Phytophthora ramorum* infection or decline resulting from other agents. *Other decline* tree in severe decline due to agents other than *P. ramorum*. *Other dead* tree dead due to agents other than *P. ramorum*. *All Pr* all trees (live or dead) with *P. ramorum* canker symptoms. *Bottom* graphs: *Early Pr* live trees with *P. ramorum* cankers only. *Late Pr* live trees with *P. ramorum* cankers plus beetle boring or *Annulohypoxylon thouarsianum* fruiting bodies. *Dead Pr* tree dead due to *P. ramorum* infection

caused by all other agents (0.76 % per year) (Fig. 25.8). SOD-associated mortality develops in discrete pulses that occur several years after wet spring conditions that favor infection (Swiecki and Bernhardt 2013). Mortality associated with other factors (commonly canker rot and wood decay fungi) has shown much less year-to-year variability over the same time period. Among tanoaks, the SOD mortality rate (2.4 % per year) was about 3.4 times that for all non-SOD causes (0.7 % per year). Overall, SOD incidence and mortality tend to increase faster and reach higher levels in tanoak stands than in oak stands (Fig. 25.8). Mortality rates measured in forests without SOD (Swiecki and Bernhardt 2008c) are similar to those attributed to non-SOD causes in Fig. 25.8.

If conditions for infection are favorable, a strong pulse of mortality can develop within a few years after *P. ramorum* first becomes established in an area. Many of the trees that are either highly susceptible or exposed to high levels of inoculum from adjacent or overtopping California bay are infected and killed early in the epidemic. Especially in oak forests, subsequent pulses of disease may be less dramatic because fewer trees at high risk of SOD remain.

25.8 Disease Management

Options for managing SOD are discussed under the standard categories of exclusion, eradication, protection, and resistance.

25.8.1 Exclusion

Introduction of *P. ramorum* will only result in disease if suitable hosts are present and environmental conditions are favorable for pathogen infection, reproduction, and survival. Models that predict the risk of *P. ramorum* infection based on host and climate variables indicate that the greatest risk of SOD establishment is in the coastal areas from central to northern California (Meentemeyer et al. 2004; Kliejunas 2010). Excluding *P. ramorum* from these favorable environments can prevent SOD from becoming established in new areas beyond the range of natural dispersal.

25.8.1.1 Nursery Stock

Phytophthora ramorum was originally introduced into California forests through movement of contaminated nursery stock (Kliejunas 2010; Croucher et al. 2013). Since that time, federal and state regulations and inspections have been implemented to prevent the movement of *P. ramorum*-infested nursery stock (USDA APHIS 2012). Confounding factors that make nursery detection difficult include: an extensive host list and the possibility of still-undiscovered hosts, symptoms that may be confused with other problems, asymptomatic infections, including root infections on some hosts (Dart and Chastagner 2007), fungicide use, which can mask but not eradicate *P. ramorum* infections.

Inspections continue to detect *P. ramorum* in nursery plants and inter- and intrastate shipment of nursery plants, indicating that movement of nursery stock can still serve to introduce *P. ramorum* to new areas (COMTF 2014).

Nursery-grown plants that are most commonly infested with *P. ramorum* include species and varieties of *Camellia*, *Rhododendron*, *Pieris*, and *Viburnum* (Tjosvold et al. 2005). Nursery-grown plants should not be planted where spores produced on the plants could be dispersed into native stands or where contaminated soil or water runoff could reach native stands.

25.8.1.2 Plant Material–Pruning Waste, Wood

Phytophthora ramorum can be transported by moving infected leaves from California bays. Infected leaves can collect on vehicles and be moved to new locations. Infected California bay leaves dropped on the ground may produce *P.*

ramorum spores that could be splashed to low leaves of susceptible species and initiate a new infestation.

Although cankers on intact oak and tanoak trees do not appear to produce sporangia under normal field conditions, chlamydospores can be formed within infected wood (Parke et al. 2007). Under wet conditions, sporangia can be produced on the cut surfaces of wood from trees with *P. ramorum* cankers (Davidson and Shaw 2003; Davidson et al. 2008). Therefore, movement of firewood cut from SOD-infected trees poses a risk of transporting *P. ramorum* to noninfested areas. State and federal regulations prohibit movement of firewood cut from SOD hosts out of quarantined infested areas.

25.8.1.3 Soil

Moist soil on hiking boots and bicycle tires has been shown to spread SOD (Davidson et al. 2005; Cushman et al. 2008). Vehicles driven on nonsurfaced roads that pass through lands infested with *P. ramorum* may also spread contaminated soil, especially when conditions are muddy. Footwear and vehicles should be cleaned of soil and associated plant debris before leaving infested areas and before entering new areas.

25.8.1.4 Water

Watercourses that drain SOD-affected watersheds or receive runoff from contaminated nurseries can contain spores of *P. ramorum* (Aram and Rizzo 2013, 2014). Untreated water from potentially infested streams should not be used for irrigation, dust control on roads, or similar purposes. Water can be treated with ultrafiltration, chemicals (chlorine, ozone), or UV radiation to eliminate *Phytophthora* spores.

25.8.2 Eradication

The longest-running attempt to eradicate a *P. ramorum* infestation began in Oregon in 2001, when the pathogen was detected in five tanoak stands in an oblong area of about 14.6 ha (Kanaskie et al. 2013). Aerial imagery suggested that some of the infestations dated to at least 1998 or 1999. A cooperative interagency effort was undertaken with the goal of eradicating the pathogen by cutting and burning all symptomatic host plants and a buffer of symptomless hosts. The Oregon Department of Agriculture also set up a quarantine area encompassing the infested sites to prevent movement of host material out of the area.

In this very favorable environment, with mild, wet conditions year round and extensive stands of susceptible tanoak, *P. ramorum* was not eradicated. New infested areas were found in successive years. Most were adjacent to or near known infested sites, but new detections were sometimes found 3–5 km, and in one instance of 20 km, from known sites (Kanaskie et al. 2013).

Because the latent period between trunk infection and mortality can be 2 years or more, aerial and ground detection surveys were unlikely to detect the actual edge of each infested area. Treatment buffers extending 100 m beyond apparent infestations have not been sufficient to contain the pathogen. Disease has continued to spread predominantly in the prevailing storm wind direction. The number of new sites was correlated with successive years of wet spring weather. Although the pathogen was not successfully eradicated in Oregon after 11 years of intensive efforts, it appears that host removal around known infested sites has slowed the spread of the pathogen (Kanaskie et al. 2013).

25.8.3 Protection

25.8.3.1 Removing Hosts That Support *P. ramorum* Sporulation

Foresters have long manipulated stands to favor one species over another. In California forests, California bay serves as the main source of *P. ramorum* spores that infect SOD-susceptible oak species. Removing California bays can greatly increase the likelihood that susceptible oaks will escape, or in some cases recover from, infection. Responses of oaks to *P. ramorum* vary greatly, with many trees expressing resistant or tolerant reactions to infection (Swiecki and Bernhardt 2013). California bay removal can be used to protect oaks across a range of spatial scales, from large blocks to small localized patches. In ongoing long-term controlled studies involving California bay removal, results to date have shown reduced spore loads and a much lower incidence of new infections in treated compared to nontreated areas.

Even in areas where extensive removal of California bays to protect oaks is not practical, it may be helpful to remove highly susceptible California bays that facilitate carryover of inoculum through unfavorable years. Individual California bay trees vary in their susceptibility to foliar *P. ramorum* infections (Anacker et al. 2008; Meshriy et al. 2006). California bay trees also vary with respect to how many infected leaves they retain over the dry season (Swiecki and Bernhardt 2007, 2008a; Davidson et al. 2011). Because *P. ramorum* does not affect the survival of California bay, even highly disease-prone trees are not eliminated from the population by natural selection.

Host removal can at best provide some suppression of SOD in tanoak. Removal of California bay from noninfected tanoak stands may delay SOD establishment, but *P. ramorum* can invade tanoaks stands that lack California bay. Experience from the Oregon eradication attempts (above) suggests that removal of tanoak can slow but not stop disease spread.

25.8.3.2 Chemical Protectants

Field studies to determine if fungicides can reduce SOD incidence or severity in mature trees were initiated several years after the pathogen was identified and are still ongoing (Garbelotto et al. 2002). Phosphites (also known as phosphonates) have been the main focus for chemical control of SOD because of their high level of environmental safety and very low nontarget toxicity (USEPA 1998, 2006). Phosphites are selective, systemic fungicides that have been used to manage *Phytophthora* diseases for many years (Guest and Grant 1991).

Phosphites (most commonly potassium phosphite) can be applied to trees via stem injection, bark or foliar spray, and soil drench. In greenhouse tests, soil drench applications have not been effective against SOD (Garbelotto et al. 2007). Foliar applications are difficult to execute on large trees and may require high volumes of spray. Low volume aerial application of phosphite by helicopter to mature tanoaks in Oregon suppressed *P. ramorum* to some degree, but infections were not completely prevented (Kanaskie et al. 2010).

Phosphite applied via stem injection or bark spray application reduced *P. ramorum* canker size on potted coast live oaks that were artificially inoculated (Garbelotto et al. 2007; Garbelotto and Schmidt 2009). The effect appeared to last at least 18 months after treatment. Branches cut from coast live oaks after treatment with a bark spray application developed smaller lesions than branches from nontreated trees when inoculated in the laboratory with *P. ramorum* (Garbelotto and Schmidt 2009).

Field tests of injection and bark spray phosphite applications have yet to yield convincing results. Post-infection bark spray applications have not been effective, and preventative bark spray applications have failed to lower SOD incidence and mortality rates in treated tanoak trees compared to nontreated trees in several studies (Swiecki and Bernhardt 2013). Injection treatments at label rates of potassium phosphite have caused significant phytotoxicity in injected tanoaks and coast live oaks. Injection holes exhibited prolonged bleeding (up to several years) and necrosis in the phloem and xylem. Recent studies have shown that phytotoxicity can be avoided by using more dilute potassium phosphite solutions, but the efficacy of reduced rates in large trees is unknown. Although phosphites are effective against *Phytophthora* root rots because they accumulate in roots, it is not clear whether phosphite concentrations sufficient to prevent or limit *P. ramorum* cankers can be reached in the phloem of mature trees.

25.8.4 Genetic Resistance

Individual trees in the SOD-susceptible species vary greatly in their susceptibility. Many bleeding cankers on coast live oak become inactive within a year or two after bleeding is first seen (Swiecki and Bernhardt 2010, 2013; Bernhardt and Swiecki 2014). These cankers fail to expand and cease bleeding. They are not colonized by secondary agents and may become undetectable after one to several years. Small cankers (usually less than 10 cm across) are most likely to become inactive. Although individual cankers can become inactive, trees with inactive cankers can develop new cankers on other portions of the trunk if conditions become favorable for establishment of new infections.

Genetic differences between individual host trees appear to influence susceptibility to infections caused by *P. ramorum,* although environmental factors also play a role. If sufficient levels of genetic resistance are present, it may be possible to select oaks and tanoaks with higher levels of resistance to *P. ramorum* for restoration of affected forests (Hayden et al. 2011, 2013). Research is underway to determine if phenolics in the phloem of coast live oaks are correlated with resistance (Nagle et al. 2011).

In situ selection for resistant genotypes should occur naturally in tanoak stands, but selection for a more resistant population will be slowed by the fact that SOD-related mortality is commonly patchy and incomplete. Practical tests that would allow for identification and culling of highly susceptible genotypes could be used to accelerate selection toward a more resistant population.

25.9 Management of SOD-Affected Forests

Many of the forests now affected by SOD previously had complete or nearly complete canopy cover. In forests with overlapping tree canopies, scattered mortality due to SOD can result in small canopy gaps that are quickly erased by growth of overstory or understory trees. However, mortality of dominant trees in relatively open stands can cause significant changes in canopy cover and forest structure. Fast growing native species like Douglas-fir (*Pseudotsuga menziesii*) commonly invade canopy gaps caused by SOD mortality. Without thinning, this regeneration can form dense, unsustainable stands that pose greater fire hazard than the pre-SOD forest. In addition, weedy annuals and exotic perennials such as broom species (*Cytisus, Genista, Spartium* spp.) can also invade canopy gaps, degrading habitat quality and increasing fire hazard.

Alterations in the forest environment due to SOD may also favor other pests or diseases that can further destabilize the habitat. The root pathogen *P. cinnamomi* has been associated with tree mortality in multiple northern California forests that have also been impacted by SOD (Fichtner et al. 2010; Swiecki et al. 2011). Loss of overstory oaks due to SOD can increase soil temperatures and may increase soil moisture levels, which may favor reproduction of *P. cinnamomi*. Root rot caused by *Phytophthora cinnamomi* causes decline and death of California bay and Pacific madrone, two native trees that are not killed by SOD.

Before *P. ramorum* became established in California, SOD-susceptible oaks and tanoaks typically had low mortality rates and little or no active management was necessary to maintain forests dominated by these species. *Phytophthora ramorum* has greatly changed the stability and sustainability of these native forests. Stands can undergo dramatic changes in canopy cover and vegetation composition within

10 years once SOD becomes established. Active management is now needed in many SOD-affected forests to direct forest succession toward desired vegetation types and to restore lost ecosystem services.

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References

Anacker BL, Rank NE, Hüberli D et al (2008) Susceptibility to *Phytophthora ramorum* in a key infectious host: landscape variation in host genotype, host phenotype, and environmental factors. New Phytol 177:756–766

Aram K, Rizzo DM (2013) New insights into the ecology of *Phytophthora ramorum* in streams. In: Frankel SJ, Kliejunas JT, Palmieri KM, Alexander JM tech. coords. Proceedings of the sudden oak death fifth science symposium. Gen. Tech. Rep. PSW-GTR-243. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 45–47

Aram K, Rizzo DM (2014) Decaying leaf litter supports *Phytophthora ramorum* and endemic *Phytophthora* species in streams. http://www.apsnet.org/meetings/Documents/2014_meeting_abstracts/aps2014abO48.htm. Accessed 27 Mar 2015

Aram K, Swiecki T, Bernhardt E et al (2011) Canyon live oak (*Quercus chrysolepis*) is susceptible to bole infection by *Phytophthora ramorum*. Phytopathology 101:S8

Bernhardt E, Swiecki TJ (2014) Visualizing sudden oak death, Part 3: resistant reactions in coast live oak [Video file]. Retrieved from http://www.youtube.com/watch?v=NYaIJS8aqV0

California Oak Mortality Task Force [COMTF] (2014) Current California Oak Mortality Task Force newsletter, August 2014 report. http://www.suddenoakdeath.org/news-and-events/current-newsletter/. Accessed 31 Aug 2014

Chandelier A, Heungens K, Werres S (2014) Change of mating type in an EU1 lineage isolate of *Phytophthora ramorum*. J Phytopathol 162:43–47. doi:10.1111/jph.12150

Chastagner G, Oak S, Omdal D et al (2010) Spread of *P. ramorum* from nurseries into waterways—implications for pathogen establishment in new areas. In: Frankel SJ, Kliejunas JT, Palmieri KM, tech. coords. Proceedings of the sudden oak death fourth science symposium. Gen. Tech. Rep. PSW-GTR-229. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 22–26

Croucher PJP, Mascheretti S, Garbelotto M (2013) Combining field epidemiological information and genetic data to comprehensively reconstruct the invasion genetics of the sudden oak death agent *Phytophthora ramorum* (Stramenopila: Oomycetes) in California. Biol Invasions 15:2281–2297. doi:10.0007/s10530-013-0453-8

Cushman JH, Cooper M, Meentemeyer RK, et al (2008) Human activity and the spread of *Phytophthora ramorum*. In: Frankel SJ, Kliejunas JT, Palmieri KM, tech. coords. Proceedings of the sudden oak death third science symposium. Gen. Tech. Rep. PSW-GTR-214. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 179–180

Dart NL, Chastagner GA (2007) High recovery rate of *Phytophthora* from containerized nursery stock pots at a retail nursery highlights potential for spreading exotic oomycetes. Online. Plant Health Prog. doi:10.1094/PHP-2007-0816-01-BR

Davidson JM, Shaw CG (2003) Pathways of movement for *Phytophthora ramorum*, the causal agent of sudden oak death. Sudden Oak Death Online Symp. doi:10.1094/SOD-2003-TS

Davidson JM, Rizzo DM, Garbelotto M et al (2002) *Phytophthora ramorum* and sudden oak death in California. II. Transmission and survival. In: Standiford RB, McCreary D, Purcell KL, tech. coords. Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. Gen. Tech. Rep. PSW-GTR-184. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 741–749

Davidson JM, Wickland AC, Patterson HA et al (2005) Transmission of *Phytophthora ramorum* in mixed evergreen forest in California. Phytopathology 95:587–596

Davidson JM, Patterson HA, Rizzo DM (2008) Sources of inoculum for *Phytophthora ramorum* in a redwood forest. Phytopathology 98:860–866

Davidson JM, Patterson HA, Wickland AC et al (2011) Forest type influences transmission of *Phytophthora ramorum* in California oak woodlands. Phytopathology 101:492–501

Duniway JM (1976) Movement of zoospores of *Phytophthora cryptogea* in soils of various textures and matric potentials. Phytopathology 66:877–882

Englander L, Browning M, Tooley PW (2006) Growth and sporulation of *Phytophthora ramorum in vitro* in response to temperature and light. Mycologia 98:365–373

Erwin DC, Ribeiro OK (1996) *Phytophthora* diseases worldwide. American Phytopathological Society Press, St. Paul

Fichtner EJ, Lynch SC, Rizzo DM (2009) Survival, dispersal, and soil-mediated suppression of *Phytophthora ramorum* in a California redwood-tanoak forest. Phytopathology 99:608–619

Fichtner EJ, Rizzo DM, Swiecki TJ et al (2010) Emergence of *Phytophthora cinnamomi* in a sudden oak death-impacted forest. In: Frankel SJ, Kliejunas JT, Palmieri KM, tech. coords. Proceedings of the sudden oak death fourth science symposium. Gen. Tech. Rep. PSW-GTR-229. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 320–321

Frankel SJ (2008) Sudden oak death and *Phytophthora ramorum* in the USA: a management challenge. Aust Plant Pathol 37:19–25

Frankel SJ, Shea PJ, Haverty MI, tech. coords. (2006) Proceedings of the sudden oak death second science symposium: the state of our knowledge Gen. Tech. Rep. PSW-GTR-196. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, 571 p

Frankel SJ, Kliejunas JT, Palmieri KM, tech. coords. (2008) Proceedings of the sudden oak death third science symposium. Gen. Tech. Rep. PSW-GTR-214. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, 491 p

Frankel SJ, Kliejunas JT, Palmieri KM, tech. coords. (2010) Proceedings of the sudden oak death fourth science symposium. Gen. Tech. Rep. PSW-GTR-229. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, 378 p

Frankel SJ, Kliejunas JT, Palmieri KM, et al. tech. coords. (2013) Proceedings of the sudden oak death fifth science symposium. Gen. Tech. Rep. PSW-GTR-243. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, 169 p

Garbelotto M, Schmidt DJ (2009) Phosphonate controls sudden oak death pathogen for up to 2 years. Calif Agric 66:10–17

Garbelotto M, Svihra P, Rizzo DM (2001) Sudden oak death syndrome fells three oak species. Calif Agric 55:9–19

Garbelotto M, Rizzo DM, Marais L (2002) *Phytophthora ramorum* and sudden oak death in California: IV. Preliminary studies on chemical control. In: Standiford R, McCreary D, Purcell KL, tech. coords. 5th symposium on California oak woodlands: oaks in California's changing landscape. Gen. Tech. Rep. PSW-GTR-184. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 811–818

Garbelotto M, Davidson JM, Ivors K et al (2003) Non-oak native plants are main hosts for sudden oak death pathogen in California. Calif Agric 57:18–23

Garbelotto M, Schmidt DJ, Harnik TY (2007) Phosphite injections and bark application of phosphite + Pentrabark™ control sudden oak death in coast live oak. Arboricul Urban For 33:309–317

Grünwald NJ, Goss EM, Ivors K et al (2009) Standardizing the nomenclature for clonal lineages of the sudden oak death pathogen, *Phytophthora ramorum*. Phytopathology 99:792–795

Guest D, Grant B (1991) The complex action of phosphonates as antifungal agents. Biol Rev 66:159–187

Hansen E (2008) Rethinking *Phytophthora*– research opportunities and management. In: Frankel SJ, Kliejunas JT, Palmieri KM., tech. coords. Proceedings of the sudden oak death third science symposium. Gen. Tech. Rep. PSW-GTR-214. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 5–14. http://www.treesearch.fs.fed.us/pubs/29767. Accessed 7 Dec 2012

Hayden KJ, Nettel A, Dodd RS et al (2011) Will all the trees fall? Variable resistance to an introduced forest disease in a highly susceptible host. For Ecol Manage 261:1781–1791

Hayden KJ, Garbelotto M, Dodd R et al (2013) Scaling up from greenhouse resistance to fitness in the field for a host of an emerging forest disease. Evol Appl 6:970–982. doi:10.1111/eva.12080

Ivors K, Garbelotto M, DeVries I et al (2006) Microsatellite markers identify three lineages of *Phytophthora ramorum* in US nurseries, yet single lineages in US forest and European nursery populations. Mol Ecol 15:1493–1505

Kanaskie A, Hansen E, Sutton W et al (2010) Aerial application of Agri-Fos® to prevent sudden oak death in Oregon tanoak forests. In: Frankel SJ, Kliejunas JT, Palmieri KM Proceedings of the sudden oak death fourth science symposium. Gen. Tech. Rep. PSW-GTR-229. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 225–232

Kanaskie A, Hansen E, Goheen EM, et al. (2013) Detection and eradication of *Phytophthora ramorum* from Oregon forests, 2001–2011. In: Frankel SJ, Kliejunas JT, Palmieri KM, Alexander JM, tech. coords. Proceedings of the sudden oak death fifth science symposium. Gen. Tech. Rep. PSW-GTR-243. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 3–13

Kelly M, Meentenmeyer RK (2002) Landscape dynamics of the spread of sudden oak death. Photogramm Eng Remote Sens 68:1001–1009

Kelly M, Tuxen KA, Kearns FR (2012) OakMapper. http://www.oakmapper.org. Accessed 13 July 2012

Kliejunas JT (2010) Sudden oak death and *Phytophthora ramorum*: a summary of the literature. Gen. Tech. Rep. PSW-GTR-234. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, 181 p

Maloney PE, Lynch SC, Kane SF et al (2005) Establishment of an emerging generalist pathogen in redwood forest communities. J Ecol 93:899–905

Mascheretti S, Croucher P, Vettraino A et al (2008) Reconstruction of the sudden oak death epidemic in California through microsatellite analysis of the pathogen *Phytophthora ramorum*. Mol Ecol 17:2755–2768

McPherson BA, Erbilgin N, Wood DL et al (2008) Attraction of ambrosia and bark beetles to coast live oaks infected by *Phytophthora ramorum*. Agric For Entomol 10:315–321

Meentemeyer R, Rizzo D, Mark W et al (2004) Mapping the risk of establishment and spread of sudden oak death in California. For Ecol Manage 200:195–214

Meshriy M, Hüberli D, Harnik T, Meentemeyer R (2006) Variation in susceptibility of *Umbellularia californica* (bay laurel) to *Phytophthora ramorum*. In: Frankel SJ, Shea PJ, Haverty MI, tech. coords. Proceedings of the sudden oak death second science symposium: the state of our knowledge. Gen. Tech. Rep. PSW-GTR-196. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 87–89

Moralejo E, Denman S, Beales P, Meentemeyer R (2007) The ability of key tree and non-tree hosts to support inoculum production of *P. ramorum*. RAPRA deliverable report 27. http://rapra.csl.gov.uk. Accessed 14 Mar 2012

Nagle AM, McPherson BA, Wood DL et al (2011) Relationship between field resistance to Phytophthora ramorum and constitutive phenolic chemistry of coast live oak. For Pathol 41:464–469

Parke JL, Oh E, Voelker S et al (2007) *Phytophthora ramorum* colonizes tanoak xylem and is associated with reduced stem water transport. Phytopathology 97:1558–1567

Rizzo DM, Garbelotto M, Davidson JM et al (2002) *Phytophthora ramorum* as the cause of extensive mortality of *Quercus* spp. and *Lithocarpus densiflorus* in California. Plant Dis 86:205–214

Svihra P (2001) Diagnosis of SOD: case study of a scientific process. Calif Agric 55:12–13

Swiecki TJ, Bernhardt EA (2002) Evaluation of stem water potential and other tree and stand variables as risk factors for *Phytophthora ramorum* canker development in coast live oak. In: Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. Gen. Tech. Rep. PSW-GTR-184. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, pp 787–798. http://danr.ucop.edu/ihrmp/proceed/swiecki02.pdf

Swiecki TJ, Bernhardt E (2003) Relationships between *Phytophthora ramorum* canker (sudden oak death) and failure potential in coast live oak. Vacaville: Phytosphere Research. 57 p. http://phytosphere.com/publications/P_ramorum_coast_live_oak_failure_report_Oct_2002.pdf. Accessed 27 Aug 2012

Swiecki TJ, Bernhardt EA (2004) *Phytophthora ramorum* canker (sudden oak death) in coast live oak and tanoak: factors affecting disease risk, disease progression, and failure potential. 2003–2004 contract year annual report. Phytosphere Research, Vacaville, 35 p. http://phytosphere.com/publications/2003–2004_Case-control_Pramorum_annual_report.pdf. Accessed 27 Aug 2012

Swiecki TJ, Bernhardt EA (2005) *Phytophthora ramorum* canker (sudden oak death) in coast live oak and tanoak, 2000–2004: factors affecting disease risk, disease progression, and failure potential. 2004–2005 contract year annual report. Phytosphere Research, Vacaville, 41 p. http://phytosphere.com/publications/2004–2005_Case-control_Pramorum_annual_report.pdf. Accessed 27 Aug 2012

Swiecki TJ, Bernhardt EA (2007) Influence of local California bay distribution on the risk of *Phytophthora ramorum* canker (sudden oak death) in coast live oak. Phytosphere Research, Vacaville, 30 p. http://phytosphere.com/publications/Influence_bay_distribution_SOD_coast_live_oak.pdf. Accessed 27 Aug 2012

Swiecki TJ, Bernhardt E (2008a) *Phytophthora ramorum* canker (sudden oak death) in coast live oak and tanoak, 2000–2007: factors affecting disease risk, disease progression, and failure potential. 2007–2008 contract year annual report. Phytosphere Research, Vacaville, 40 p. http://phytosphere.com/publications/Phytophthora_case-control2007–2008.htm. Accessed 27 Aug 2012

Swiecki TJ, Bernhardt E (2008b) Increasing distance from California bay reduces the risk and severity of *Phytophthora ramorum* canker in coast live oak. In: Frankel SJ, Kliejunas JT, Palmieri KM, tech. coords. Proceedings of the sudden oak death third science symposium. Gen. Tech. Rep. PSW-GTR-214. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 181–194. http://www.fs.fed.us/psw/publications/documents/psw_gtr214/psw_gtr214_181–194_swiecki.pdf. Accessed 27 Aug 2012

Swiecki TJ, Bernhardt E (2008c) Impacts of *Phytophthora ramorum* canker and other agents in Sonoma County forests. In: Merenlender A, McCreary D, Purcell KL, tech. (eds) Proceedings of the sixth symposium on oak woodlands: today's challenges, tomorrow's opportunities. Gen. Tech. Rep. PSW-GTR-217. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 209–233. http://www.fs.fed.us/psw/publications/documents/psw_gtr217/psw_gtr217_209.pdf. Accessed 27 Aug 2012

Swiecki TJ, Bernhardt E (2010) Long-term trends in coast live oak and tanoak stands affected by *Phytophthora ramorum* canker (sudden oak death). In: Frankel SJ, Kliejunas JT, Palmieri KM, tech. coords. Proceedings of the sudden oak death fourth science symposium. Gen. Tech. Rep. PSW-GTR-229. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 207–209. http://www.fs.fed.us/psw/publications/documents/psw_gtr229/psw_gtr229_207.pdf. Accessed 8 Dec 2012

Swiecki TJ, Bernhardt EA (2013) A reference manual for managing sudden oak death in California. Gen. Tech. Rep. PSW-GTR-242. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, 129 p

Swiecki TJ, Bernhardt E, Drake C et al (2006) Relationships between *Phytophthora ramorum* canker (sudden oak death) and failure potential in coast live oak. In: Frankel SJ, Shea PJ, Haverty MI, tech. coords. Proceedings of the sudden oak death second science symposium: the state of our knowledge. Gen. Tech. Rep. PSW-GTR-196. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 427–453. http://www.fs.fed.us/psw/publications/documents/psw_gtr196/psw_gtr196_007_064Swiecki.pdf. Accessed 27 Aug 2012

Swiecki TJ, Bernhardt E, Garbelotto M et al (2011) The exotic plant pathogen *Phytophthora cinnamomi*: a major threat to rare *Arctostaphylos* and much more. In: Willoughby JW, Orr BK, Schierenbeck KA, Jensen NJ (eds) Proceedings of the CNPS 2009 conservation conference: strategies and solutions. California Native Plant Society, Sacramento, pp 367–371

Swiecki TJ, Bernhardt E, Aram K et al (2013) Diagnosis and management of *Phytophthora ramorum* in canyon live oak, an atypical bole canker host. In: Frankel SJ, Kliejunas JT, Palmieri KM, Alexander JM, tech. coords. Proceedings of the sudden oak death fifth science symposium. Gen. Tech. Rep. PSW-GTR-243. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 80–83. 169 p

Tjosvold SA, Buermeyer KR, Blomquist C et al (2005) Nursery guide for diseases of *Phytophthora ramorum* on ornamentals: diagnosis and management, Publication No 8156. University of California Agriculture and Natural Resources, Oakland

Tjosvold SA, Chambers DL, Koike S et al (2006) Epidemiology of *Phytophthora ramorum* infecting rhododendrons under simulated nursery conditions. In: Frankel SJ, Shea PJ, Haverty MI, tech. coords. Proceedings of the sudden oak death second science symposium: the state of our knowledge. Gen. Tech. Rep. PSW-GTR-196. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, pp 459–461. http://www.fs.fed.us/psw/publications/documents/psw_gtr196/psw_gtr196_007_068Tjosvold.pdf. Accessed 8 Dec 2012

U.S. Environmental Protection Agency [USEPA] (1998) Mono- and di-potassium salts of phosphorous acid (076416) fact sheet. http://www.epa.gov/opp00001/chem_search/reg_actions/registration/fs_PC-076416_1-Oct-98.pdf. Accessed 23 Jan 2013

U. S. Environmental Protection Agency [USEPA] (2006) Phosphorous acid and its ammonium, sodium, and potassium salts (076002) mono- and di-potassium salts of phosphorous acid (076416) Federal Register notices. http://www.epa.gov/oppbppd1/biopesticides/ingredients_keep/fr_notices/frnotices_076002.htm. Accessed 28 Jan 2013

U.S. Department of Agriculture, Animal and Plant Health Inspection Service [USDA APHIS] (2012) APHIS list of regulated hosts and plants proven or associated with *Phytophthora ramorum* (January 2012). http://www.aphis.usda.gov/plant_health/plant_pest_info/pram/downloads/pdf_files/usdaprlist.pdf. Accessed 16 Mar 2012

University of California–Berkeley (2012) SODMAP project. Forest pathology and mycology laboratory. http://sodmap.org. Accessed 13 July 2012

Van Poucke K, Franceschini S, Webber JF et al (2012) Discovery of a fourth evolutionary lineage of *Phytophthora ramorum*: EU2. Fung Biol 116:1178–1191

Vettraino AM, Huberli D, Garbelotto M (2008) *Phytophthora ramorum* infection of coast live oak leaves in Californian forests and its capacity to sporulate in vitro. Aust Plant Pathol 37:72–73

Vettraino AM, Sukno S, Vannini A et al (2010) Diagnostic sensitivity and specificity of different methods used by two laboratories for the detection of *Phytophthora ramorum* on multiple natural hosts. Plant Pathol 59:289–300

Webber JF, Mullett M, Brasier CM (2010) Dieback and mortality of plantation Japanese larch (*Larix kaempferi*) associated with infection by *Phytophthora ramorum*. New Dis Rep 22:19. doi:10.5197/j.2044-0588.2010.022.019

Werres S, Marwitz R, Veld WAMI et al (2001) *Phytophthora ramorum* sp. nov., a new pathogen on *Rhododendron* and *Viburnum*. Mycol Res 105:1155–1165

Widmer TL (2009) Infective potential of sporangia and zoospores of *Phytophthora ramorum*. Plant Dis 93:30–35

Chapter 26
Polyphagous Shot Hole Borer and *Fusarium* Dieback in California

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Abstract The Polyphagous Shot Hole Borer (Coleoptera: Curculeonidae: Scolytinae), *Euwallacea* sp. near *fornicatus*, is an ambrosia beetle native to Asia that has been introduced into Israel, California, and South Africa. The beetle maintains a symbiotic relationship with three species of fungi that it vectors between host trees by carrying spores within a mandibular mycangium. These ambrosial fungi are inoculated into host trees and are the sole nutritional source for the adults and the larvae. Unfortunately for forest and resource managers, one of the fungi, *Fusarium euwallaceae*, is a moderately virulent pathogen and is responsible for causing a dieback disease in susceptible hosts. High levels of infestation of susceptible host trees have resulted in high levels of mortality. The currently recognized host range for the beetle-fungus complex includes more than 200 tree species that can be attacked by the beetle, more than 100 species that can support growth of the fungus, and 37 species that can be used as a reproductive host by the beetles. Many of these reproductive hosts are important agricultural crops, components of the California urban forest, or components of native riparian forest communities. Management is currently focused on monitoring using visual inspections or trapping, sanitation using solarization or chipping, and direct control using contact or systemic insecticides. Future management approaches will include planting resistant or unsuitable host trees and biological control. As more information about the biology and ecology of the insect-fungus complex is developed, it may be possible to develop strategies for limiting spread within and among regions of the world with Mediterranean climates.

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26.1 Wood Borers and Ambrosia Beetles

As international trade and movement of people increases, there are increased movements of insects to new environments. This has become a particular problem with wood borers and ambrosia beetles (Haack 2006). The emerald ash borer, a buprestid native to Asia, has killed hundreds of thousands of trees in central North America where it has been accidentally introduced and threatens to invade the Mediterranean forests of the west (Herms and McCullough 2014). The redbay ambrosia beetle was also introduced into southeastern North America where, in combination with a highly pathogenic fungus, is killing large numbers of native trees (Mayfield et al. 2013).

Scolytinae bark beetles have a wide spectrum of symbiotic associations with fungi (Paine et al. 1997; Six and Wingfield 2011). At one end of the spectrum are species that may be associated with fungi that contaminate the external surface of the body or with phoretic mites. At the other end of the continuum are beetles whose sole source of nutrition are the fungi vectored into new host trees. The ambrosia beetles may be associated with one or more symbiotic fungi which are cultivated on the walls of the beetle's galleries (Batra 1985). Fungi are carried between hosts in special ectodermal pouches known as mycangia that protect and culture the fungi (Batra 1963). The ambrosia beetles may colonize a range of host species and may also be associated with both living and dead or dying trees.

26.2 Polyphagous Shot Hole Borer Biology

The Polyphagous Shot Hole Borer (Scolytinae: *Euwallacea* sp. nr. *fornicatus*) (PSHB) is an invasive ambrosia beetle that has recently been found spreading throughout southern California (Eskalen et al. 2012). Based on morphological characteristics, the PSHB was initially identified as the Tea Shot Hole Borer (Scolytinae: *Euwallacea fornicatus*) (TSHB). However, Mendel et al. (2012) noted that *E. fornicatus* established in Israel exhibited previously undocumented host preferences. The two were distinguished as separate species based on DNA samples collected in California compared to those collected from tea plantations in Sri Lanka. There were significant differences in nuclear and mitochondrial DNA sequences which distinguished PSHB as a cryptic species (P. F. Rugman-Jones and R. Stouthamer, unpublished data). Until a full taxonomic evaluation and navigation of the numerous revisions that have occurred in the genus *Euwallacea* has been finished, the common name of Polyphagous Shot Hole Borer was adopted by Eskalen et al. (2013). The appellation "Polyphagous" refers to the broad range of trees attacked by the beetle rather than the different kinds of fungi eaten.

The first documentation of PSHB in California was in 2003 on black locust (*Robinia pseudoacacia*) (Eskalen et al. 2012). However, no fungal damage was recorded at the time. It was not until 2012 that nine avocado trees exhibiting branch dieback were observed in Los Angeles County (Eskalen et al. 2012). The cultivars that were attacked consisted of Hass, Bacon, Fuerte, and Nabal (Eskalen et.al. 2012). Branch dieback is due to the disease *Fusarium* dieback which is caused by fungal invasion of the vascular elements of the tree, which prevents transport of water and nutrients to the branches (Eskalen et al. 2012; Freeman et al. 2013). Before this the only prior reports of damage caused by PSHB were on avocado in Israel (Mendel et al. 2012). Trees in Israel started showing symptoms of beetle attack in 2005 which includes a characteristic accumulation of white exudate around penetration site (Mendel et al. 2012). Because ambrosia beetles do not feed on the wood itself, the sawdust that is created during tunneling is cleaned out by the mother (Batra 1985) and often accumulates around the entrance to the gallery. Active galleries created by PSHB can often be found by the accumulation of sawdust on the bark of the tree along with discoloration around the gallery entrance (Fig. 26.1).

The mycangia of PSHB is located in a cuticular invagination associated with the mandibles. The beetle maintains a symbiotic relationship with three different fungal species that are carried within the fungus-bearing structure. The first is *Fusarium euwallaceae* which is the causal agent of *Fusarium* dieback (Freeman et al. 2013). The other two are an *Acremonium* and a *Graphium* species (Lynch et al. 2015).

Fig. 26.1 Water soaking and frass accumulation around polyphagous shot hole borer entry sites on the trunk of a coast live oak (*Quercus agrifolia*)

Sequences obtained from fungal isolates were deposited in Genbank under under accession numbers: JQ723753, JQ723760, JQ723756, and JQ723763 (Eskalen et al. 2012).

Female polyphagous shot hole borers are 1.8–2.5 mm in length and range from brown to black in color. Males are 1.5–1.67 mm in length, light brown to black in color, and lack wings (Fig. 26.2). Long distance dispersal and gallery formation is strictly limited to females. Males are only able to disperse by walking to adjacent galleries on the same host. Males are less common than females and galleries will usually only contain one to two males. The exception to this is in galleries created by unmated females. The beetles have a haplo-diploid sex determination system, which means that diploid fertilized eggs give rise to females and haploid unfertilized eggs give rise to males. Consequently, galleries created by unmated females will consist of only male progeny.

Galleries are only about as wide as the female beetle and are initially dug to a depth of about 15 mm into the tree. As the initial gallery is formed, the fungal symbionts are established on the walls using spores carried in the mycangia. If fungal growth is sufficient, the female will lay approximately five eggs at the end of the initial gallery before starting to expand the gallery further. The growing fungal mats are grazed upon by both larvae and adults throughout their entire occupation of the gallery (Fig. 26.3). Larvae remain in the area which they hatched and stay in a clumped distribution throughout the gallery, even when pupating. After pupation, both sexes reach a teneral adult stage that is characterized by lack of fully developed wings and lighter coloration.

While in the gallery, the beetles will mate with their siblings and continue to feed on the fungi growing on the walls. During this time, the mycangia of the females will be filled with fungal spores that will be transported to the next parental gallery. Adult beetles may remain within their natal gallery past maturation and disperse at irregular intervals. Dispersing females may either fly from their natal host to search for a new suitable host tree or they may recolonize the same host tree. The stimuli associated with

Fig. 26.2 Female polypgagous shot hole borer *Euwallacea sp. nr. Fornicatus*

Fig. 26.3 Cross section of a branch heavily colonized by the polyphagous shot hole borer. The gallery walls are lined with ambrosial fungal growth and the vascular tissue is stained

the decision to disperse or recolonize are currently very poorly understood but may possibly be associated with densities of occupied galleries and condition of the natal host.

Damage to host trees is characterized by different symptoms, depending on the species attacked. The tree may exhibit signs of *Fusarium* dieback in the branches (Fig. 26.4). Dieback symptoms include wilting branches, discolored leaves, and breaking of heavy branches (Mendel et al. 2012). These symptoms will be typically observed on primary branches as a result of the symbiotic fungi blocking water movement through the plant vascular system (Eskalen et al. 2013) (Fig. 26.5). However, PSHB can start galleries in branches as small as 2 cm in diameter and almost any age (Mendel et al. 2012). On the trunk of the tree the most common symptom of beetle invasion is the presence of staining or discoloration of the bark around the entry hole due to necrosis of the tissue (Eskalen et al. 2013). Some tree species will also respond to attack with gum deposition around the attack site. Infested avocado exhibits a unique response where large deposits of white and powdery exudate composed of the sugar perseitol form around the entry hole (Mendel et al. 2012).

Infested trees have been located in Los Angeles, San Diego, Riverside, and Orange County in southern California. Records of the beetles' movement are tracked using trap baited with an attractant lure (quercivorol) set up along the borders of the known infested areas in order to identify when the beetle has moved into new territory. Known host species are also visually inspected for signs of attack. The earliest mapped infestations in 2012 covered an area that included Los Angeles, Pasadena, Pomona, and Seal Beach (Eskalen et al. 2015. Distribution map). The following year, in 2013, the infestations had expanded its borders in each direction

Fig. 26.4 Dieback in boxelder (*Acer negundo*) heavily colonised by the polyphagous shot hole borer and infected with the symbiotic *Fusarium euwallacea*

Fig. 26.5 Vascular staining associated with beetle galleries and infection by the symbiotic fungus

to include Brentwood, Altadena, Ontario, and Laguna Beach. During 2014 PSHB expanded its range northwest to Sunland above the Verdugo Mountains and east into Corona. This trend has continued in 2015 where the only new captures of PSHB are north and west in the lower Santa Susanna Mountains and Woodland Hills. Research is currently underway to determine the temperature development rates and thermal tolerances of the beetles to predict the potential limits of the infested areas.

Unfortunately, a different type of PSHB was discovered outside the previously infested area. The two types are distinguished by having different fungal complements and different mitochondrial DNA sequences (A. Eskalen and R. Stouthamer, unpublished data). The first type found in California has been named the Los Angeles type and the second type is named the San Diego type, based on the county that each were first recorded. The San Diego type has been mostly located around the city of Escondido with recent captures in the city of San Diego.

The infested areas of Los Angeles County include the Los Angeles Arboretum and the Huntington Library and Botanical Gardens. These botanical gardens contain a wide variety of identified tree species and cultivars. Trees in these collections were surveyed in order to estimate the range of possible hosts within California. Of the 335 tree species in 85 families that were examined 207 of them showed symptoms consistent with attack (Eskalen et al. 2013). More than 100 of the tree species were susceptible to colonization by *F. euwallaceae* (Eskalen et al. 2013), which indicates that even if the beetle doesn't reproduce inside that tree that it may still suffer the effects of *Fusarium* dieback. The number of trees species that supported reproductive success for PSHB was 19 species (Eskalen et al. 2013). That number has expanded to a list of 37 species. California native forest species that are threatened include box elder (*Acer negundo*), big leaf maple (*Acer macrophyllum*), California sycamore (*Platanus racemosa*), Gooding's black willow (*Salix goodingii*), red willow (*Salix laevigata*), white alder (*Alnus rhambifolia*), cottonwood (*Populus fremontii*), black cottonwood (*Populus trichocarpa*), Engelmann oak (*Quercus engelmannii*), valley oak (*Quercus lobata*), and coast live oak (*Quercus agrifolia*) (Eskalen et al. 2013). Of these trees, PSHB has a strong preference for box elder. However, work is currently underway to evaluate susceptibility and suitability of the reproductive hosts.

To estimate the potential impact PSHB could have on an urban forest, a comparison was made between a list of common street trees and the list of trees that support either or both fungus and beetle growth. It was determined that 48 % of street trees belong to a species that are suitable for fungal colonization and that 26 % of street trees are a suitable host for beetle development (Eskalen et al. 2013). Urban tree species on this list include Japanese maple, English oak, mimosa, mesquite, and camellia (Eskalen et al. 2013).

A similar comparison was made to estimate the threat of PSHB to agricultural crops. The fungus *F. euwallacea* was able to colonize avocado, eastern mulberry, olive, macadamia, Turkish hazelnut, loquat, peach, and grapevine (Eskalen et al. 2013). Of these crops only avocado supported beetle development (Eskalen et al. 2013). Trees of agricultural significance that were not attacked by PSHB include date palm, pomegranate, fig, apple, and citrus (Eskalen et al. 2013). Agricultural trees that PSHB attacked but did not support fungal growth were cassava, Japanese persimmon, Japanese crabapple, and eastern black walnut (Eskalen et al. 2013).

Two reproductive hosts of exotic origin are of particular note. The first is castor bean (*Ricinus communis).* Castor bean is a favored reproductive host of the Los Angeles type (Eskalen et al. 2013) and is considered an obnoxious weed because of the toxic seeds and aggressive growth characteristics. The second is Tree of Heaven (*Alianthus altissima*). It is also considered an aggressive weedy tree species that will establish thick stands in disturbed habitats. Due to the widespread nature of these two weedy species, they may function as potential alternate hosts of PSHB that can facilitate reestablishment of the beetle in managed areas or allow for a population of beetles to move between areas if castor bean patches or *Alianthus* stands exist in between and act as corridors for invasion across the interfaces between urban, agricultural, and native forest communities.

26.3 Approaches for Management

The biology of the polyphagous shot hole borer limits potential options for management of the insect to reduce the number of affected trees. Females emerge from the natal galleries already inseminated, so there is no known sex pheromone for the insect. There does not appear to be an aggregation pheromone as has been identified for many other species of bark beetles. Consequently, survey and detection has been limited to visual inspections until very recently. The discovery of the response to quercivorol (p-menth-2-en-1-ol) has made it possible to trap beetles in the landscape. This discovery should make it possible to both delimit infestations and to monitor the movement of individuals. Because of the high risk of tree mortality, quarantine, detection, and restriction of movement of infested or potentially infested host material is critical to limiting tree loss.

Disposal of infested trees and wood residues provides challenge for forest managers. Sanitation is critical to reduce the population of beetles within an area, eliminate human-aided dispersal of the insects, and to prevent on-site emergence and reinfestation of trees. It is possible to chip or grind infested material to kill the beetles in the wood. Material chipped to sizes 2.5 cm or less prevented any emergence of adults. Chipping material to approximately 5 cm in size did not completely prevent emergence of the adults, but the population was reduced by more than 90 %. An alternative approach to chipping for sanitation is to use solarization. Covering infested log sections with 2 ml clear plastic in the summer months in southern California raised the temperatures within the log pile to more than 60 °C when the daily ambient temperatures had an average maximum of 32 °C and eliminated any signs of beetle activity within six weeks (Jones and Paine 2015). Unfortunately, solarization in the cooler fall and winter seasons has not proven to be effective.

It may be possible to use direct control with insecticides to reduce the risk of infestation of individual high value trees. Synthetic pyrethroid contact insecticides have been demonstrated to be effective at establishing a barrier to beetles attempting to penetrate through the bark during colonization. There are systemic insecticides that have proven effective against other wood borers (McCullough et al. 2015), but these could be acting either on adults when they feed on foliage or on adults and larvae tunneling in the wood. Unlike the many other wood borers, the ambrosia beetles do not feed on the wood; rather, they only feed on the fungi. Consequently, it remains unclear whether they would contact the systemic insecticides in a way to acquire a toxic dose. However, their absolute reliance on fungi for nutrition may provide another opportunity for chemical control. It may be possible to apply a fungicide either systemically or in conjunction with a bark penetrant to kill the fungal symbionts and deprive the beetles of their source of nutrition. All of these options are the subject of ongoing investigations.

The identified list of susceptible or suitable hosts continues to change as the beetles encounter new potential host species. Although the range of potential hosts does change, it is clear that there are some species that are regularly infested (e.g., box elder) and others that are not (e.g., conifers). Thus, it is possible to generate a series of recommendations to landscape and forest managers of high risk tree species to either carefully monitor in established landscapes or to avoid when replanting. Careful host selection should be practiced to limit future risk from the ambrosia beetle.

The other option for long term management of the beetle is establishing biological control. Once it can be clearly established how many species of beetles have become established and where their native range is in Asia, it will be possible to conduct exploration in those areas for suitable natural enemies. Investigators have collected a number of candidate fungi, nematode, and arthropod natural enemies in preliminary trips and these opportunities will be pursued in the future. Unfortunately, because the ambrosia beetle species appear to be new to science, the amount of historical collection data for the beetles. Comparable historical data for the natural enemies is essentially nonexistent. Biological control remains an important option, but will not be established in a short time frame.

26.4 Risk to Mediterranean Forests

Although native range of the polyphagous shot hole borer appears to be in Asia, there is substantial risk to forest tree communities in Mediterranean environments. In fact, the beetle is currently found in three of the five continents with Mediterranean climates. It was first discovered infesting avocado groves in Israel (Mendel et al. 2012; Freeman et al. 2013) along the eastern rim of the Mediterranean Sea. Fortunately, the number of suitable host trees either in the urban landscape or in native forests is limited. Consequently, it has not been reported to have spread. However, because the beetle is well established there is a very significant risk of movement to other parts of the region. The California experience indicates that some species of *Quercus*, *Salix*, *Alnus*, and *Platanus* are highly susceptible (Fig. 26.6). Species in these plant genera are at high risk. Movement of the beetle from currently infested areas with low host densities to areas with higher host densities could accelerate the spread of the insect throughout the Mediterranean Basin.

The beetle is also reported from South Africa, again from avocado. It is unclear how long the beetle has been in the southern part of the continent or whether it has moved from the areas dominated by summer rainfall the Mediterranean environments with winter precipitation. However, because the beetle is already present, the susceptible hosts in native and introduced host trees are at risk. There is the potential for both geographic spread and for the host range to expand as the beetles encounter new host species.

As noted previously, the polyphagous shot hole borer is well established in southern California. To date, the emphasis of research investigations has focused on the insect as a pest of commercial agriculture (avocados) or of landscape trees. However, there is also a critical need to understand the risk to native forest systems. The highly susceptible hosts that have been identified to date include very important constituents of the riparian forests and of native savannah or oak woodland ecosystems in California. Many of these are adjacent to urban developments that include susceptible urban forest tree species. The interface between the native and urban landscapes presents a very high risk for movement of the insects, something already observed in the southern California mountains. The valuable riparian forests in the

Fig. 26.6 Red willow (*Salix laevigata*) branch heavily infested by the polyphagous shot hole borer. The density of parental galleries structurally weakened the branch and contributed to structural failure in a wind storm

canyons have been colonized by the insect and trees at lower elevations adjacent to urban areas have been killed. It is not yet clear whether further spread will be restricted by low temperatures at higher elevations.

Because we do not know how the beetle/disease complex was introduced into any of the three currently infested areas, there is limited available analysis assessing risk for future introduction. If we knew how and from where, it would be possible to develop a monitoring strategy. However, we do know where it has currently been established and there is some information available regarding hosts at risk. Consequently, it now may be possible to evaluate risk of range expansion in invaded areas or risk of movement from invaded areas to new parts of the world.

References

Batra L (1963) Ecology of ambrosia fungi and their dissemination by beetles. Trans Kans Acad Sci 66:213–236

Batra L (1985) Ambrosia beetles and their associated fungi: research trends and techniques. Proc Indiana Acad Sci 94:137–148

Eskalen A, Gonzalez A, Wang DH et al (2012) First report of *Fusarium* sp. and its vector tea shot hole borer (*Euwallacea fornicatus*) causing *Fusarium* dieback on avocado in California. Plant Dis 96:1070

Eskalen A, Stouthamer R, Lynch SC et al (2013) Host range of *Fusarium* Dieback and Its Ambrosia Beetle (Coleoptera: Scolytinae) vector in Southern California. Plant Dis 97:938–951

Eskalen A, Feirer S, Drill S, et al (2015) PSHB/FD distribution map. http://eskalenlab.ucr.edu/distribution.html

Freeman S, Sharon M, Maymon M et al (2013) *Fusarium euwallaceae* sp. nov. a symbiotic fungus of *Euwallacea* sp., an invasive ambrosia beetle in Israel and California. Mycologia 105:1595–1606

Haack RA (2006) Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can J For Res 36:269–288

Herms DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu Rev Entomol 59:13–30

Jones ME, Paine TD (2015) Effect of chipping and solarization on emergence and boring activity of the polyphagous shot hole borer in southern California. Environ Entomol (in press)

Lynch SC, Twizeyimana M, Mayorquin JS et al (2015) Identification, pathogenicity, and abundance of *Acremonium pembeum* sp. nov. and *Graphium euwallaceae* sp. nov.- two newly discovered mycangial associates of the polyphagous shot hole borer (*Euwallacea* sp.) in California. *Mycologia* in review

Mayfield AE, MacKenzie M, Cannon P et al (2013) Suitability of California bay laurel and other species as hosts for the non-native red bay ambrosia beetle and granulate ambrosia beetle. Agric For Entomol 15:227–235

McCullough DG, Mercader RJ, Siegert W (2015) Developing and integrating tactics to slow ash (Oleaceae) mortality caused by emerald ash borer (Coleoptera: Buprestidae). Can Entomol 147:349–358

Mendel Z, Protosav A, Sharon M et al (2012) An Asian ambrosia beetle *Euwallacea fornicatus* and its novel symbiotic fungus *Fusarium* sp. pose a serious threat to Israeli avocado industry. Phytoparasit Online publication. doi:10.1007/s12600-012-0223-7

Paine TD, Raffa KF, Harrington TC (1997) Interactions among scolytid bark beetles, their associated fungi, and live host conifers. Annu Rev Entomol 42:179–206

Six DL, Wingfield MJ (2011) The role of pathogenicity in bark beetle-fungus symbioses: a challenge to the classic paradigm. Annu Rev Entomol 56:255–272

Chapter 27
Air Pollution

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Abstract The most important regional impacts of air pollution in Mediterranean forests arise from ozone and nitrogen deposition. Primary pollutants from urban centers, and hot summers lead to high photochemical activity for ozone formation in many Mediterranean regions. Ozone concentrations are typically high in rural and wildland areas removed from urban centers, and thus have the potential to impact Mediterranean forests. Ozone regularly exceeds concentrations where plant damage is expected in southern Europe and California. Chile has moderate ozone, while concentrations are typically lower in the Mediterranean regions of southern Africa and Australia. Anthropogenic nitrogen deposition primarily arises from atmospheric nitrogen oxides and ammonia. Nitrogen deposition is also high in southern Europe and California. Plant and insect community impacts of air pollution have been most studied in California. Although pollution exposure is also high in the Mediterranean basin, forest impacts there have not been widely studied. In California, both ozone and nitrogen deposition have been associated with increased bark beetle attacks and tree mortality. Other changes in insect herbivore communities have also been observed. We found that nitrogen deposition may affect the relationship between fruittree leafrollers and leaf expansion of California black oak. During a leafroller outbreak, trees with nitrogen addition treatments had lower densities of leafrollers, less leaf damage, and leaves had expanded further during early spring sampling.

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27.1 Introduction

Changes to forest vegetation in response to anthropogenic air pollution and the accompanying changes in insect communities or herbivore performance are mainly associated with exposure to O_3 and with the effects of increased nitrogen additions to the forest. Both of these pollution effects are increased by anthropogenic emissions of NO_X and volatile organic compounds (VOCs) in urban regions and the subsequent increased formation of ozone and ammonium nitrate as a result of these primary emissions. NO_X and VOCs are emitted during the combustion of fossil or vegetative fuels (Finlayson-Pitts and Pitts 2000). This can include mobile emission sources such as emissions from gasoline or diesel powered vehicles and stationary emission sources such as emissions from coal- or oil-fired power plants. For example, 1996 emissions of NO_X in the United States (Finlayson-Pitts and Pitts 2000) came from on-road vehicles (30 %), fuel combustion + electrical utility (28 %), non-road engines and vehicles (19 %), fuel combustion – industrial (13 %), fuel combustion – other (5 %) and all other (5 %). And emissions for VOCs came from solvent utilization (33 %), on-road vehicles (29 %), non-road engines and vehicles (13 %), miscellaneous (3 %), all other (15 %).

The majority of primary nitrogen oxides are emitted from combustion sources in the form of NO(g) (Finlayson-Pitts and Pitts 2000). In the presence of ozone, $HO_2^{\cdot}$ or RO_2 (an alkyperoxy radical), NO is oxidized to NO_2 via the following:

$$NO(g) + O_3(g) \rightarrow NO_2(g) + O_2(g) \tag{27.1}$$

$$NO(g) + HO_2(g) \rightarrow NO_2(g) + OH(g) \tag{27.2}$$

$$NO(g) + RO_2(g) \rightarrow NO_2(g) + RO(g) \tag{27.3}$$

Ozone is formed by the photolysis of $NO_2(g)$, OH(g) is formed by the photolysis of O_3 followed by the reaction of O^1D with H_2O and $HO_2(g)$ and $RO_2(g)$ are formed from the reactions of hydroxyl (and at night, nitrate) radicals with gas phase VOCs. Thus, the relative concentrations of NO_X and VOCs control the concentration of O_3 in a complex manner described by an ozone isopleth (Finlayson-Pitts and Pitts 2000). The isopleth shown in Fig. 27.1 is calculated using the EPA EKMA model (Committee 1991). All ozone isopleths have the same general features, whether model calculated or experimentally determined. In general, at low NO_X concentrations, the concentration of ozone is not significantly influenced by the concentrations of VOCs and the system is NO_X limited. For example, if the atmospheric system behaves as shown in Fig. 27.1, if the NO_X concentration is constant at 0.08 ppm, as the concentration of VOC increases from negligible to about 0.06 ppm the ozone concentration will increase up to 0.20 ppm. However, as a result of increasing VOC concentration further, the system will pass over the $VOC/NO_X = 8/1$ crest line and increasing VOC concentration will push the ozone concentrations to about 0.24 ppm (the next isopleth) line, but ozone will not increase above that even

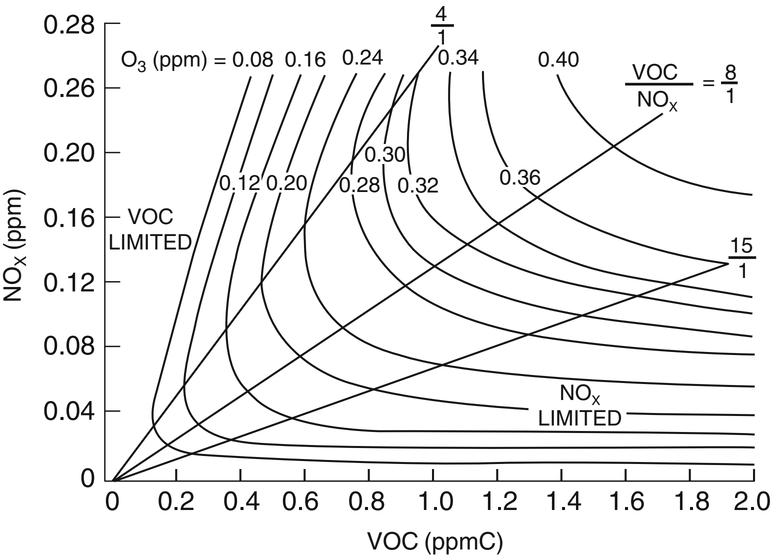

Fig. 27.1 Ozone isopleth diagram calculated from the EPA EKMA model (From Rethinking the Ozone Problem in Urban and Regional Air Pollution, Committee on Tropospheric Ozone, Nsyional Research Council, The National Academies Press, 2015, p. 155)

at very high concentrations of VOC. Conversely at a constant NO_X concentration of 0.24 ppm, ozone will increase at all increasing concentration of VOC as the ridge line is not crossed. However, at low VOC concentrations, O_3 concentrations can decrease with increasing NO_X as NO reacts with O_3 and NO_2 competes with VOC for the OH (g) radical by the irreversible formation of nitric acid:

$$NO_2(g) + OH(g) \rightarrow HNO_3(g) \quad (27.4)$$

Nitric acid usually reacts rapidly reacts with ammonia to form particulate ammonium nitrate:

$$HNO_3(g) + NH_3(g) \rightarrow HH_4NO_3(s) \quad (27.5)$$

Reactions 27.4 and 27.5 contribute to forest system nitrogen deposition. Nitric acid may also be formed at night through the nitrate radical. However, since O_3 and NO_2 do not coexist at night this pathway will usually not be important.

For the isopleth diagram shown in Fig. 27.1, the ridge in the ozone concentrations occurs at a ratio of $VOC/NO_X = 8/1$. The existence of a ridge is a typical feature for any given urban area. For any given environment the details of the isopleth diagram will differ somewhat from that shown in Fig. 27.1, but the features will be the same (e.g. see Finlayson-Pitts and Pitts 2000, pp. 882–886). The VOC limited region is typical of the condition seen in highly polluted urban areas, whereas the NO_X limited region is typical of locations downwind of urban and suburban centers.

Thus the NO_X limited region can be important in determining the chemistry occurring in a Mediterranean forest area.

Because the key reactions in the chemistry described above are photochemistry driven by the solar flux, the actual concentration of ozone produced with a given concentration of NO_X and VOCs will be dependent on season and cloud cover. The maximum concentration will be produced during clear weather during the summer. Concentrations of ozone produced with the same precursor conditions, but much lower solar flux, i.e. during the winter, will be significantly lower.

The second anthropogenic pollution effect which can negatively impact Mediterranean forests is atmospheric nitrogen deposition. Human activities have more than doubled the amount of nitrogen entering terrestrial ecosystems. Major sources of airborne emissions of these nitrogenous compounds include burning of fossil fuels and forest biomass, emissions from nitrogen enriched soils, and volatilization from livestock operations. Approximately 80 % of global nitric oxide emissions and 70 % of ammonia emissions arise from human sources (Vitousek et al. 1997). The major avenue for nitrogen deposition impacts to a forest is through the deposition or either ammonia or nitrate, with the effect of other nitrogen containing anthropogenic pollutants, e.g. NO_2, being less important. The major route for this deposition is either the dry deposition of ammonium nitrate formed by reaction (27.5) or the wet deposition in fog or rain of ammonium nitrate, nitric acid and ammonia. In most Mediterranean ecosystems, dry deposition is the dominate pathway for atmospheric nitrogen deposition (Ochoa-Hueso et al. 2011). Nitrogen additions to forest systems will occur in all regions due to natural processes. However, nitrogen inputs can be significantly increased due to the chemistry of anthropogenic NO_X and VOC emissions as described above. The relative importance of nitrogen deposition to Mediterranean forests in various areas of the world has been reviewed (Ochoa-Hueso et al. 2011).

27.2 Ozone and Nitrogen Deposition in Mediterranean Climate Zones

Mediterranean forests are characterized by dry summers and rainy winters. Summers are typically hot in low-lying inland locations but can be cool near some seas or at higher elevations. Winters are typically mild to cool in low-lying locations but can be cold in inland and higher locations. There are five Mediterranean climate zones, on the west coast of continents in the mid-latitudes. These are (in order of the pollution information available in each):

- The Mediterranean Basin
- The California chaparral and woodlands ecoregion from central California southward.
- The Chilean Matorral
- The Cape Province – Western Cape of South Africa
- The Southwest Australia corner area

Table 27.1 Typical ranges of ozone concentrations and nitrogen deposition for Mediterranean climate zones

	Ozone (ppb)		Nitrogen deposition (kg ha^{-1} year^{-1})	
	Summer average	Hourly peak	Typical range	Peak
Southern Europe (Northern Italy)	60	120	10–20	38
California (western slopes)	70	140	30–70	71
California (interior forests)	60	120	2–5	
Chile	50	80	2.8	
Africa	25	50	<2	13
Australia	20–40	60–70	NA	

A summary of typical pollution inputs in each of these zones is given in Table 27.1. Examples of known anthropogenic ozone and nitrogen deposition impacts in each zone follow.

27.3 The Mediterranean Basin

27.3.1 Pollution

Extensive ozone monitoring at rural background stations has been conducted by the European Environment Agency to determine the exposure of European agricultural areas to ozone. The 2010 results from analysis of this data set are given in Fig. 27.2. The AOT40 results given in Fig. 27.2 refer to the summer growing season accumulated dose of ozone over a threshold of 40 ppb and is the sum of differences between hourly concentration greater than 40 ppb (80 · μg/m^3) and 40 ppb. The European program uses a default growing season of May–July and a default crop-height of 1 m. Maximum summer vegetative dose of ozone is highest along the Mediterranean Coast with maximum inland impact from southeastern France, through northern Italy and into northwestern Greece. Correspondingly, these would be the regions where impacts on Mediterranean forests would be expected to be the most significant.

A review by Paoletti (2006) gives 5 year (2000–2004) mean monthly diurnal average ozone concentrations at rural sites (and a few suburban sites) in Italy (Fig. 27.3). The line in the middle of each ozone summary insert in Fig. 27.3 corresponds to 45 ppb ozone. The trends at the various locations shown in Fig. 27.3 are consistent with the spatial distribution expected from the 2010 summary in Fig. 27.2. It is interesting to note the particularly high concentrations seen at the suburban site in Sicily, consistent with the data shown in Fig. 27.2. As noted in Fig. 27.3, the winter diurnal ozone maxima averages are significantly lower than the summer concentrations.

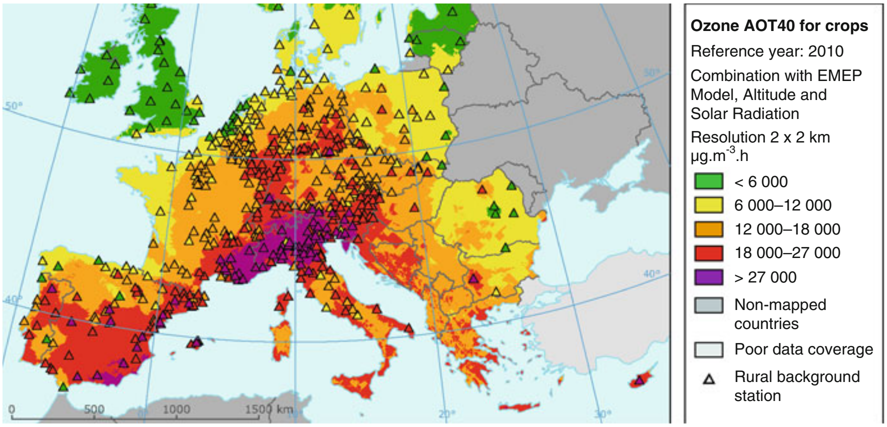

Fig. 27.2 Ozone AOT40 for crops, reference year 2010 (From the European Environment Agency (http://www.eea.europa.eu/legal/copyright))

Nitrogen deposition to the Mediterranean basin forest ecosystem has been shown to lead to deleterious effects, with the majority of the data related to Italy (Ochoa-Hueso et al. 2011). Most studies on nitrogen effects do not establish a clear tie between anthropogenic pollution and observed effects. However, a recent study by Ferretti et al. (2014) has shown a clear relationship between dry nitrate plus ammonium throughfall which is probably related to ammonium nitrate production from NO_X and O_3 chemistry. The study did not show a strong relationship between nitrogen deposition effects and ozone. However, this is not surprising because nitrate formation is not linearly related to ozone formation (see Sect. 27.1). Nitrogen deposition in rural and forest areas has been estimated at 10–20 kg $ha^{-1}year^{-1}$ in Spain, about 13 kg $ha^{-1}year^{-1}$ in Italy, and 15 kg $ha^{-1}year^{-1}$ in Greece (Ochoa-Hueso et al. 2011).

27.3.2 Forest Impacts in the Mediterranean Basin

Ozone concentrations in wide areas of southern Europe regularly exceed critical levels that have been shown to be damaging to plants. Crop damage and reduced yields associated with ozone exposure have been reported in many regions of southern Europe (Fumagalli et al. 2001; Mills et al. 2011), particularly in Italy (Fagnano et al. 2009; Picchi et al. 2010; González-Fernández et al. 2014), Greece (Vlachokostas et al. 2010), and Spain (Gimeno et al. 1999; Delgado-Saborit and Esteve-Cano 2008). In spite of chronic ozone exposure, forests in the Mediterranean basin have not been widely studied for ozone impacts (Bussotti and Gerosa 2002; Paoletti 2006). A 10 years monitoring program in forest plots throughout Europe did show a correlation between increasing crown transparency and ozone levels (Klap et al.

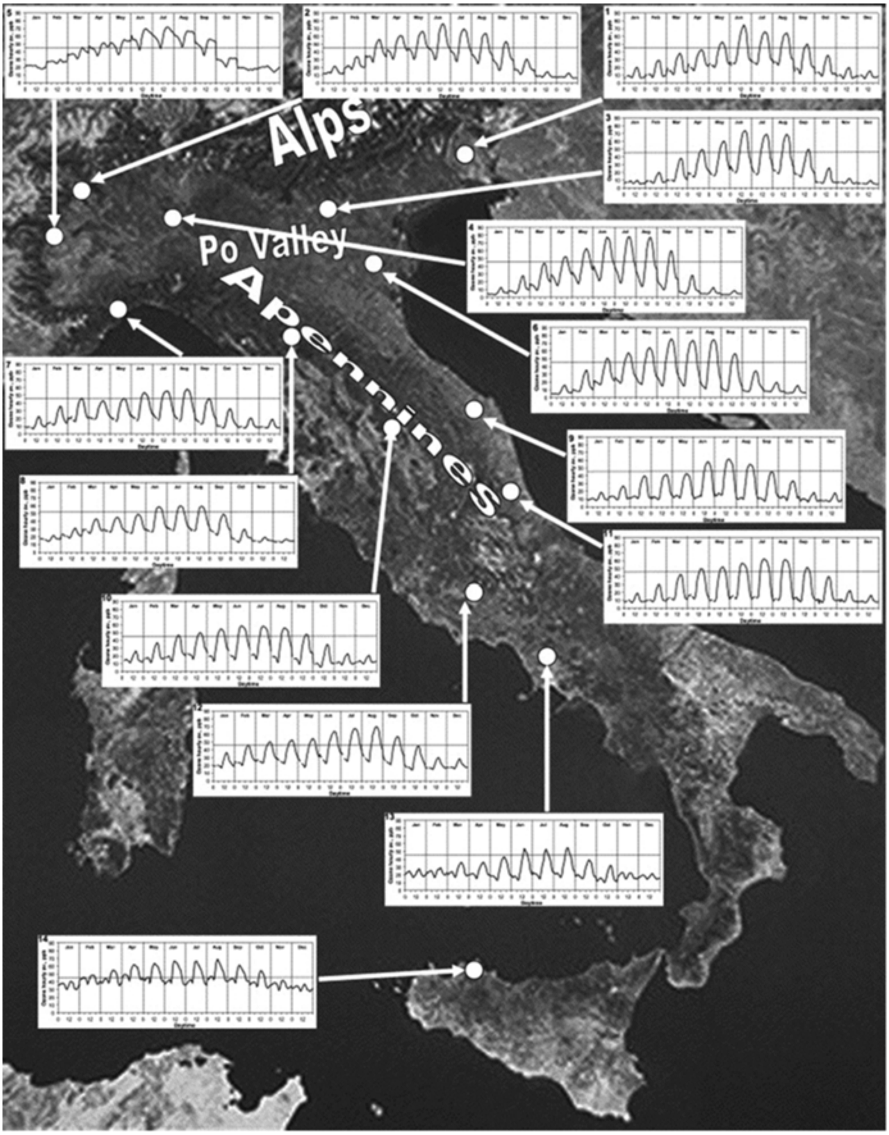

Fig. 27.3 Location and mean daily trend of O_3 concentrations per month. Numbers in the upper-left corner of each graph show the O_3 monitoring stations as in Table 27.1. According to Noirfalise (1987), Italian natural vegetation south of the Po Valley, except the highest Apennines elevations, is classified as Mediterranean (Figure and Title from Paoletti 2006)

2000). The relationship was stronger for mesic species such as European beech, but less pronounced for xeric species such as holm oak. However, crown transparency is affected by a wide variety of factors, and this correlation is inconclusive in regards to determining ozone impacts for forests in Europe.

After symptoms of ozone injury were identified in southern California (Stark et al. 1968), these symptoms were also recognized for some forest species in the Mediterranean basin. Ozone injury has been most widely described for Aleppo pine (*Pinus halepensis*) in several Mediterranean countries including Spain (Gimeno et al. 1992; Barnes et al. 2000; Sanz et al. 2000), Greece (Gimeno et al. 1992; Velissariou et al. 1992), Italy (Soda et al. 2000) and Israel (Naveh et al. 1980). Ozone injury has also been observed of many other Mediterranean tree species (Bussotti and Gerosa 2002; Paoletti 2006). Additionally, ozone sensitivity has been determined individually for many Mediterranean tree species using chamber fumigation experiments (Bussotti and Gerosa 2002; Paoletti 2006). It is generally accepted that, in spite of chronic high ozone concentrations in the Mediterranean basin, plant adaptations to the Mediterranean climate also buffer against ozone uptake and subsequent plant damage so that plant damage from ozone exposure has been less in Mediterranean forests than for irrigated agricultural crops and more mesic areas of Europe (Bussotti and Gerosa 2002; Paoletti 2006). However, ozone exposure may predispose trees to attack by insects or pathogens. Cork oak seedlings (*Quercus suber*) that were fumigated with ozone and then inoculated with endophytic fungi under natural conditions in a forest stand had more fungal isolates compared to control seedlings (Paoletti et al. 2007). However, impacts of ozone on insects and pathogens in Mediterranean forests have not been studied.

Mediterranean forests are often considered N limited, therefore N additions to these forests through atmospheric deposition have the potential to alter patterns of plant growth, plant chemistry and competitive interactions among plant species, which in turn may affect herbivory and insect communities. Some effects of N deposition or N addition experiments have been recorded for Mediterranean plants, but overall there is limited information for Mediterranean plant communities outside of California (Ochoa-Hueso et al. 2011). However, in Mediterranean forests, water is a main factor limiting plant growth, which will mitigate plant responses to N deposition (Phoenix et al. 2006; Sanz Pérez et al. 2007). Changes in soil nutrient cycling due to nitrogen deposition have been recorded in forests in Italy (Ferretti et al. 2014), Greece (Michopoulos et al. 2004) and Spain (Blanes et al. 2013; Ochoa-Hueso et al. 2013). Altered foliar nutrient ratios and increased basal growth were related to nitrogen deposition for forests in Italy (Ferretti et al. 2014). Higher trophic levels have not been studied.

27.4 California

27.4.1 Pollution

The ecosystem areas of interest are the forests of the San Bernardino and the Sierra Nevada Mountains. The major emission areas impacting the California Mediterranean ecosystems are the San Francisco Bay region, the San Joaquin Valley, and the South Coast Air Basin (Los Angeles and the Inland Empire). The U.S. Environmental Protection Agency combines daily ozone data from over 148 sampling sites run by

30 California air quality monitoring districts to produce a Daily Combined AQI map for the region (http://www.airnow.gov/index.cfm?action=airnow.mapsarchive-calendar). Ozone episodes are frequently seen during the summer. An example is shown for July 30, 2014 (Fig. 27.4a). The large yellow zone (Moderate) between Los Angeles and Sacramento covers the San Joaquin Valley with a few orange areas (USG) imbedded around the major urban areas in the Valley. The general direction of transport each day is to the east. This transport results in the large orange area with a small red (Unhealthy) area which is centered over the Sierra Mountains. This increased ozone in the mountain regions is frequently seen in the central Sierra Mountains. The highest concentrations of ozone in the Los Angeles area are also to the east of the city center and represent increased ozone production as pollutants are transport east into the Inland Empire and the San Bernardino Mountains. In contrast, during the winter, ozone episodes can frequently occur in the populated areas, particularly in the San Joaquin Valley which frequently has strong, shallow inversions (Fig. 27.4b). Winter concentrations are usually much lower in the South Coast Air Basin. In addition, during the winter, transport of ozone in to the mountains is much reduced for both the Sierra and San Bernardino Mountains (Fig. 27.4b).

Ozone concentrations in the forests in both the Sierra Nevada (Lake Tahoe area) and the San Bernardino Mountains have been reported (Zielinska et al. 2012; Burley et al. 2015). Results for the Lake Tahoe area study are shown in Fig. 27.5, where the location of 2 weeks passive ozone monitor sample collection is indicated in the panel to the left and the average results seen during the summer of 2010 is given in the panel to the right (Zielinska et al. 2012; Burley et al. 2015). Highest concentrations were seen at the lower elevation sites to the west (1250 m) and decrease towards the western rim of the Lake Tahoe Basin (2225 m). These results suggest that the elevated ozone concentrations in the region are due to the transport of polluted air from the San Joaquin Valley. An earlier study using passive samplers for a 2 weeks period in August 1999 covered the entire Sierra Nevada mountain range (Bytnerowicz et al. 2014). Results obtained in the Lake Tahoe area were very similar to those given in Fig. 27.5. However, the concentrations of ozone were about twice those seen in 2010. Similar high impacts were seen towards the southern end of the Sierra Nevada range with high ozone to the east of Fresno and Bakersfield.

Similar conditions also impact the San Bernardino Mountains east of Los Angeles. As indicated by the data for Wednesday, July 30, 2014 (Fig. 27.4a). The concentrations of ozone will frequently increase during the summer as polluted air from the Los Angeles area is transported east across the urban Inland Empire towards the San Bernardino Mountains, resulting in increased ozone in the forests in these mountains.

Hourly averaged concentrations of O_3, NO_X and NO_2 were obtained during July and August, 2005 at Riverside CA, just west of the San Bernardino Mountains (Eatough et al. 2008). These data provide insight into the factors controlling the concentration of ozone in air being transported toward the mountains. The relationships during daytime hours of NO_X to O_3 and NO_2 to O_3 are shown in Fig. 27.6a and b, respectively. The inverse relationships shown in Fig. 27.6a and b suggests ozone scavenging by NO and competition of the NO_2 molecule for the $OH^{\cdot}$ radical, thus

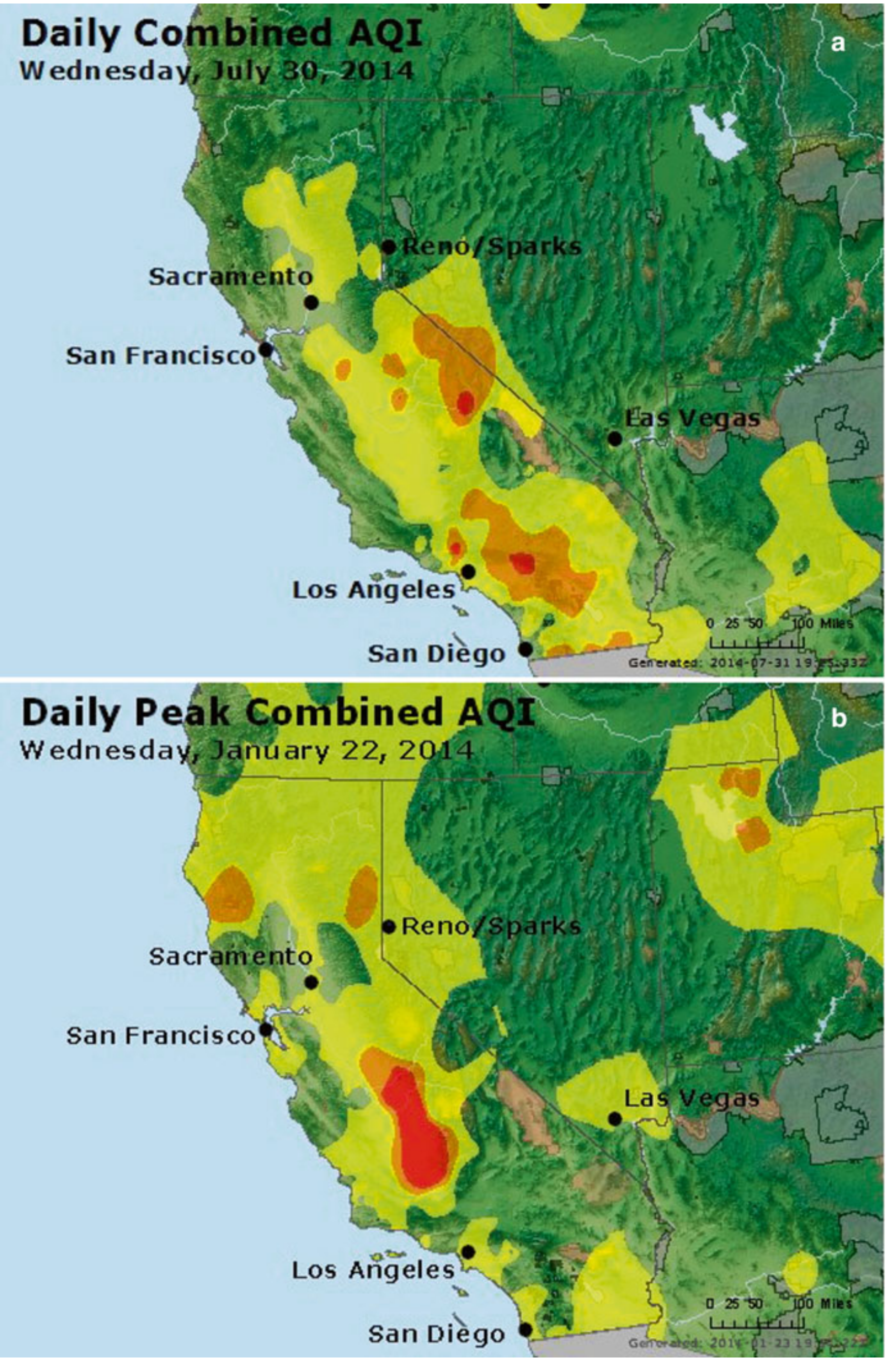

Fig. 27.4 Air quality index for California for Wednesday July 30, 2014 **(a)** and Wednesday, January 22, 2014 **(b)** (From archived maps in http://www.airnow.gov/)

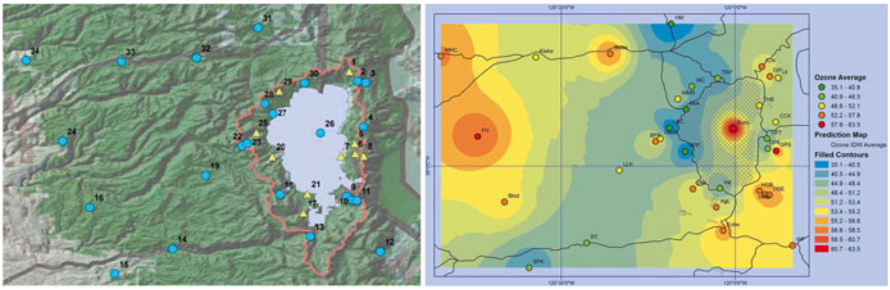

Fig. 27.5 Results of the 2010 Lake Tahoe Study (Zielinska et al. 2012). The study monitoring network is shown on the *left*. Regular passive sampler sites are marked with *blue circles*, and mega sites where: active ozone monitors were also located are marked with *yellow triangles*. The study average ozone impact is shown on the *left*

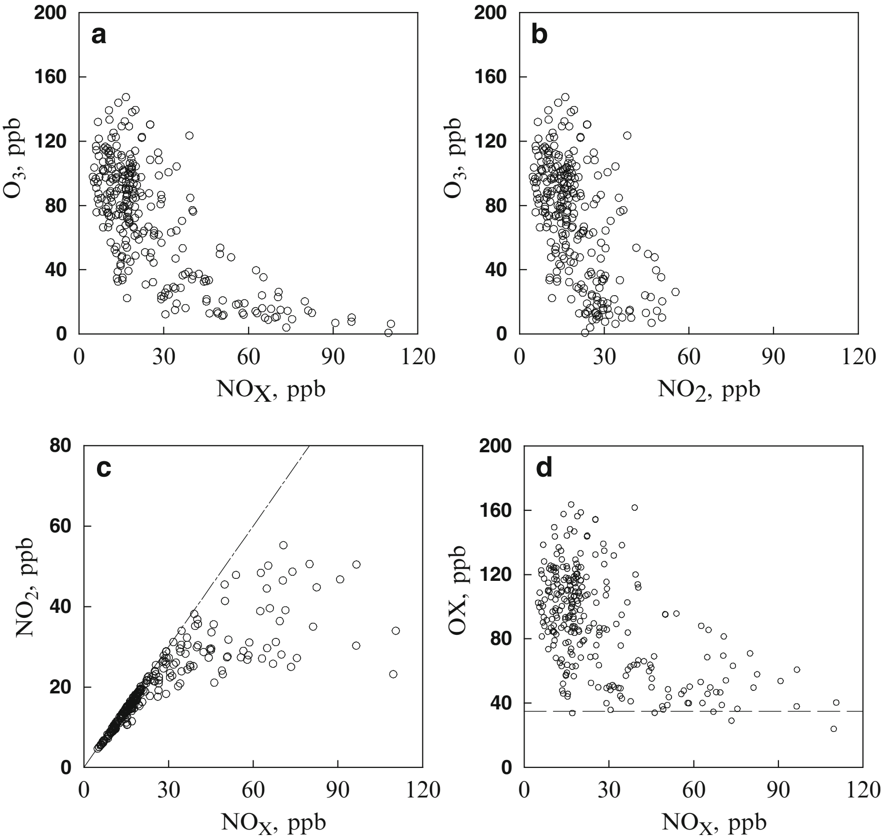

Fig. 27.6 Results of the 2005 Riverside study. Comparison of the O_3 concentrations to that of NO_X (**a**) or NO_2 (**b**) indicate the formation of ozone is VOC limited. The comparison of NO to NO_X (**c**) indicates the atmospheric system is oxidant limited. The comparison of $OX = O_3 + NO_2$ (**d**) indicates the background concentration of oxidant is about 38 ppb and the system is oxidant limited

limiting the formation of ozone. The downward trend of the O_3/NO_X and O_3/NO_2 relationships indicates an oxidant limited air mass, with VOC concentrations low, relative to NO_X (Finlayson-Pitts and Pitts 2000). This conclusion is further strengthen by Fig. 27.6c, showing NO_2 plotted against NO_X. Close to 100 % of the NO_X is present as NO_2 at concentrations below 30 ppb. The linearity of the data deteriorates at concentrations of NO_X above 30 ppb. At concentrations of NO_X above 60 ppb, the relative NO_2 concentrations plateau out, indicative of the lack of oxidant species to convert NO to NO_2, typical of an urban VOC limited atmosphere.

An analysis of the NO_x and O_3 data can also be carried out using the method described by Clapp and Jenkin (2001). Figure 27.6d shows the oxidant concentration, $[NO_2]+[O_3]$ (defined as OX), plotted against the NOx concentration ($NOx = NO + NO_2$) for daylight hours. The lower limit of the data represents the regional contribution to the oxidant concentration. The difference between this lower limit and the measured OX concentration represents the local contribution to the oxidant concentration. The regional contribution to the oxidant concentration is 38 ppb. The oxidant concentrations above this background are highest at low NO_X concentrations. This results in the linear relationship in NO_2 and NO_X below 30 ppb (Fig. 27.6c) and the decreasing concentration of oxidant above the background level corresponds to the oxidant limited region where not all NO_X is converted to NO_2. The relatively large amount of scatter in Fig. 27.6d may due to the scavenging of NO_2 by the OH radical to produce HNO_3 (which is rapidly converted to NH_4NO_3) instead of O_3. Associated with this chemistry, afternoon peaks of from 10 to

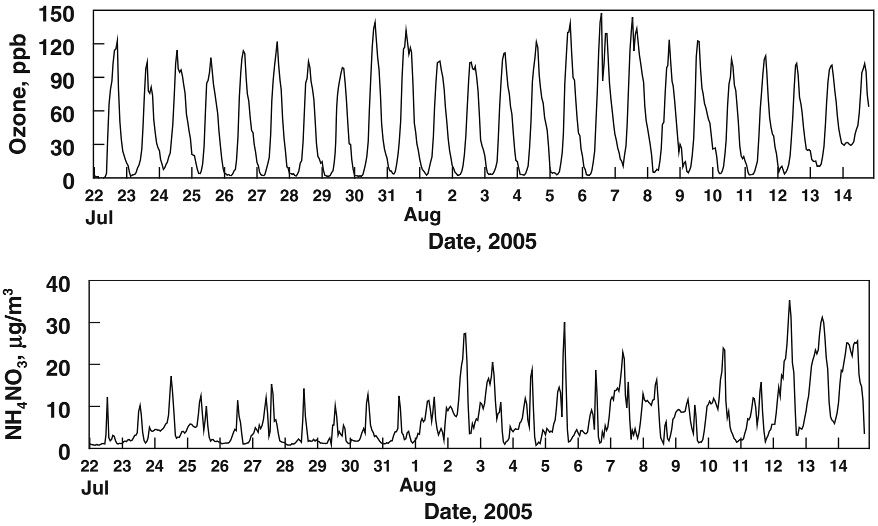

Fig. 27.7 The diurnal variation in ozone and fine particulate ammonium nitrate during the 2005 Riverside study

35 · µg m^3 of ammonium nitrate were seen every day. As the air masses are transported further to the east, this will contribute to nitrogen deposition in the forests of the San Bernardino Mountains. This daily formation of ozone and ammonium nitrate in the Riverside study is shown in Fig. 27.7.

The California Air Resources Board has measured eight hour, or more recently, hourly averaged concentrations of ozone (as well as extensive measurements of PM) at the Crestline monitoring station located at the western edge of the San Bernardino Mountains, just 20 km north of San Bernardino (in the Inland Empire region of the South Coast Air Basin) at the top of the front range of the mountains at an elevation of 1400 m. Ozone at Crestline has consistently been higher than that measured at San Bernardino, Riverside, Upland or Fontana, urban areas located in the populated valley just below the station in the Inland Empire region of the basin. For example, data given in a modeling study of an August 1997 ozone episode gave eight hour maximum concentrations of about 130 ppb at Crestline and 110 ppb at Fontana (Environ 2002). Likewise in an analysis of July 2002 and July 2003 data (Schwartz 2005) daily hourly ozone maximum concentrations at Crestline reached 140 ppb and averaged about 20 % higher than daily maximum concentrations at Upland in the valley.

An extensive study of N deposition in both the Sierra Nevada and San Bernardino Mountains has been reported by the U.S. Department of Agriculture Forest Service (Fenn et al. 2008). This included 17 throughfall study sites in the Sierra Nevada Mountains covering the length of the San Joaquin Valley and 9 throughfall study sites in the San Bernardino Mountains. A companion set of ozone measurements has also been made at many of the same sampling sites in the San Bernardino Mountains (Bytnerowicz et al. 2008). Some conclusions about the relative importance of anthropogenic pollution from the Los Angeles basin on ozone in the San Bernardino Mountains can be made from the Bytnerowicz et al. (2008) data. The long-term data which have been collected at the Crestline sampling station (Environ 2002; Bytnerowicz et al. 2008) show that ozone concentrations at this location at the eastern edge of the Los Angeles basin are clearly influenced by ozone production in the Inland Empire as pollutants are transport east across the South Coast Air Basin, with concentrations of ozone being consistently higher at Crestline than in the valley to the east where the pollutants originated, Additional ozone formation occurs during the transport of pollutants from the basin into the mountains. These ozone concentrations drop only slightly as pollutants are transported further east across the San Bernardino Mountains.

The strong influence of urban pollution associated with the production of ammonium nitrate during pollutant transport is also indicated by the extensive N deposition data available for both the San Bernardino and Sierra Nevada Mountain forests. The changes in concentration of transported ozone and ammonium nitrate will be quite different during transport into an effected ecological region. While ozone effects exposed vegetation, ozone removal by the vegetation is minimal during transport (Bytnerowicz et al. 2008). In contrast, scavenging of ammonium nitrate by

Table 27.2 Site comparison for BF and CP

	BF	CP
Elevation (meters)	1900	1600
[a]Average annual precipitation (mm)	534	994
[a]Average annual temperature (°C)	10.6	12.9
[b]Ozone (ppb): Summertime average peak values	91.3	101.6
[c]Nitrogen deposition as throughfall: kg N ha^{-1} $year^{-1}$	8.8	70

[a]Annual precipitation and temperature were calculated from data obtained from the San Bernardino County Water Resources Division. Additional precipitation data was obtained from Fenn and Poth (2004). Yearly precipitation was recorded from October of the year listed through September of the following year. Precipitation data covered 1956–1993 for CP and 1975, 1977–1979 and 1991–1998 for BF. Temperature data spanned 1992–1997 for BF and 1956–1991 for CP

[b]Summer ozone concentrations were obtained from continuous ozone monitors at Crestline (California Air Resources Board, public information) and Barton Flats (Atmospheric Deposition Group, USDA PSW Research Station) for June through September 2002. Summertime peak concentration was the average of peak hourly concentrations for each day

[c]Fenn et al. (2008)

a forest canopy is very efficient and concentrations of ammonium nitrate will decrease during transport unless new photochemical production is quite high. This is reflected in the Forest Service multi-site data for N deposition (Fenn et al. 2008). For example, the Crestline site (Table 27.2), has the highest throughfall nitrogen deposition of any site in the network, 71 kg ha^{-1} $year^{-1}$, while Strawberry Peak, located 8 km to the east, has a nitrogen deposition rate of just 39 kg ha^{-1} $year^{-1}$. Barton Flats is located about 20 km to the southeast of Crestline, and 10 km east of the start of the San Bernardino Mountains, has a deposition rate of 9 kg $ha^{-1}year^{-1}$. Camp Angelus, located 8 km west of Barton Flats and on the same transport path from the basin as Barton Flats, has a deposition rate of 13 kg ha^{-1} $year^{-1}$. These data indicate the major contributor to N deposition in the San Bernardino Mountains is ammonium nitrate produced from pollutants in the South Coast Air Basin. Similar results are seen for the Sierra Nevada Mountains N deposition sites (Fenn et al. 2008). There the highest throughfall nitrogen deposition sites are all located on the western front of the range, close to the San Joaquin Valley. The highest deposition measured at those sites is Greenhome, 18 kg ha^{-1} $year^{-1}$, just east of Bakersfield. It is interesting to note that the deposition rates east of the larger pollution centers of Fresno and Sacramento are all less than half that value. A 1999 study of ozone in the Sierra Nevada Mountains indicated highest concentrations to the east of Sacramento, Fresno and Bakersfield (Bytnerowicz et al. 2014), with the highest ozone impacts to the east of Sacramento. The highest N deposition, however, is seen east of Bakersfield. It is possible that emissions from the oilfields around the Bakersfield area may make a significant contribution to the formation of ammonium nitrate (Pang et al. 2002).

27.4.2 Forest Impacts in California

Southern California was the first Mediterranean region where air pollution impacts on forests were documented. Ozone was recognized as a possible factor for increasing the susceptibility of pines to bark beetle in the 1960s in the San Bernardino Mountains of southern California. Ponderosa pine trees showing greater oxidant injury were more frequently infested by western pine beetle and mountain pine beetle (Stark et al. 1968). Ozone damaged trees had several characteristics that were associated with increased bark beetle susceptibility, including lower resin flow rates, lower resin exudation pressure and an increased rate of resin crystallization (Stark and Cobb 1969). Other symptoms of ozone injury documented for pines in the San Bernardino Mountains include decreased radial growth (Miller 1992), reduced fine root mass and reduced belowground allocation of carbohydrates (Grulke et al. 1998), chlorotic mottling of needles and reduced needle retention (Miller 1973; Miller and Rechel 1999).

Forty years later in 2003, during a bark beetle outbreak under drought conditions a strong association between ozone injury and beetle attack and tree mortality was observed (Eatough Jones et al. 2004). By this time, nitrogen deposition was also recognized as a significant factor affecting forests in California (Fenn et al. 1996; Grulke and Balduman 1999; Takemoto et al. 2001). In 1996, previous to the 2003 bark beetle outbreak, long-term fertilization plots were established by the USDA Forest Service Pacific Southwest Research Station Forest Fire Laboratory to examine the impacts of ozone and nitrogen in southern California forests. During the beetle outbreak, surveys of trees from fertilization plots showed that, in addition to the effects of ozone, nitrogen additions were also associated with increased beetle attack and tree mortality (Eatough Jones et al. 2004). Ozone injury to forest trees and symptoms resulting from anthropogenic N deposition have also been observed in the Sierra Nevada Mountains in California (Bytnerowicz et al. 2003), but this area has not been as well studied as the San Bernardino Mountains.

Although research relating herbivore performance to N deposition has been limited, the few studies available suggest insects respond similarly to N deposition and more conventional N fertilization (Erelli et al. 1998; Throop and Lerdau 2004). Fertilization has been widely documented to increase leaf N concentrations and water content and decrease leaf toughness (Mattson 1980; Waring and Cobb 1992). N fertilization may decrease concentrations of C-based secondary plant chemistry which are often detrimental to arthropod herbivores (Bryant et al. 1983). However, many plant processes, including plant growth and leaf development (Dickson and Isebrands 1991; Ingestad and Agren 1991) are affected by changes in plant N availability. The timing of budburst and leaf expansion may affect the performance and survival of leaf-feeding arthropod herbivores (Hunter 1992; Wait et al. 1998; Forkner et al. 2008; Butt et al. 2010). This is particularly true for foliage feeding herbivores specialized to feed during the period of leaf expansion (Forkner et al. 2008).

Nitrogen additions have also been shown to influence herbivore communities in California forests. Herbivore communities of California black oak and bracken fern were both more characterized by chewing herbivores at sites with high air pollution compared to low pollution sites (Eatough Jones and Paine 2006; Eatough Jones et al. 2008, 2011). Nitrogen enrichment may also influence interactions at higher trophic levels. In an ant-exclusion experiment, ants visiting extrafloral nectaries on bracken fern decreased oviposition for sawflies, the main herbivore of bracken fern in southern California (Eatough Jones and Paine 2012). Nitrogen additions were associated with higher ant abundance, although this increase in ant abundance did not have a significant impact on sawfly oviposition.

27.4.2.1 California Black Oak and Leafroller Outbreak

Although a growing number of studies have examined the relationship between syncrorony of arthropod herbivores with budburst on arthropod populations, few studies have examined the relationship between N additions, leaf expansion and arthropod herbivore populations. Wait et al. (1998) examined the effect of plant fertilization on leaf expansion in eastern cottonwood and two foliage feeding beetles. They found for this tree, where leaves are continuously initiated, that changes in leaf development rather than changes in leaf chemistry accounted for differences in herbivore feeding behavior.

Changes in patterns of growth and leaf expansion in response to fertilization may also be important for trees producing a single flush of new foliage in the spring. Lepidoptera that feed and complete development during the period of leaf expansion on deciduous trees may be affected if leaf expansion is altered by nitrogen fertilization. Forkner et al. (2008) found that oak-feeding Lepidoptera feeding only during the period of leaf expansion had much higher variation in population density from year to year than Lepidoptera that fed throughout the summer. They conclude that factors that exacerbate asynchrony of Lepidoptera feeding with budburst will impact spring feeding Lepidoptera, especially those with limited mobility.

We examined the relationship between nitrogen additions and an oak-feeding Lepidoptera in the San Bernardino Mountains. For this study, we focused on Lepidoptera on California black oak that complete larval development during the period from budburst to the completion of leaf expansion, since synchrony with budburst and leaf expansion is of greatest importance for this life history strategy (Forkner et al. 2008). Fruittree leafroller (*Archips argyrospila*: Torticidae) is the most common defoliator of California black oak in southern California (Swiecki et al. 2006). In California forests, *A. argyrospila* has one generation per year and completes development during the period of leaf expansion. Leafroller egg masses overwinter, and neonate leafrollers emerge as buds are beginning to swell and open. Neonate leafrollers feed on leaf tissue in the buds under the bud scales (Fig. 27.8). As leaves begin to expand, leafrollers tie leaves together and feed in this shelter. Leafrollers finish larval development as leaves reach full expansion, and pupate in the leaves, with the pupae secured by leaf-tying. Adults emerge, mate and lay egg masses in early summer.

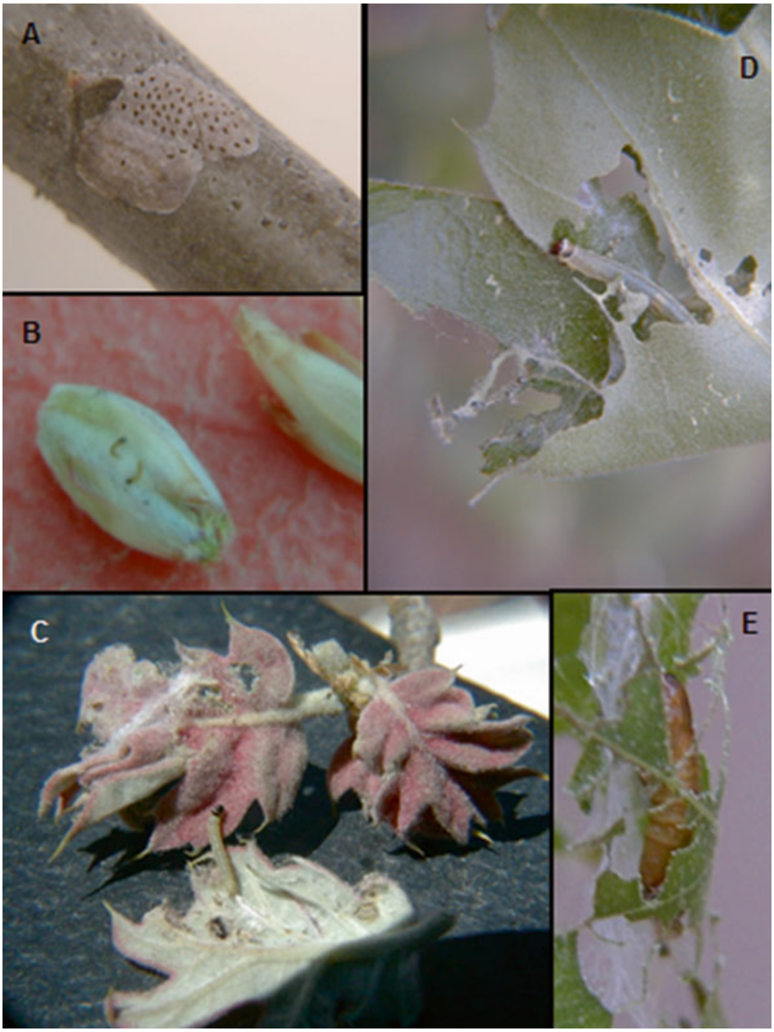

Fig. 27.8 Development of the fruitree leafroller. Overwintering egg mass (**a**); Neonate larvae feeding in buds (**b**); young larvae tying expanding leaves (**c**); late instar larvae feeding in tied leaves (**d**); pupa in foliage (**e**)

During a 3 years study from 1998 to 2000, we collected California black oak foliage monthly from bud break in May through August (Eatough Jones et al. 2008). *A. argyrospila* was the dominant leaf-feeding Lepidoptera in all years (≥70 % of all individuals collected). In California forests, foliar damage is to California black oak is generally low, but trees may be defoliated during occasional outbreaks. The last recorded outbreak of *A. argyrospila* occurred in the San Bernardino Mountains between 1999 and 2003 (Swiecki et al. 2006). Since one of the areas heavily impacted by the outbreak was a site where ongoing studies examining the impacts of nitrogen and ozone on California black oak and its herbivores, we were able to monitor the dynamics of the outbreak on trees with different levels of nitrogen additions.

27.4.2.2 Methods

Long-term fertilization plots were established at two locations in the mixed conifer zone of the San Bernardino Mountains (San Bernardino County, CA) along a west/east gradient for N deposition and ozone (Fenn and Poth 2001). One site, Camp Paivika (CP; 34°14′05″ N, 117°19′25″ W), was near the town of Crestline and the other site was in the Barton Flats area (BF; 34°10′10″ N, 116°54′25″ W), 42 km east-southeast of CP. The western-most site at CP has been impacted by high levels of N deposition while the more eastern site at BF has received lower input from atmospheric N (Table 27.2). Ten trees at each site were fertilized with Nitroform® (BFC Chemicals, Wilmington, Delaware) slow-release fertilizer (38-0-0) at a rate equivalent to 150 kg N $ha^{-1}year^{-1}$, and ten trees were left as unfertilized controls as described in Eatough Jones et al. (2008). Nitrogen fertilization treatments began in the fall of 1997 and continued annually through the duration of the study.

Lepidoptera and foliage were collected twice during each growing season from 1998 to 2000. Sampling dates were determined by plant phenology. The first sample was collected after bud-break, during the period of rapid leaf expansion. The second sample was collected as the foliage reached full expansion. Fruit tree leafroller larvae were identified and counted for each sample. Herbivore damage was estimated quantitatively as described in Eatough Jones et al. (2008). For samples collected in 2000, leaf length was measured on 10 randomly selected leaves from each tree and each sampling period. Leaf total N and % water were determined for each sample (Eatough Jones et al. 2008). Differences in foliage growth and damage among treatments at each site and within each year were tested by ANOVA and evaluates at $\alpha = 0.05$ using SAS Institute Inc (2010). Correlations between leafroller abundance and plant characteristics within each site were evaluated using Pearson correlation coefficients.

27.4.2.3 Results and Discussion

While sampling oak foliage at the high pollution site CP, during the spring of 2000, we noticed that leaves from control trees had much higher rates of damage than leaves from fertilized trees. Both damage to leaves and abundance of leafrollers was significantly higher for control trees compared to fertilized trees, both during early leaf expansion and at full expansion (Fig. 27.9 and Table 27.3). At full expansion, when the differences in leaf damage were most striking, total N, and leaf length did not differ between fertilized and control trees, and were not correlated with leaf roller abundance (Table 27.4). Water content was significantly lower for leaves from control trees, but this was directly related to the high levels of damage for control trees (Fig. 27.10). Total leaf N was significantly higher at CP compared to the low

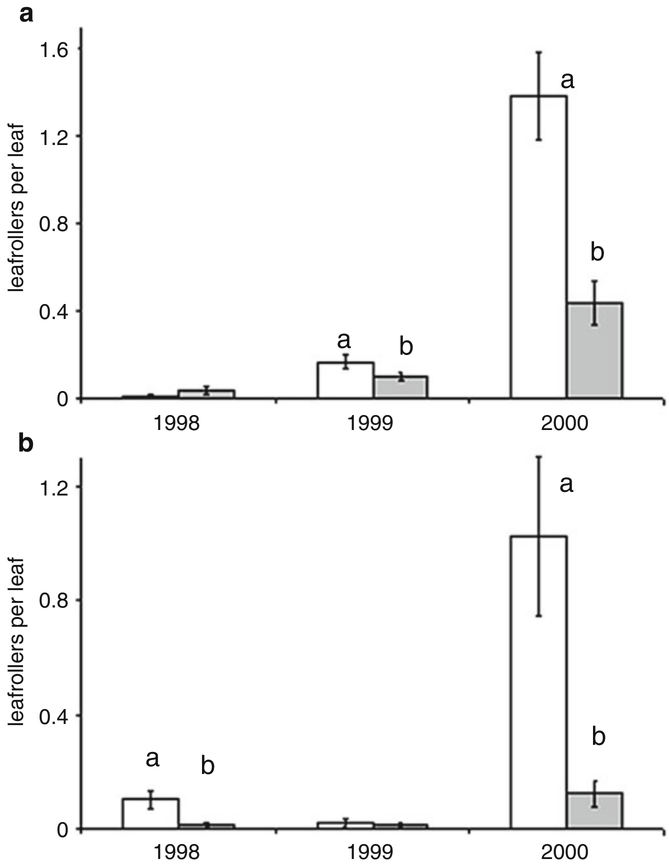

Fig. 27.9 Leafroller abundance (mean and s.e.) at the high pollution site, CP, during early leaf expansion (**a**), and at full leaf expansion (**b**). *White bars* indicate control trees and *gray bars* indicate trees with nitrogen addition treatments. Within each year, bars with different letters are significantly different

pollution site. At both sites, total N tended to be higher on fertilized trees, but was not significantly different among control and fertilized trees at either site.

When we examined leaves for the high pollution site from control and fertilized trees during the period of early leaf expansion, neither water content nor total N differed among treatments. However, leaves from fertilized trees were significantly longer than leaves from control trees (Fig. 27.11). Leafroller abundance was significantly negatively correlated with leaf length (Table 27.4). While the differences in were not as striking in 1998 and 1999 when leafroller populations were lower, leaf roller abundance and damage also tended to be higher during leaf expansion for control plots (Fig. 27.9). The leafroller outbreak did not impact the low pollution site at BF. There, leafroller abundance was slightly higher on fertilized trees compared to control trees (Fig. 27.12). Damage remained low and was not significantly different for control and fertilized trees. However, like the high pollution site, for the

Table 27.3 ANOVA statistics for leafroller abundance and leaf variables

	Leafrollers		Damage		Water		Total N		Leaf length	
	F	p	F	p	F	p	F	p	F	p
1998 expanding	1.38	0.27	0.81	0.50	3.62	0.02				
1998 full expansion	9.93	<0.001	3.63	0.02	28.42	<0.001	17.68	<0.001		
1999 expanding	8.56	<0.001	22.86	<0.001	3.68	<0.001				
1999 full expansion	1.02	0.39	6.11	0.002	4.58	0.008	6.22	0.006		
2000 expanding	20.87	<0.001	10.71	<0.001	0.46	0.72	8.33	<0.001	18.71	<0.001
2000 full expansion	12.13	<0.001	50.08	<0.001	11.37	<0.001	17.23	<0.001		

Table 27.4 Pearson correlation coefficients for leafroller abundance compared to leaf variables for expanding leaves and leaves at full expansion in 2000

	Expanding leaves				Full expansion			
	CP		BF		CP		BF	
	r	P	r	P	r	P	r	P
Damage	0.55	0.01	0.57	0.01	0.65	0.002	0.25	0.28
Water	0.15	0.42	–0.27	0.25	–0.73	<0.001	0.14	0.54
Total N	–0.36	0.05	–0.23	0.35	–0.11	0.58	0.35	0.13
Leaf length	–0.57	0.001	0.08	0.73	–0.22	0.26		

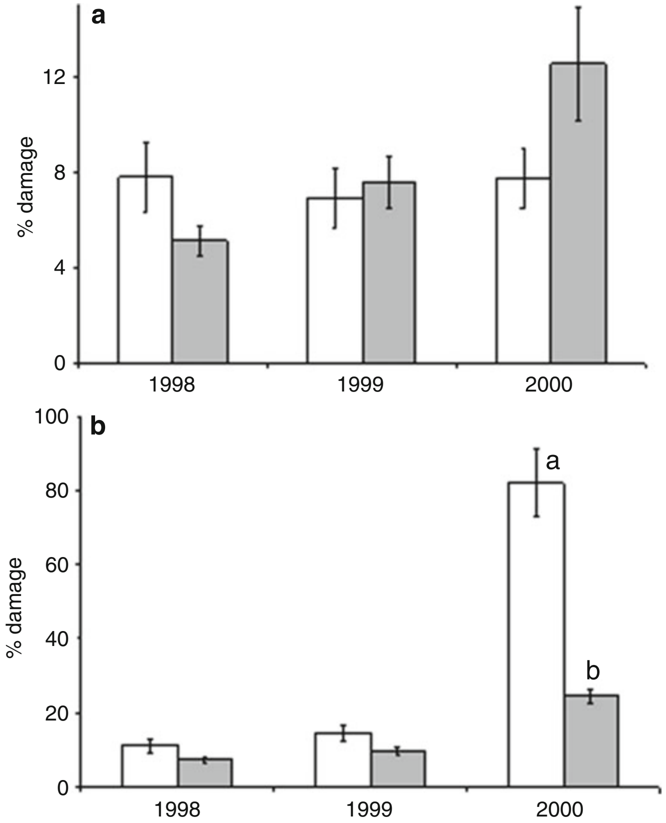

Fig. 27.10 Leaf damage during the period when leaves reached full expansion (mean and s.e.) at the low pollution site, BF (**a**) and the high pollution site, CP (**b**), *White bars* indicate control trees and *gray bars* indicate trees with nitrogen addition treatments. Within each year, bars with different letters are significantly different

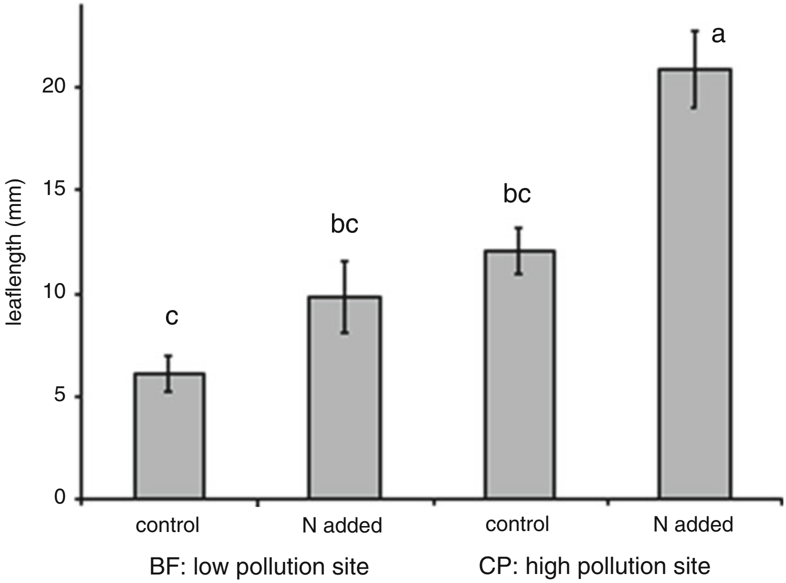

Fig. 27.11 Leaf length during early leaf expansions (mean and s.e.) during spring 2000, Bars with different letters are significantly different

samples collected during early leaf expansion, leaves from fertilized trees were longer than leaves from fertilized trees (Fig. 27.11).

We found that the strongest factor associated with differences in leafroller abundance during early expansion was the leaf length. If nitrogen additions changed the timing of bud burst, or changed the rate of leaf expansion, this could intensify asynchrony between leafroller development and leaf expansion. Increased asynchrony has been found to impact spring feeding Lepidoptera, especially those such as fruit-tree leafroller that feed only during the period of leaf expansion (Forkner et al. 2008). We found that leaves collected from fertilized trees during leaf expansion had longer leaves than control trees. While this did not impact leafroller abundance at the low pollution site, where leafroller populations remained low throughout the study period, it did affect leafroller populations at the high pollution site, which was impacted by a leafroller outbreak.

27.5 The Chilean Matorral

The Chilean Matorral Mediterranean Forest region constitutes a 100 km-wide strip extending along the central part of the Chilean coast. The major population centers which effect the concentrations of ozone and ammonium nitrate in this ecoregion are Santiago (population 6.3 million) located in the central portion of the Matorral,

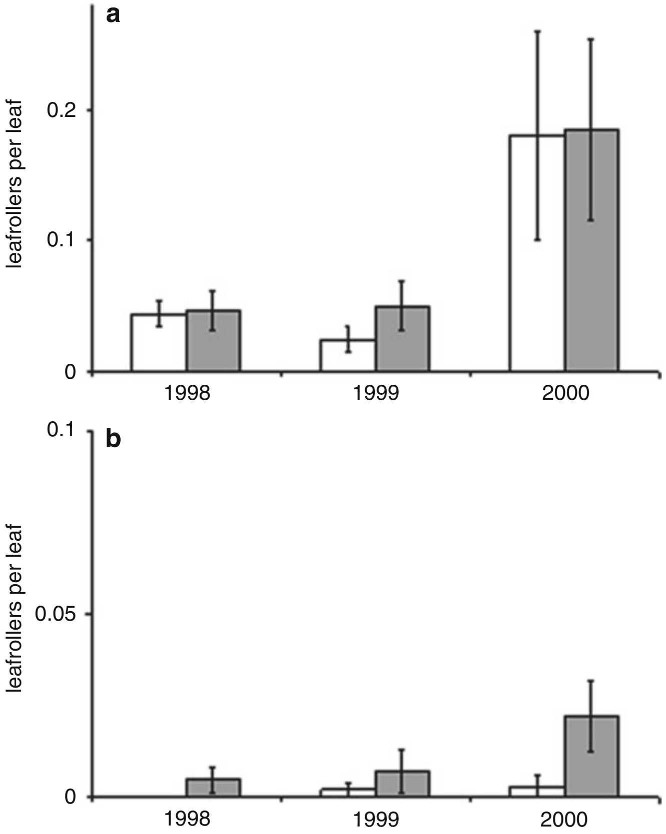

Fig. 27.12 Leafroller abundance (mean and s.e.) at the low pollution site, BF, during early leaf expansion (**a**), and at full leaf expansion (**b**). *White bars* indicate control trees and *gray bars* indicate trees with nitrogen addition treatments

about 60 km inland and the Greater Valparaiso Metropolitan area (population 0.8 million) located on the coast about 40 km north of Santiago and the major seaport for Chile. Several studies of ozone, nitrogen oxides and VOC have been conducted in Santiago (Gramsch et al. 2006; Elshorbany et al. 2009; Seguel et al. 2012). These studies indicate formation of ozone in the metropolitan area is VOC limited (Elshorbany et al. 2009; Seguel et al. 2012) (e.g. see Fig. 27.1), that ozone concentration have decreased since 2005 due to pollution control measures, and that current daytime average ozone concentrations are 40–60 ppb, with maximum hourly concentrations of 60–80 ppb (Seguel et al. 2012). An informative study of the potential impact of urban emissions on the Matorral was conducted in the Valparaiso Metropolitan region and further east at Los Andes (population 60,000 and 60 km north east of Valparaiso and 60 km north of Santiago) (Toro et al. 2013). Prevailing winds from the coast carry the emission from Valparaiso towards Los Andes. Hourly

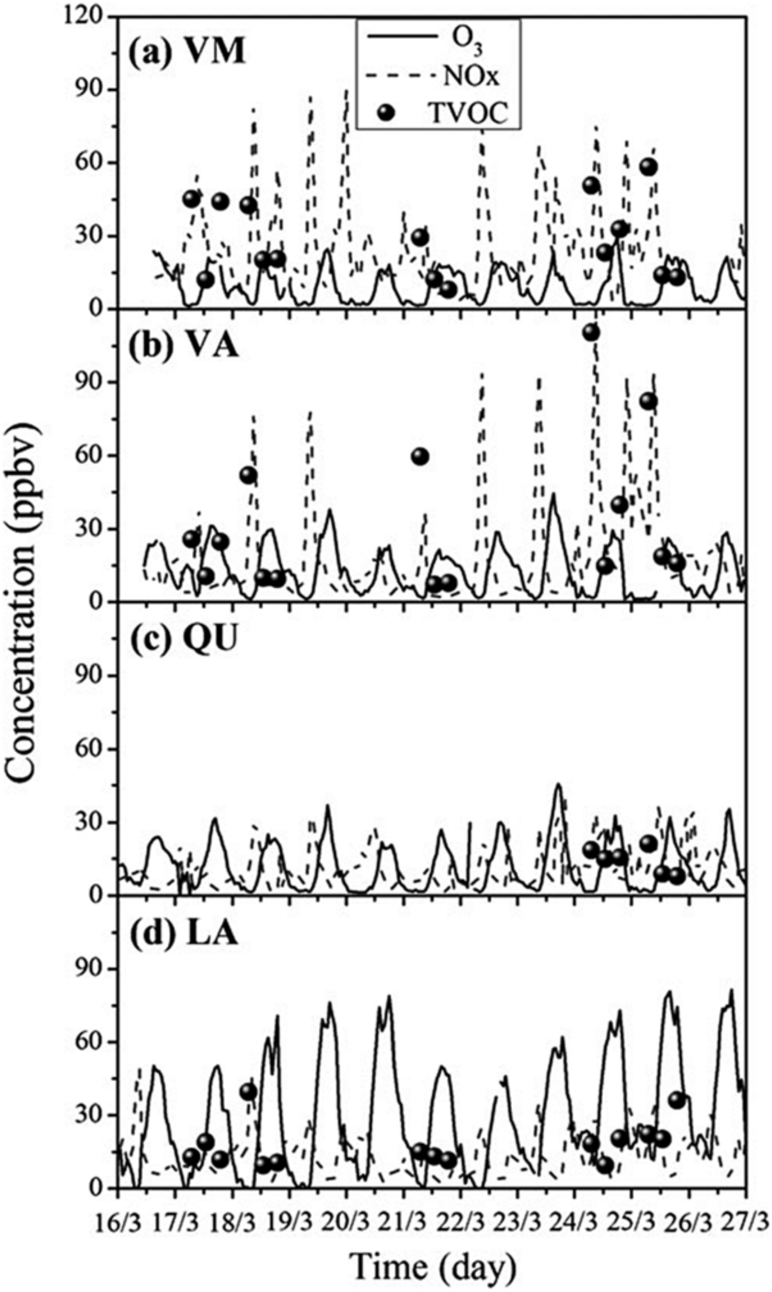

Fig. 27.13 The time series of the variation of ozone, NOx, and total VOC concentration (TVOC) in the Valparaiso region (hourly averaged concentrations over a 12 day period in March) in urban areas of Viña del Mar (VM) and Villa Alemana (VA), in the suburban area of Quillota (QU) and in the more rural area of Los Andes (LA) (From Toro, 2013)

averaged concentrations of O_3, VOC and NO_X were measured over a 12 days period in March (late summer) in Viña del Mar and Villa Alemana in Valparaiso, in Quillota just northeast of the Metropolitan area and in Los Andes (Fig. 27.13). As was the case in Santiago, ozone formation in the Valparaiso Region is VOC limited (Toro et al. 2013). Both NO_X and VOC are highest in the Valparaiso Region (Fig. 27.13a and b) where the majority of the emissions occur. The drop in measured NO_X on March 21 occurred during the weekend. Both VOC and NO_X concentrations decrease as you move out of the metropolitan area into Quillota (Fig. 27.13c) and finally further east to Los Andes (Fig. 27.13d). The maximum ozone concentrations in Las Andes are more than twice that seen in metropolitan areas of Viña del Mar and Villa Alemana. This reflects the increase in ozone production with decrease in NO_X, in a VOC limited ozone production system. Similar increases in ozone would be expected as pollutants for Santiago are moved east into the Matorral. This increase in ozone will also be associated with an increase in ammonium nitrate. Nitrogen deposition in Chile has been estimated to be approximately 2.8 kg ha^{-1} $year^{-1}$ (Ochoa-Hueso et al. 2011).

27.6 The Cape Province: Western Cape of South Africa

The Mediterranean Forest Region in South Africa includes the southern tip defined roughly by Cape Town to Port Elizabeth. Ozone measurements in Southern Africa have generally focused on the non-Mediterranean Forest regions of central and north South Africa (Zunckel et al. 2004). The exception to this is a combination of passive and active ozone monitoring programs at the South Africa Cape Point Global Atmospheric Watch station. This site generally measures ozone transported to the coastal station from the west and does not represent Cape urban ozone concentrations. Major ozone production is generally believed to occur in northern South Africa and the adjoining countries to the north in connection with Savannah fires. The most extensive study of emissions from Savannah fires occurred during the Safari 2000 study (Hobbs 2001). Tropospheric ozone during the period of the SAFARI 2000 study was mapped using TOMS satellite data (http://svs.gsfc.nasa.gov/cgi-bin/details.cgi?aid=2018). Maximum ozone impacts from transported air from the west (influenced by Amazon fire emissions) are illustrated in Fig. 27.14. The high concentrations of ozone reaching the western South African coast decreased rapidly as the transported ozone was titrated by NO from Savannah fires. Concentrations increased again as air masses were transported across the African continent and the NO_X/VOC chemistry lead to ozone formation. Examples of such impacts in the Cape Town region are possible, but were not shown in the Safari 2000 results. The maximum ozone concentrations in air masses from the west as measured at the Africa Cape Point Global Atmospheric Watch station (Zunckel et al. 2004) were about half those shown in Fig. 27.14. Ozone impacts on wildland communities in South Africa have not been studied. Nitrogen deposition in western South Africa is likely less than 2 kg ha^{-1} $year^{-1}$ (Ochoa-Hueso et al. 2011). Herbarium

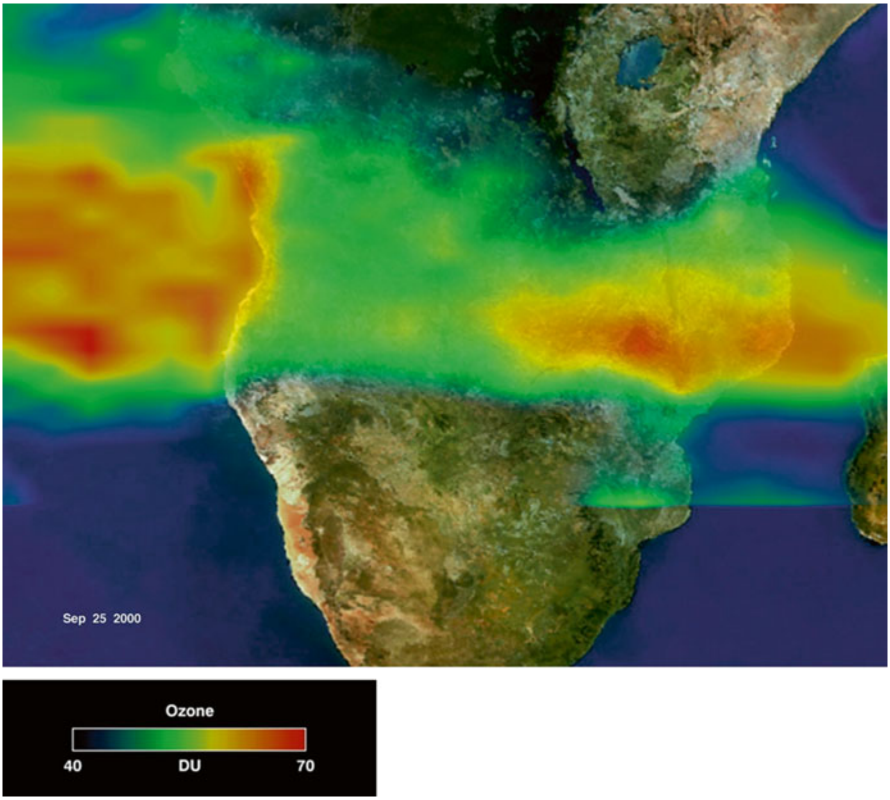

Fig. 27.14 NASA/Goddard Space Flight Center Scientific Visualization Studio map of tropospheric ozone from satellite mapping for September 25, 2000

samples of bryophytes collected from fynbos shrublands near Cape Town show a significant increase in foliar nitrogen that corresponds with increasing urbanization in the region (Wilson et al. 2009).

27.7 The Southwest Australia Corner Area

Mediterranean Forest Regions in Australia are located on the western coast of West Australia, where the major urban area is Perth (population 2.0 million) and in the southeast corner of South Australia, the location of Adelaide (population 1.3 million). Emission of NO_X and VOCs from both these urban areas would be expected to impact the nearby forest ecosystems through both the production of ozone and nitrogen. Ozone has been monitored by the EPA of each Australian state in their respective capital for several decades (South Australian EPA 2008; West Australia

EPA 2007). In both locations exceedances of the ozone standard is infrequent, ozone concentrations are much lower than in the more industrialized part of Australia, and annual ozone averages about 40 ppb in Perth and about 29 ppm in Adelaide. It is clear that the potential for impact of both ozone and nitrogen deposition on the surrounding Mediterranean forests is much lower than in the Mediterranean basin, California or Chile, and probably lower than South Africa.

27.8 Conclusions

The combination of warm summer climate and large urban centers of Mediterranean regions makes these areas likely regions of high summer ozone. Since ozone is formed by photochemical reactions as a secondary pollutant, ozone concentrations are often higher in forest and wildland regions than in urban centers. Ozone regularly exceeds concentrations where plant damage is expected in extensive areas of southern Europe and California. Ozone is also a concern in Matorral forests of Chile. Current ozone concentrations are lower in the Mediterranean regions of Africa and Australia, and are not likely directly damaging to forest systems there. Ozone injury to forest trees has been recorded in the Mediterranean basin and in California. Other Mediterranean region forests have not been studied. Impacts of ozone on insect communities have been documented in California. In particular, ozone injury to pines was associated with increased attacks and tree mortality due to bark beetles.

Dry deposition of ammonium nitrate is a major form of nitrogen deposition is Mediterranean regions. In wildland regions of the Mediterranean basin that have been studied, nitrogen deposition is typically 10–20 kg ha^{-1} $year^{-1}$. In California, nitrogen deposition can be very high (30–70 kg ha^{-1} $year^{-1}$) for forests along the western slopes of the Sierra Nevada and San Bernardino Mountains. However, there is steep west-east gradient for nitrogen deposition, and deposition is much lower in interior forests. In southern Europe, a few studies have examined nitrogen deposition in forest systems and observed changes in soil processes, foliar nutrient ratios and basal growth. In California, nitrogen deposition, like ozone, has been associated with increased tree mortality due to bark beetles for ponderosa and Jeffrey pine. Nitrogen deposition has impacted soil chemistry, foliar nutrients and plant growth. Changes in insect herbivore communities have also been recorded along the west-east nitrogen deposition gradient. For California black oak, trees with higher rates of N addition had much lower rates of defoliation during a fruittree leafroller outbreak. Leafrollers time feeding and development with budburst and leaf expansion. Changes in leaf expansion for fertilized trees were associated with lower leafroller abundance and less leaf damage during outbreak conditions. Nitrogen deposition is increasing in Africa, Chile and to a lesser extent in Australia, but forest impacts have not been addressed in these areas.

References

Barnes J, Gimeno B, Davison A et al (2000) Air pollution impacts on pine forests in the Mediterranean basin. In: Ne'eman G, Trabaud L (eds) Ecology, biogeography and management of *Pinus halepensis* and *P. brutia* forest ecosystems in the Mediterranean basin. Backhuys Publishers, Leiden, pp 391–404

Blanes MC, Viñegla B, Salido MT et al (2013) Coupled soil-availability and tree-limitation nutritional shifts induced by N deposition: insights from N to P relationships in *Abies pinsapo* forests. Plant Soil 366:67–81

Bryant JP, Chapin FS, Klein DR (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos 40:357–368

Burley J, Theiss S, Bytnerowicz A et al (2015) Surface ozone in the Lake Tahoe Basin. Atmos Environ 109:351–369

Bussotti F, Gerosa G (2002) Are the Mediterranean forests in Southern Europe threatened from ozone? J Mediterr Ecol 3:23–34

Butt C, Quiring D, Hébert C et al (2010) Influence of balsam fir (*Abies balsamea*) budburst phenology on hemlock looper (*Lambdina fiscellaria*). Entomol Exp Appl 134:220–226

Bytnerowicz A, Arbaugh MJ, Alonso R (2003) Ozone air pollution in the Sierra Nevada: distribution and effects on forests. Elsevier, Boston

Bytnerowicz A, Arbaugh M, Schilling S et al (2008) Ozone distribution and phytotoxic potential in mixed conifer forests of the San Bernardino Mountains, southern California. Environ Pollut 155:398–408

Bytnerowicz A, Fenn A, Long JW (2014) Science synthesis to support socioecological resilience in the Sierra Nevada and southern Cascade Range. General technical report PSW-GTR-247. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany. Chapter 8.1. http://www.fs.fed.us/psw/publications/documents/psw_gtr247/chapters/psw_gtr247_chapter8_1.pdf

Clapp LJ, Jenkin ME (2001) Analysis of the relationship between ambient levels of O_3, NO_2 and NO as a function of NO_x in the UK. Atmos Environ 35:6391–6405

Committee on Tropospheric Ozone, National Research Council (1991) Rethinking the ozone problem in urban and regional air pollution. The National Academies Press, Washington, DC. http://www.nap.edu/openbook.php?record_id=1889&page=165

Delgado-Saborit JM, Esteve-Cano VJ (2008) Assessment of tropospheric ozone effects on citrus crops using passive samplers in a western Mediterranean area. Agric Ecosyst Environ 124:147–153

Dickson RE, Isebrands JG (1991) Leaves as regulators of stress response. In: Mooney HA, Winner WE, Pell EJ (eds) Response of plants to multiple stresses. Academic, San Diego, pp 3–34

Eatough Jones M, Paine TD (2006) Detecting changes in insect herbivore communities along a pollution gradient. Environ Pollut 143:377–387

Eatough Jones M, Paine TD (2012) Ants impact sawfly oviposition on bracken fern in southern California. Arthropod Plant Interact 6:283–287

Eatough Jones M, Paine TD, Fenn ME et al (2004) Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. For Ecol Manage 200:67–76

Eatough Jones M, Paine TD, Fenn ME (2008) The effect of nitrogen additions on oak foliage and herbivore communities at sites with high and low atmospheric pollution. Environ Pollut 151:434–442

Eatough Jones M, Fenn ME, Paine TD (2011) The effect of nitrogen additions on bracken fern and its insect herbivores at sites with high and low atmospheric pollution. Arthropod Plant Interact 5:163–173

Eatough DJ, Grover BD, Woolwine WR et al (2008) Source apportionment of 1h semi-continuous data during the 2005 Study of Organic Aerosols in Riverside (SOAR) using positive matrix factorization. Atmos Environ 42:2706–2719

Elshorbany YF, Kleffmann J, Kurtenbach R et al (2009) Summertime photochemical ozone formation in Santiago, Chile. Atmos Environ 43:6398–6407

Environ (2002) Proximate modeling of weekday/weekend ozone differences for Los Angeles. http://www.crcao.org/reports/recentstudies00-02/A-36A1_WDWEmodeling_31jul02.pdf

Erelli MC, Ayres MP, Eaton GK (1998) Altitudinal patterns in host suitability for forest insects. Oecologia 117:133–142

Fagnano M, Maggio A, Fumagalli I (2009) Crops' responses to ozone in Mediterranean environments. Environ Pollut 157:1438–1444

Fenn ME, Poth MA (2001) A case study of nitrogen saturation in western U.S. forests. In: Galloway J, Cowling E, Erisman JW, Wisniewski J, Jordan C (eds) Optimizing nitrogen management in food and energy production and environmental protection: proceedings of the 2nd international nitrogen conference on science and policy. A.A. Balkema Publishers, Lisse, pp 433–439

Fenn ME, Poth MA (2004) Monitoring nitrogen deposition in throughfall using ion exchange resin columns: a field test in the San Bernardino Mountains. J Environ Qual 33:2007–2014

Fenn ME, Poth MA, Johnson DW (1996) Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. For Ecol Manage 82:211–230

Fenn ME, Jovan S, Yuan F et al (2008) Empirical and simulated critical loads for nitrogen deposition in California mixed conifer forests. Environ Pollut 155:492–511

Ferretti M, Marchetto A, Arisci S et al (2014) On the tracks of nitrogen deposition effects on temperate forests at their southern European range – an observational study from Italy. Glob Chang Biol 20:3423–3438

Finlayson-Pitts BJ, Pitts JN (2000) Chemistry of the upper and lower atmosphere: theory, experiments, and applications. Academic, San Diego

Forkner RE, Marquis RJ, Lill JT et al (2008) Timing is everything? Phenological synchrony and population variability in leaf-chewing herbivores of *Quercus*. Ecol Entomol 33:276–285

Fumagalli I, Gimeno BS, Velissariou D et al (2001) Evidence of ozone-induced adverse effects on crops in the Mediterranean region. Atmos Environ 35:2583–2587

Gimeno BS, Velissariou D, Barnes JD et al (1992) Daños visibles por ozono en acículas de *Pinus halepensis* Mill. en Grecia y España. Ecología 6:131–134

Gimeno BS, Bermejo V, Reinert RA et al (1999) Adverse effects of ambient ozone on watermelon yield and physiology at a rural site in Eastern Spain. New Phytol 144:245–260

González-Fernández I, Calvo E, Gerosa G et al (2014) Setting ozone critical levels for protecting horticultural Mediterranean crops: case study of tomato. Environ Pollut 185:178–187

Gramsch E, Cereceda-Balic F, Oyola P et al (2006) Examination of pollution trends in Santiago de Chile with cluster analysis of PM_{10} and ozone data. Atmos Environ 40:5464–5475

Grulke NE, Balduman L (1999) Deciduous conifers: high N deposition and O_3 exposure effects on growth and biomass allocation in ponderosa pine. Water Air Soil Pollut 116:235–248

Grulke NE, Andersen CP, Fenn ME et al (1998) Ozone and nitrogen deposition reduces root biomass of ponderosa pine in the San Bernardino Mountains, California. Environ Pollut 103:63–73

Hobbs PV (2001) Summary of flights and types of data collected aboard the University of Washington Convair-580 research aircraft in the SAFARI-2000 study in Southern Africa from 10 August through 18 September 2000. Technical report for SAFARI 2000 Field Project, Cloud and Aerosol Research Group, University of Washington, Seattle. http://daac.ornl.gov/S2K/guides/s2k_CV580.html

Hunter MD (1992) A variable insect–plant interaction: the relationship between tree budburst phenology and population levels of insect herbivores among trees. Ecol Entomol 17:91–95

Ingestad T, Agren GI (1991) The influence of plant nutrition on biomass allocation. Ecol Appl 1:168–174

Klap JM, Voshaar JHO, de Vries W et al (2000) Effects of environmental stress on forest crown condition in Europe. Part IV: statistical analysis of relationships. Water Air Soil Pollut 119:387–420

Mattson WJ (1980) Herbivory in relation to plant nitrogen content. Annu Rev Ecol Syst 11:119–161

Michopoulos P, Baloutsos G, Economou A et al (2004) Effects of nitrogen deposition on nitrogen cycling in an Aleppo pine stand in Athens, Greece. Sci Total Environ 323:211–218

Miller PR (1973) Oxidant-induced community change in a mixed conifer forest. In: Advances in chemistry series, No 122. Air pollution damage to vegetation. Symposium, Los Angeles. Mar 31–Apr 1, 1971. American Chemical Society, Washington, DC, pp 101–117

Miller PR (1992) Mixed conifer forests of the San Bernardino Mountains, California. In: Olson RK, Binkley D, Bohm M (eds) The response of western forests to air pollution, vol 97, Ecological studies. Springer, New York, pp 461–497

Miller PR, Rechel J (1999) Temporal changes in crown condition indices, needle litterfall, and collateral needle injuries of ponderosa and Jeffrey pines. In: Miller PR, McBride JR (eds) Oxidant air pollution impacts in the Montane forests of Southern California, vol 134, Ecological studies. Springer, New York, pp 164–178

Mills G, Hayes F, Simpson D et al (2011) Evidence of widespread effects of ozone on crops and (semi-)natural vegetation in Europe (1990–2006) in relation to AOT40-and flux-based risk maps. Glob Chang Biol 17:592–613

Naveh Z, Steinberger EH, Chaim S et al (1980) Photochemical air pollutants: a threat to Mediterranean coniferous forests and upland ecosystems. Environ Conserv 7:301–309

Noirfalise A (1987) Map of the natural vegetation of the member countries of the European Community and the Council of Europe. Council of Europe, CEC, Luxembourg

Ochoa-Hueso R, Allen EB, Branquinho C et al (2011) Nitrogen deposition effects on Mediterranean-type ecosystems: an ecological assessment. Environ Pollut 159:2265–2279

Ochoa-Hueso R, Maestre FT, de los Rios A et al (2013) Nitrogen deposition alters nitrogen cycling and reduces soil carbon content in low-productivity semiarid Mediterranean ecosystems. Environ Pollut 179:185–193

Pang Y, Eatough NL, Wilson J et al (2002) Effect of semivolatile material on PM2.5 measurement by the PM2.5 federal reference method sampler at Bakersfield, California. Aerosol Sci Technol 36:289–299

Paoletti E (2006) Impact of ozone on Mediterranean forests: a review. Environ Pollut 144:463–474

Paoletti E, Anselmi N, Franceschini A (2007) Pre-exposure to ozone predisposes oak leaves to attacks by *Diplodia corticola* and *Biscogniauxia mediterranea*. Sci World 7:222–230

Phoenix GK, Hicks WK, Cinderby S et al (2006) Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. Glob Chang Biol 12:470–476

Picchi V, Iriti M, Quaroni S et al (2010) Climate variations and phenological stages modulate ozone damages in field-grown wheat. A three-year study with eight modern cultivars in Po Valley (Northern Italy). Agric Ecosyst Environ 135:310–317

Sanz Pérez V, Castro Díez P, Valladares F (2007) Growth versus storage: responses of Mediterranean oak seedlings to changes in nutrient and water availabilities. Ann For Sci 64:201–210

Sanz MJ, Calatayud V, Calvo E (2000) Spatial pattern of ozone injury in Aleppo pine related to air pollution dynamics in a coastal-mountain region of eastern Spain. Environ Pollut 108:239–247

SAS Institute Inc. (2010) SAS, Version 9.3. Cary, North Carolina

Schwartz J (2005) Rethinking the California Air Resources Board's ozone standards. American Enterprise Institute for public policy research. Publication 23145. http://www.aei.org/wp-content/uploads/2011/10/20050912_Schwartzwhitepaper.pdf

Seguel RJ, Raúl GE, Morales S et al (2012) Ozone weekend effect in Santiago, Chile. Environ Pollut 162:72–79

Soda C, Bussotti F, Grossoni P et al (2000) Impacts of urban levels of ozone on *Pinus halepensis* foliage. Environ Exp Bot 44:69–82

South Australia EPA. 2008. South Australia's Air Quality (2008) http://www.epa.sa.gov.au/xstd_files/Air/Report/air_quality_2008.pdf

Stark RW, Cobb FW (1969) Smog injury, root diseases and bark beetle damage in ponderosa pine. Calif Agric 23:13–15

Stark RW, Miller PR, Cobb FW Jr et al (1968) Incidence of bark beetle infestation in injured trees. Hilgardia 39:121–126

Swiecki TJ, Tedmund J, Bernhardt EA (2006) A field guide to insects and diseases of California oaks. USDA Forest Service General Technical Report PSW-GTR-197, 156 pp

Takemoto BK, Bytnerowicz A, Fenn ME (2001) Current and future effects of ozone and atmospheric nitrogen deposition on California's mixed conifer forests. For Ecol Manage 144:159–173

Throop HL, Lerdau MT (2004) Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. Ecosystems 7:109–133

Toro RA, Donoso CS, Seguel RA et al (2013) Photochemical ozone pollution in the Valparaiso Region, Chile. Air Qual Atmos Health 7:1–11

Velissariou D, Davison AW, Barnes JD et al (1992) Effects of air pollution on *Pinus halepensis* (Mill.): pollution levels in Attica Greece. Atmos Environ 26:373–380

Vitousek PM, Aber JD, Howarth RW et al (1997) Human alteration of the global nitrogen cycle: sources and consequences. Ecol Appl 7:737–750

Vlachokostas C, Nastis SA, Achillas C et al (2010) Economic damages of ozone air pollution to crops using combined air quality and GIS modelling. Atmos Environ 44:3352–3361

Wait DA, Jones CG, Coleman JS (1998) Effects of nitrogen fertilization on leaf chemistry and beetle feeding are mediated by leaf development. Oikos 82:502–514

Waring GL, Cobb NS (1992) The impact of plant stress on herbivore population dynamics. In: Bernays EA (ed) Insect-plant interactions, vol 4. CRC Press, Boca Raton, pp 167–227

West Australia EPA (2007) State of the environment report. http://www.epa.wa.gov.au/AbouttheEPA/SOE/Documents/2_WA_SOE2007_ATMOSPHERE.pdf

Wilson D, Stock WD, Hedderson T (2009) Historical nitrogen content of bryophyte tissue as an indicator of increased nitrogen deposition in the Cape Metropolitan Area, South Africa. Environ Pollut 157:938–945

Zielinska BK, Bytnerowicz A, Gertler AW et al (2012) Distribution of ozone and ozone precursors in the Lake Tahoe Basin. In: Presentation at 2012 Tahoe science conference: Incline Village, NV, 22 May 2012. http://tahoescience.org/wp-content/uploads/2012/06/Zielinska-Barbara-presentation.pdf

Zunckel M, Venjonoka K, Pienaar JJ et al (2004) Surface ozone over southern Africa: synthesis of monitoring results during the Cross Border Air Pollution Impact Assessment project. Atmos Environ 38:6139–6147

Chapter 28
Responses of Mediterranean Forest Phytophagous Insects to Climate Change

François Lieutier and Timothy D. Paine

Abstract The present characteristics of the Mediterranean forest ecosystems are the results of millennia of human action under a particular climate. As in all forested ecosystems, insects play an essential role in their functioning. Consequently in these regions, tree insect relationships are extremely dependent on both social and climatic factors. Because these later two parameters are expected to largely change along the twenty-first century, considerable changes in the functioning of Mediterranean forest ecosystems are also expected, partly as results of modification of tree-insect interactions. Our reflection in that chapter is to try and foresee how the characteristics of phytophagous insects and their relationships with host tress could evolve during the twenty-first century, as results of climate changes in relation with social factors. Our starting point is a description of the present biological characteristics of Mediterranean forests and their phytophagous insects. Considering then the various scenarios of climate change, we present what the consequences for the Mediterranean trees and forests could be, and then the consequences for the phytophagous insects in terms of abundance, survival, phenology, spatial range, host tree quality, and biodiversity. We conclude by replacing the tree-phytophagous insects' relationships in the context of complex interactions, reality of forest ecosystem functioning.

28.1 Introduction

Climate change is now a concrete fact. Its effects have consequences on all aspects of the biosphere functioning, of which forests are essential elements. Because they act at all trophic levels of forest ecosystems (except primary production) through

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hundred thousands of species and billions of individuals, insects are a major component of forest processes. As consequence of their particular climatic characteristics, Mediterranean forests seem especially exposed to drastic changes resulting from climate modifications. The broad object of the present chapter is a reflection on how relationships between insects and trees may evolve in Mediterranean forests in the context of climate change, from here to the end of the twenty-first century. To simplify the reflection, we focus on phytophagous insects.

The Mediterranean type ecosystems are all located in coastal regions, mostly on poor and shallow soils (Fischlin et al. 2007). The five Mediterranean regions cover a total area of about 3.4 million km^2, representing 8.3 % of the earth's land surface, 9.4 % of its population and roughly 1 % of the world vegetation (Boydak and Dogru 1997). Seventy-three percent of their forested areas are in the Mediterranean Basin, 10 % in California, 10 % in Southwestern Australia, 4 % in Central Chile, and 3 % in the Cape Region (Rundel 1998). Alone, the Mediterranean Basin contains 1.8 % of the world forest, 1.5 % of its standing volume, and 1.1 % of its biomass (Boydak and Dogru 1997). In the followings, we focus on Mediterranean forests of the Northern hemisphere, mainly on the Mediterranean Basin, but with comparisons to California.

Forests are basic structural elements of the Mediterranean type ecosystems (Quézel and Médail 2003). However, the present characteristics of most Mediterranean forests largely result from the action of many anthropic factors, especially the triptych cultivation-fire-grazing, which have acted in concert for a very long time (several thousand years in the Mediterranean Basin). Over 500 million people live now in the 25 countries of the Mediterranean Basin (Boydak and Dogru 1997), which gives an idea of the human pressure that has been, and continues to be, exerted on the forested areas in that region. Although they have been present everywhere in the Mediterranean Basin, the anthropic factors have resulted in diversified forest contexts we see today. Two third of the forests are located on the northern rim, where they cover 20–30 % of the land in countries of Southern Europe. The rest is approximately equally shared between North Africa and the Middle East but covers in these regions respectively 1–8 % and 5–10 % of the land depending on the country (Scarascia-Mugnozza et al. 2000). This contrasted situation results from both climate and social factors (Sect. 28.2.4) that are still operating and are likely to be exacerbated, especially in a changing climatic world. Moreover, climate change is accompanied by other environmental changes, such as human population growth, agricultural change and development of silvicultural methods for forest sustainability. Both climate and social factors will thus shape the future characteristics and the functioning of the Mediterranean forested ecosystems and consequently tree-insect interactions. In our reflection on climate change effects, we must thus keep in mind the social aspects.

The already observed and possible future consequences of climate change for forest insect communities and their relationships with trees have already often been the subject of many papers from temperate and boreal regions. Studies have also been developed in Mediterranean regions but to a much lesser extent. However, even considering direct climatic effects only, transferring results from temperate or boreal ecosystems to Mediterranean ecosystems is difficult and hazardous. Maximum temperatures may reach values causing negative effects on insects of Mediterranean ecosystems, while temperature increase may still have positive effects in temperate and boreal areas. Precipitation also may change more drastically in Mediterranean areas than in the other two regions or vary in opposite direction. Summer temperatures and droughts may cause serious problems to both insects and trees in Mediterranean areas, but not necessarily in temperate areas, where they could be favorable to insects. Indeed, there are many examples of different or opposite effects of climate change on living organisms, between temperate or boreal ecosystems and the Mediterranean ones. Among those examples, effects of CO_2 increase on tree growth are most often still positive in temperate and boreal areas but are already largely negative for some tree species in Mediterranean areas, due to water limitations (Nageleisen et al. 2010). As result of temperature rise, a general increase of the number of plant species in the European summits (due to migrations to higher elevations) has been reported between 2001 and 2008 in all the 13 boreal-temperate mountain regions (52 summits), while a general decrease (no possibility to migrate at higher elevation) has been observed during the same period in all the 4 Mediterranean mountain regions (14 summits) (Pauli et al. 2012). In southern California Mountains, the dominant forest species increased in average elevation by 65 m over the last 30 years, apparently in response to regional climate change (Kelly and Goulden 2008). Consequently, the examples that we shall use to present our reasoning will be chosen almost exclusively in the Mediterranean areas.

In a first step, we shall present the biological characteristics of the Mediterranean forest ecosystems, for then tentatively inferring the consequences for the characteristics and behavior of the Mediterranean forest insects. In a second step, the foreseen climate modifications in the Mediterranean areas will be presented, followed by their possible effects on trees and forests. Finally, we shall try and evaluate the possible consequences of these changes for the relationships between trees and forest insect communities. Meanwhile, the social aspects will be taken into account, not in a special discussion but at several occasions to show how their consequences can be strongly linked to those of climate change.

28.2 Characteristics of the Mediterranean Forest Ecosystems

Compared to temperate forest ecosystems, the major characteristics of the Mediterranean forests are their complexity and their heterogeneity, regarding both physical (climate, soil, topography …) and biological (landscape, biogeography, flora, fauna …) components. In addition, they have been submitted to dramatic modifications by human actions.

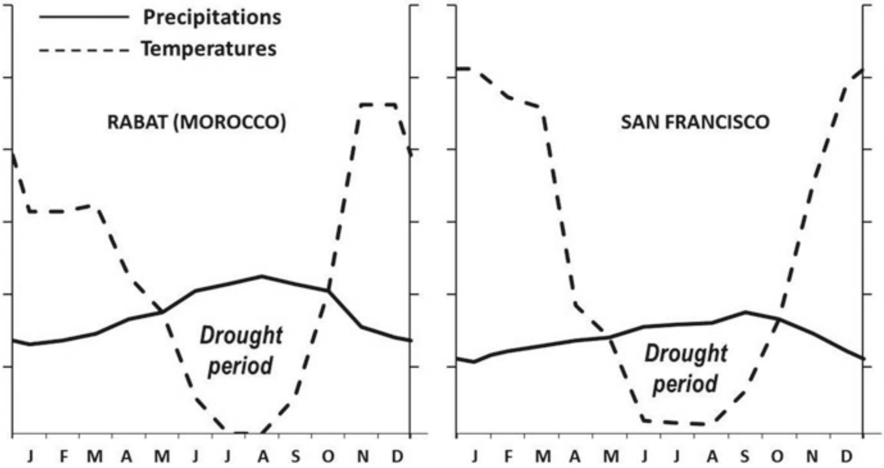

Fig. 28.1 Climatic diagrams of Rabat (Morocco) (65 m elevation; mean temperature 17.3 °C; precipitation 523 mm) and San Francisco (California) (16 m elevation; mean temperature 13.6 °C; precipitation 561 mm) (From Quézel and Barbero (1989), modified)

28.2.1 Climate

Hot dry summers and mild rainy winters with high seasonal contrasts characterize the Mediterranean climate, with periodic droughts in synchrony with high temperatures (Fig. 28.1). The climatic heterogeneity is very high, especially with a dry season from one to six months, depending on localities. Completed by a high topographic heterogeneity, this climatic heterogeneity results in many local microclimates, and consequently in a high number of forest types: evergreen forests, coniferous forests, deciduous forests, with various species and various tree densities in each case (Rundel 1998; Quézel and Médail 2003; Lefevre and Fady, Chap. 2).

28.2.2 Vegetation

Mediterranean forests have been moderately affected by the ice age and have been refugees for many plant and animal species of the tertiary period, some of which being still present. In all Mediterranean regions, vegetation is dominated by sclerophyllous and evergreen and drought deciduous woodlands (Rundel 1998). In both the Mediterranean Basin and California, sclerophyllous forest is the most expanded plant community and, although the parent bedrock in California is not limestone typically associated with the Mediterranean Basin, similar vegetation structures are recognizable. This ecological convergence clearly appears in the altitudinal zonation, making it possible to connect most Californian recognized forest structures to the classical altitudinal zonation defined in the Mediterranean Basin (Quézel and

Médail 2003). Mediterranean plants including trees are generally drought resistant, even xerophyllic, with abundant ligneous structures and low water content. Mediterranean oaks for example are considered the most tolerant oaks to drought (Timbal and Aussenac 1996; Manes et al. 2006). Mediterranean plants are also known to be frequently rich in volatile substances (among which terpenes). Aside of these climate adaptations, many plant characteristics are also the result of human actions (Sect. 28.2.4).

Compared to temperate forest ecosystems, Mediterranean forests are also characterized by a lower leaf area index (Hickler et al. 2012), a moderate biomass and a moderate primary productivity, mainly consequences of summer droughts. However, for these last two parameters, they have the highest root/total plant ratios (about 50 %) among the world forests (Saugier et al. 2001 *in* Stuart Chapin et al. 2002), also an adaptation to drought. Consequence of these high ratios, pest attacks on aerial parts may be more dramatic for the Mediterranean plants than for those of other ecosystems. One may thus wonder if their generally high content in volatile compounds could be related to the necessity to defend their aerial parts against aggressions. However, root/shoot biomass ratio varies among species and, for a same species, depends on sites (Pausas 1999a). Plant communities in Mediterranean areas have been considered as highly resilient to disturbances until now, probably as a result of both their high ecological diversity and their evolutionary history of disturbance (Lavorel 1999). In particular, on the Northern rim of the Mediterranean Sea, forests have generally recovered rapidly from fire and grazing, because of their efficient regeneration strategies (Sect. 28.2.4) and because disturbances have often modified species relative abundance rather than species composition (Quézel and Médail 2003).

28.2.3 A High Biodiversity Level

Contrary to temperate and boreal forests, Mediterranean forests and especially those of the Mediterranean Basin are composed of many isolated and often small-sized patches of stands, as consequences of combination of various paleogeographic, climatic, and ecological processes, as well as of ancient and omnipresent human action (Quézel and Médail 2003; Lefevre and Fady, Chap. 2). This defines a large number of distinct and more or less isolated communities with patchy distribution, resulting in many boundaries (ecotones), less spatial buffering, high biodiversity (at both species and communities levels) and high endemism. Mediterranean Basin as well as the other four Mediterranean ecosystems belongs to list of the 25 world biodiversity hot spots (Myers et al. 2000). There are 30,000 plant species in the Mediterranean Basin over an area of 2.3 million km^2 and similarly, 4400 plant species live on 324,000 km^2 in the Californian Mediterranean region (Quézel and Médail 2003; Lefevre and Fady, Chap. 2).

Compared to the medio-european forests, species richness and level of endemism of woody species is particularly high in the Mediterranean forests of Europe and

California. The Mediterranean Basin gathers 201 woody plant species or subspecies exclusive or highly preferential of the Mediterranean forests (endemism level 69 %), California 77 species (endemism level 45 %), whereas only 46 are exclusive or highly preferential of the medio-European forests (endemism level 34 %) (Quézel and Médail 2003). In the Mediterranean basin, many endemic tree species or subspecies such as *Pinus nigra laricio* in Corsica, *Pinus nigra dalmatica* in Croatian islands, *Abies nebrodensis* in Sicilia or *Cedrus libani brevifolia* in Cyprus, are found in large islands, but also in continental areas for several firs (*Abies pinsapo*, *Abies maroccana*, *Abies numidica*, *Abies cilicica*), oaks (*Quercus afares* in North Africa and *Quercus lusitanica* in Portugal), *Cupressus atlantica* in the High Atlas, or *Argania spinosa* and *Acacia gummifera* in south-western Morocco (Barbero et al. 1995; Quézel and Médail 2003). According to (Scarascia-Mugnozza et al. 2000) and (Quézel and Médail 2003), there is a total number of 100 tree species in the Mediterranean Basin, including 11 pine species, 10 fir species and 20 oak species, whereas 30 tree species in total, 7 pine species, 2 fir species and about 7 oak species are found all over the rest of Europe in an area yet 4 times higher. Similarly, there are 20 pine species in California as well as 5 fir species and 16 oak species; more than 50 % of the species of pine and 75 % of the oak species are endemic to the Mediterranean climate zones of western North America (Munz and Keck 1968).

28.2.4 Dramatic Modifications by Human Actions

Human action has had dramatic effects in all Mediterranean ecosystems. However, because many civilizations have developed successively in the Mediterranean Basin during at least 4 millennia, this region exhibits the most drastic modifications (Lefevre and Fady, Chap. 2). Each of these civilizations has indeed deforested large areas by trees harvest, grazing (even in forests), cultivation, fires, and urbanization, leading to forest fragmentation, low or null natural regeneration, soil degradation, and finally permanent non-equilibrium conditions. In the middle of the nineteenth century, 3/4 of the originally present Mediterranean forests had disappeared (Quézel 1974, in Quézel and Médail 2003). Reforestation programs have been largely developed since that period, especially on the Northern rim, but human density averages now above 110 inhabitants/km^2.

Beginning in the mid-nineteenth century, differences have developed between the Northern and the Southern rim of the Mediterranean Sea, and continue to persist. The Northern rim has been characterized by a rapid industrialization and urbanization, together with a low population growth and a decrease of the density of rural populations. Intensification of the agriculture has resulted in the abandoning of large agricultural lands and a decrease of grazing, opening large potential for natural or human- made reforestation, but also increasing fire risks. During the same period, on the Southern and Eastern rims, high population growth rates and high population density lead to large rural populations still heavily dependent on forests and natural resources for wood, food and grazing. The result has been a rapid deforestation with low or null forest regeneration, and an accelerated use of the forest resources above their renewal capacity (overgrazing and over-cutting) (Boydak and Dogru 1997; Quézel and Médail 2003). For example, during the second half of the twentieth century, 2–5 % of the wooden areas were disappearing each year in Morocco, and roughly half of the North African forests have been destroyed (Quézel and Médail 2003). Thus, on both rims but for different reasons, the forests have drastically changed.

Fragmentation is the most important consequence of deforestation and the most serious cause of biodiversity erosion and species extinction at the world scale. It causes a barrier to gene fluxes, with increasing inter-population differences. It also drastically modifies, if it does not stop, many biotic interactions, such as predator-prey or host-parasites interactions, and plant-insect interactions. Finally, the whole forest structure and functioning at the regional level is modified.

Overgrazing, especially with sheep and goats, creates a drastic decrease of the plant cover favoring erosion, disappearance of seedlings, and soil compaction, resulting in dramatic perturbations of the regeneration process. Algeria and Morocco presently support two to three times the maximum tolerable load. Forests become park-forests with trees at some distance ones from the others without low branches or sprouts and without any regeneration. Moderate controlled grazing by sheep can however be benefit through increasing the floristic diversity in the open areas or through allowing regeneration of some tree species by opening favorable niches in a dense herbaceous level (Quézel and Médail 2003).

In the Mediterranean Basin, 95 % fires have human causes, but natural fires (lightning) are largely the most frequent in the other Mediterranean ecosystems. In California, fire is a natural process which maintains diversity, productivity and stability of the ecosystem (California Mediterranean Research Learning Center 2010). If not too repetitive, fires can indeed have benefic effects such as biodiversity increase by favoring species of open areas (rapid root penetration into the soil, vigor, competition-free growth of stems …) (Boydak and Dogru 1997). Fire has thus been a determinant driver for the evolution of the Mediterranean forests through creating selective pressure leading to adaptations of plants and animals. These specific adaptations could be essential for future changes in forest communities. However, contrary to Australia and South Africa, no plant in the Mediterranean Basin is strictly dependent on fire for completing its cycle (Pausas and Vallejo 1999). The high resilience capacity of the Mediterranean forests results from both multiple possibilities of plant regrowth and colonization (sprouts, soil seed bank, serotiny, dispersion) and re-distribution of the nutrients accumulated in plants (Pausas and Vallejo 1999; Quézel and Médail 2003; Paula et al. 2009). The capacity to re-sprout allows to quickly recovering after fire. It is the most frequent strategy used by trees in the Mediterranean Basin. Re-sprouting involves various types of tree organs: zhizomes for *Quercus coccifera*, stem buds for *Quercus suber*, basal buds for the other *Quercus* species. Cone serotiny concerns only a few species, mainly *Pinus halepensis* and *Pinus brutia* and to a lesser extent *Tetraclinis articulata*, *Cupressus sempervirens*, *Pinus canariensis*, and *Pinus pinaster* (Pausas and Vallejo 1999; Quézel and Médail 2003). Latent phase of cones (without fire) can be up to 20 years in *C. sempervirens* (4–5 years for *P. halepensis*). However, in case of too repetitive fires on a same area, serious physical, chemical and biological constraints can occur, leading to selection among the initial species and finally to a dramatic decrease of biodiversity in forest species.

Reforestation through plantations is also a frequent disturbance in the Mediterranean areas, especially when it concerns exotic species. Plantations represent 12 % of the total forest area in the Mediterranean Basin, but can reach up to 40 % in North African countries, with more than 50 % of exotic species, as in the case of Morocco (Quézel and Médail 2003 and Fig. 28.2). Eucalyptuses are the most frequently introduced species, but significant areas have also been planted with exotic pines, such as *P. canariensis* and *Pinus radiata. Eucalyptus* is exigent regarding soil quality, causing rapid nutrient decrease in soils. Introduced exotic pines lead to genetic pollution of the indigenous stands through introgression and hybridization with indigenous species and finally to disappearance of the intraspecific originality of the local populations. Moreover, most planted species, be they introduced or not, are very flammable, give a slow decomposing litter and cause soil acidification (Quézel and Médail 2003).

Invasion by exotic tree species is another disturbance in the Mediterranean areas and the second threat for the world biodiversity. Moreover, invasive species are

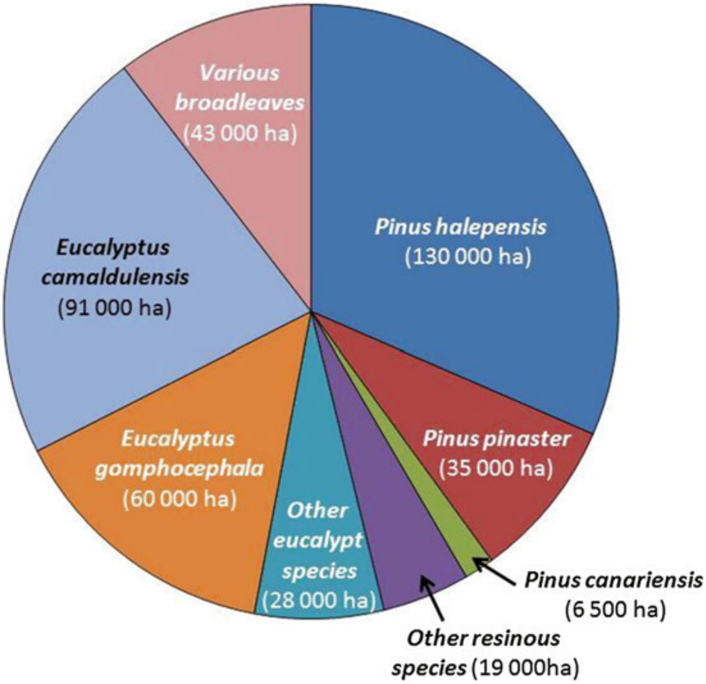

Fig. 28.2 Planted areas of various tree species in Morocco, between 1950 and 1990 (From data of Quézel and Médail (2003))

facilitated by fragmentation and urbanization. In the Mediterranean Basin, invasive trees are mainly *Ailanthus altissima*, *Robinia pseudoacacia*, and above all various *Acacia* species (of which the most dynamistic is *Acacia dealbata*) which eliminate the original species. Other introduced species (among which some originating from the Mediterranean Basin itself) can extend themselves although not as fast as the above species. They are *Abies cephalonica*, various pines among which *Pinus nigra* ssp. *nigra*, *Cedrus atlantica*, *C. sempervirens*, *Fraxinus ornus*, and *Pseudotsuga menziesii* (Quézel and Médail 2003).

As a consequence of human perturbations, Mediterranean ecosystems in general are in permanent non-equilibrium conditions and certainly among the most disturbed ecosystems in the world (Sanways 1998).

28.3 Resulting Life Traits and Behaviors of Phytophagous Forest Insects

Insects in general are characterized by high levels of narrow endemism in all Mediterranean ecosystems (Sanways 1998). Regarding forests of the Mediterranean Basin, the high levels of trees biodiversity and endemism, combined with the diversity of insect habitats available on a single tree and the various insect feeding behaviors, have very likely favored high biodiversity and narrow endemism in phytophagous forest insects, particularly for those that are specialists. Not many data exist on that aspect but there are demonstrative examples.

As many as 62 cone and seed insect species have been collected in the sole Mediterranean Basin, whereas roughly 400 species are known at the world level (Roques and El Alaoui El Fels 2005). That these species have been collected from 31 species of native conifers (with 1–13 insect species per tree species) demonstrates the role of tree biodiversity on insect biodiversity. In parallel, the percentage of endemic insect species is largely dependent on tree endemism. It indeed varies from about 90 % in *Cedrus* and *Cupressus* to 100 % in *Tetraclinis*, which are all genera endemic from the Mediterranean Basin, while it varies from around 43 % in *Abies* and *Pinus* to 57 % in *Juniperus*, genera of which the geographical range is much larger than the Mediterranean Basin (Roques and El Alaoui El Fels 2005). Nevertheless, the still high level of endemism of the insect species collected from those three non-endemic tree genera shows that characters particular to the local Mediterranean ecosystems also interfere. Similarly, 42 species or subspecies of conifer bark beetles are indigenous in the Mediterranean Basin, among which 28 endemic ones. They live on 25 native conifers, of which 15 are endemic (Lieutier et al., Chap. 6). That example also shows that trees' biodiversity and endemism can be important drivers of forest insects' biodiversity and endemism.

Combined with tree diversity, the patchy organization of the Mediterranean forest may also have been a factor of intense genetic divergence, leading to high insect species richness at the scale of the whole Mediterranean Basin. However, as for plants, insect species richness could also be due to species from boreal or eurasiatic origin, which had found refuge in the Mediterranean Basin during the ice age and have stayed there after ice melting.

Mediterranean forest insects have developed adaptations not only to trees but also to the various Mediterranean traits such as vegetation characteristics, climate and fire, or have exploited man-created particularities such as large plantations of exotics or overgrazing.

For example, the sclerophyllous vegetation is favorable to the presence of galling insects (Fernandes and Price 1992; Espírito-Santo and Fernandes 2007) which allows the Mediterranean ecosystems to possess high species diversity in that guild. Species diversity of galling insects is particularly high between latitudes 25° and 38° north and south, an area characterized by the large extent and diversity of the sclerophyllous vegetation. Always more than 12 and up to 46 insect galling species have been found in the sites located inside that latitudinal zone, whereas the species number has reached 12 maximum in the sites located outside that area (Price et al. 1998). Regions with sclerophyllous vegetation are not all Mediterranean and sclerophyllous plants are not all trees. However, the Mediterranean type ecosystems are an important component of and are all located in the considered latitudinal zone, and are characterized by the abundance of their sclerophyllous plants, especially trees.

Everywhere, climate is an important factor of adaptation of organisms to local or regional conditions. Insects are ectotherms and multiplication and growth of their populations in general are thus favored by the particularities of the Mediterranean climate, especially mild winter allowing winter development, and high temperature during all year allowing a high number of generations. This later favorable effect is particularly visible for Mediterranean species of which the geographical range is extended in latitude. For example, the bark beetle *Orthotomicus erosus* can have up to six complete generations per year in the Mediterranean Basin but only two in central Europe (Carle 1975; Mendel et al. 1985).

Many Mediterranean forest insects belong to heliophilous and thermophilous species, as it is the case of the typically Mediterranean oak xylophagous species *Coroebus undatus*, *Coroebus florentinus* (Buprestidae) and *Cerambyx cerdo* (Cerambycidae) (Du Merle and Attié 1992; Soria and Ocete 1993; Cardenas and Gallardo 2012; Jimenez et al. 2012). Although they can also be found in temperate forests, their damages are located mainly in the Mediterranean region (Bouhraoua et al. 2002; Evans et al. 2004; Sanchez-Osorio et al. 2007). The pine processionary moth *Thaumetopoea pityocampa* lives at low elevation where mild winter temperatures allow its larvae to develop upon the foliage of their host trees. They built silk nests which play the role of solar heaters during the day, from which they go out at night to feed. The species however cannot tolerate hot dry summers and consequently spends this season in an underground pupal diapause (Huchon and Demolin 1970). For these reasons, the species has been called the “winter processionary”. Interestingly as a comparison, the cedar processionary moth *Thaumetopoea bonjeani*, also a Mediterranean species, is a summer processionary, with an egg diapause during winter, but its host is located at the highest vegetation level where temperature is lower. No nest is thus necessary in winter, neither a summer pupal diapause.

The endemic Mediterranean bark beetle *Tomicus destruens* can attack its pine hosts in fall and its larvae can develop during winter, whereas all other *Tomicus* species, which live under temperate or boreal climates, always attack their host at the end of winter or in spring (Lieutier et al. 2015). Moreover, *T. destruens* causes heavy damage in its natural area, whereas the other European *Tomicus* very rarely cause extended damage (Lieutier et al. 2015). That contrast may be a consequence of the repeated summer droughts that characterize the Mediterranean climate.

Frequent fires can benefit to Mediterranean forest insects. This is the case of xylophagous insects in general and especially of those, such as bark beetles, which attack weakened trees, even in non-Mediterranean areas. As an example, *T. piniperda* is attracted by fire burned places in Sweden, mainly during the first 2 years after fire, the success of stem attacks depending on the severity of fire injury to the crown (Ehnström et al. 1995; Långström et al. 1999). In the Mediterranean Basin, the more frequent fires may have more significant effects on population dynamics of xylophagous insects. In Greece and Portugal, various pine species have been attacked by several species of bark- and wood-boring insects after forest fires (Ferreira and Ferreira 1987; Markalas 1997; Lombardero and Ayres 2011) In Spain, attacks by several bark beetles species, among which *T. destruens,* an aggressive species in the Mediterranean Basin, have been reported on fire damaged *P. pinaster*, with those of other xylophagous species such as *Buprestis novenmaculata* and *Pissodes castaneus*. These later two species, together with *T. destruens* and *T. piniperda* were among the first arrivals, (Santolamazza-Carbone et al. 2011).

Plantations of exotic tree species occupy large areas in the Mediterranean Basin and in California (Sect. 28.2) where they represent large quantities of potential resources for indigenous or exotic insects. Examples exist for both insect categories in the Mediterranean Basin as well as in California. A typical situation of indigenous Mediterranean insect exploiting plantations of exotics is that of the scale *Matsucoccus josephi* in Turkey. This insect does not cause damage on its usual host *P. brutia* but only on *P. halepensis*, a species supposedly introduced there by man (Mendel 1992). Similarly, when extending its area westwards from Eastern Europe, the fir leaf roller *Choristoneura murinana* first developed on its usual host species *Abies alba* when it established in South-Eastern France. Then however, it shifted to *C. atlantica* introduced from Morocco, where it caused important damage (Du Merle et al. 1992). Inverse situations however also exist where exotic insects adapt and cause damage to an indigenous Mediterranean host tree, as when the scale *Mastucoccus feytaudi*, introduced from Spain, invaded and destroyed *P. pinaster* stands in South-Eastern France (Schvester 1971). A third common situation is that of exotic pests following their original host in its new area. *Eucalyptus* plantations are a significant example. In all Mediterranean countries, *Eucalyptus* introductions have been followed by the arrival of several exotic insects becoming local *Eucalyptus* pests, such as the longhorn beetle *Phoracantha semipunctata* and the weevil *Gonipterus scutellatus*, followed several years later by *Phoracantha recurva*, psyllid species, and nowadays by the leaf gall wasps *Leptocybe invasa* and *Ophelinus maskeli* (Paine et al. 2011). However, none of these exotic insects have adapted to the local tree species and, inversely, indigenous Mediterranean insects never caused damage to

Eucalyptus, because this tree genus is taxonomically and chemically very far from all local tree genera. Although few exceptions exist, the possibility for an insect to establish on a novel host tree indeed largely depends on the taxonomic and/or chemical proximity between the novel and the usual host (Lieutier 2006). A similar case occurred in southern France after the introduction of *C. atlantica* from Morocco, with the aphids *Cinara cedri* and *Cedrobium laportei*, the lepidoptera *Epinotia cedricida* and the seed chalcid *Megastigmus pinsapinis* (Fabre et al. 1999; Mouna 2013).

In addition to exploiting plantations, some Mediterranean insects can take advantage of or at least adapt to overgrazing. In the Mâamora forest in Morocco, damage to roots of cork-oak seedlings by the Scarabaeidae *Sphodroxia maroccana* seem to be caused in a large part by a lack of native vegetation resulting from overgrazing (Lumaret et al. 2005). In response to grazing, white grubs have changed their feeding behavior and turned to oak seedlings, as proved by the lack of damage in sites protected from grazing where seedlings have to compete with native vegetation.

28.4 Climate Predictions for the Mediterranean Basin

The Mediterranean region might be especially vulnerable to global change (Giorgi and Lionello 2008). Observations of regional changes during the last decades together with climate change simulations have indeed "identified the Mediterranean basin as a hot spot of hydrological cycle changes" (Mariotti 2010; Carnicer et al. 2011).

The present CO_2 concentration in the atmosphere is 370 ppm whereas it was 280 ppm in 1850. As consequence, the world average temperature has increased by 0.8 °C during the twentieth century, and the 12 hottest years observed since 1880 all occurred between 1990 and 2005 (Lindner et al. 2010). However, temperature increase in the Mediterranean Basin has been much more rapid. In several Mediterranean regions such as Cyprus and Eastern Spain, temperature has increased by 1 °C during the same period (Quézel and Médail 2003). On the southern rim however, considerable differences have been reported, with mean annual temperature increases of 1 °C in Morocco, 2.5 °C in North-Eastern Algeria and Northern Tunisia, but less than 0.5 °C in Libya and Egypt, during the period 1901–1995 (Hulme et al. 2001). In the Mediterranean Basin, as in Western Europe, the length of summer heat waves have doubled and the frequency of dog-days has tripled since 1880 (Della-Marta et al. 2007). Precipitations have also changed during the last century but not in the same direction everywhere. They have generally decreased significantly on the Northern rim, as in the Montpellier region where 72 mm have been lost from May to August in 150 years (Quézel and Médail 2003), pushing the 150 mm isohyet for these months 35 km northwards (Hoff and Rambal 2000). On the southern rim at a large scale, while precipitations have decreased on average by about 10 % in Morocco and Algeria, they have increased by about 10 % in Tunisia, Libya and Egypt during the period 1901–1995 (Hulme et al. 2001). Locally however, considerable decreases can have occurred, as in the Moroccan Middle Atlas where Atlantic cedar forests are located, and where a precipitation drop of 24 % has been reported from the 1930–1980 to the 1980–2006 periods (Benziane et al. 2010). In North-Eastern Algeria and North-Western Tunisia, several drought periods have succeeded since the 1540s but the most recent (1999–2002) drought episode has been the worst since at least the fifteenth century and may be the first sign of a transition to the more arid conditions in North Africa predicted under high scenarios of CO_2 increase (see below) (Touchan et al. 2008).

The IPCC predicts that CO_2 concentration could reach 500–1250 ppm in 2100, depending on scenarios, which would correspond to a world average temperature increase of 0.3–4.5 °C compared to present (Edenhofer et al. 2014). In Southern Europe as a whole (below 47.5° latitude) and depending on scenarios, temperature would be 2.6–4.8 °C higher and precipitation 6.4–13 % lower in the 2071–2100 period compared to the 1961–1990 period (Hickler et al. 2012). If temperatures variations would thus approximately correspond to those predicted for whole Europe, decrease in precipitations would be considerably more dramatic. Predictions for precipitations are indeed −2.5 % to +2.0 % for whole Europe (Hickler et al. 2012).

On the Northern rim of the Mediterranean Sea, a doubling of CO_2 concentration in 2050, corresponding to a relatively moderate scenario according to the IPCC, would lead to an average annual temperature increase of 2 to 3 °C in Southern France, especially in summer, winter and spring, but of 3.5 °C in Southern Spain and North Africa and 2–2.5 °C in Eastern Mediterranean (Quézel and Médail 2003; Météo-France 2015), with a greater occurrence of extremely high events (Giorgi and Lionello 2008). The same moderate scenario would cause an increase of winter precipitations by 30 to 50 % on the Northern rim (Languedoc-Roussillon) in 2050, but a decrease of summer rains as well as of annual precipitations (Météo-France 2015). The summer decrease would be especially important on the Southwestern area of the Mediterranean Basin, leading to steppisation or desertification (Quézel and Médail 2003). According to Ozenda and Borel (1991 in Quézel and Médail 2003), an increase of summer average temperature by 3.8 °C (with respects to the end of the 1980s), which roughly corresponds to 2050 under a moderate IPCC scenario of CO_2 increase, would lead to a summer drought of 5 months instead of 3 months presently in Southern France (Provence). On the North African rim a moderate scenario of CO_2 increase would lead in 2080 to an increase of 1.4–1.9 °C (East to West) compared with the 1960–1990 period, while summer precipitations would continue to decrease (by 14–19 %) in the western area (Morocco and Algeria) but would not change significantly in the Eastern area (Tunisia to Egypt). Winter precipitation would be approximately stable everywhere (Hulme et al. 2001). Under a high scenario of CO_2 increase however, the temperature rise could be 4.7–6.3 °C (East to West) in 2080. Winter precipitations could decrease by 10 to 15 % in the western area (Morocco, Algeria and Tunisia) and by 20–24 % in Libya and Egypt, whereas summer precipitation could decrease by 30–63 % everywhere (Hulme et al. 2001). At long term at the scale of the whole Mediterranean Sea, precipitation decrease combined with evaporation increase would lead to crucial modifications of the Mediterranean water cycle (Mariotti 2010).

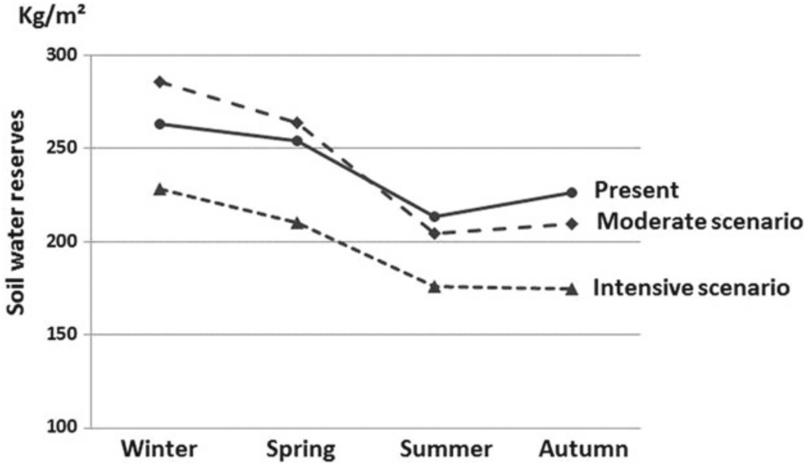

Fig. 28.3 Predictions of variations, compared to present, in soil water reserves for 2050 in Languedoc-Roussillon (Southern France) (From data of Météo-France (2015))

Soil water reserves will obviously be affected. In Southern France (Languedoc-Roussillon) for instance (Fig. 28.3) a moderate scenario of CO_2 increase predicts the following variations of the soil water reserves for 2050: +8.5 % in winter, +3.9 % in spring, −4.3 % in summer, and −7.3 % in autumn, with respect to the present situation. In the same delay and compared to the present situation, an intense scenario of CO_2 increase predicts −15.2 % in winter, −21.1 % in spring, −21.8 % in summer, and −29.4 % in autumn (Météo-France 2015). Whatever the scenario in 2100, the water reserves would decrease drastically (−9.1 % to −23.9 %) at all seasons, except in autumn for a moderate scenario (+6.4 %).

28.5 Consequences for Forest Characteristics

28.5.1 General Considerations

Mediterranean type ecosystems are identified as the terrestrial ecosystems of which biodiversity is likely to be impacted at the highest relative rate by environmental modifications resulting from concomitant changes in climate, land use, biotic exchange, nitrogen deposition and atmospheric CO_2, but land use appears a more important driver than climate (Sala et al. 2000; Fischlin et al. 2007). Consequently, direct climate effect must not be the only aspect to be taken into consideration. Human decisions in forestry (including those in response to climate change) as well as human perturbations must also be considered. Regarding forest production in relation to global change at the 2080 horizon, Vindel and Seller (2005) report on a study carried out by several European laboratories. This study has concluded that, whatever the scenarios chosen by the foresters for plantations or cuttings (economical or environmental tendency), most changes in the European Mediterranean forest will very likely continue to mainly result from forest management decisions in response to markets and public politics. It is estimated that in 2080, forest changes in response to management decisions will account for 60–80 %, while changes due to climate will be only 10–30 %, and those in response to land use 5–22 % (Vindel and Seller 2005). However, as markets and public politics will certainly be greatly influenced by climate change, forest changes will largely correspond to an indirect effect of climate. On the Southern and Eastern Mediterranean rims, the impact of the social factor in response to climate change, although different from the European one, will certainly also be very important (Sect. 28.2.4).

Mediterranean forests and especially those of the Mediterranean Basin will probably be submitted to more dramatic immediate local changes than other forest types because of less spatial buffering and non-equilibrium conditions. Changes in response to shifting climate patterns should be observed at the boundaries between communities, particularly in case of elevation gradients. In addition, owing to the high topographic, climatic and vegetation heterogeneity, very likely various changes will occur depending on the local climatic variables acting as main limiting factors, resulting in complex regional changes. Especially, droughts impacts will vary in space and time, leading to both positive and negative physiological responses of forest trees depending on sites and species (Martinez-Alonso et al. 2007; Carnicer et al. 2011).

Moderate disturbances are said to allow high levels of biodiversity and efficient ecosystem functioning (Connell 1978), and thus changing climate conditions and fires should benefit the forest ecosystems. These changes must however not be too extreme or too frequent for not exceeding the resilience capacity of the ecosystem and the species tolerances. This is precisely the main aspect of climate change with which the forests will have to cope. In fact, the major ecological impacts will come from a changing in rhythms and intensity of climate factors, especially precipitations, together with increased intra-annual and inter-annual variability and an increase of extreme unforeseeable events (Quézel and Médail 2003). Extreme conditions have indeed certainly more influence on ecosystem changes than species physiological responses to variations of average values.

Forests in general are affected by a very large diversity of abiotic and biotic drivers interacting with each other and resulting from climate change (Dale et al. 2001). Settele et al. (2014) have ranked the parameters of terrestrial ecosystems according to the degree of confidence in detection of change and attribution of their observed response to climate change. Among those which are directly concerned with forest, changes in phenology and species range shifts have the highest chance to result from climate change, whereas changes in evapotranspiration, increased tree mortality, increased primary productivity and species invasions have a low chance to be attributed to the climate change effect only, and increase in species extinction a very low chance (Fig. 28.4). We discuss below the effect of climate change on these parameters and others, in relation to trees in the present section, in relation to forest insects in Sect. 28.6.

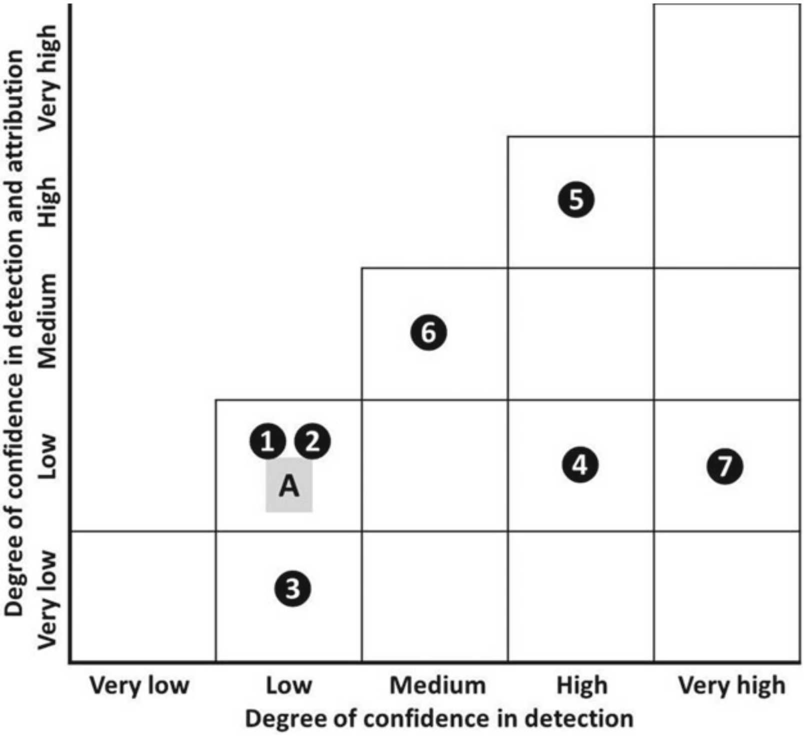

Fig. 28.4 Confidence in detection of change and attribution of observed responses of terrestrial ecosystems to climate change, for parameters directly concerned with forests. 1: Changes in evapotranspiration; 2: Increased tree mortality; 3: Increased extinctions; 4: Increased primary productivity; 5: Changes in phenology; 6: Species range shifts; 7: Invasive species; A: Evolutionary and genetic adaptation. (From Settele et al. (2014) (modified))

28.5.2 Effect of CO_2 Increase on Tree Water Use Efficiency and Primary Productivity

Increase in CO_2 should *a priori* allow a better photosynthetic efficiency and consequently should increase primary productivity, especially in C3 plants which Mediterranean trees belong to, this effect varying depending on tree species. CO_2 increase could also *a priori* induce a decrease in stomatal density and stomatal conductivity, thus conferring a higher resistance of trees to water stress (Quézel and Médail 2003). For instance indeed, the productivity of *Quercus pubescens* has doubled between 1880 and 1980 (Rathgeber et al. 1999) and, although the benefit seems less important for conifers, an increase of *P. pinaster* productivity has also been reported (Quézel and Médail 2003). Similarly, in Southern France, *P. halepensis* productivity has regularly increased during the twentieth century (Venetier et al. 2007). Experimental CO_2 increases have induced a better water economy in young *Q. ilex* and *Q. pubescens* (Tognetti et al. 1999 *in* Quézel and Médail 2003). However, productivity cannot increase indefinitely, mostly because it becomes rapidly limited by water availability even if intrinsic water use efficiency (iWUE) can increase, the more because climate change is accompanied by a decrease of soil water reserves. Moreover, nutrients quantity may also rapidly become a problem. As a result, the productivity curve of the western European forests should necessary culminate. For example, by using the temperature increase predicted by a moderate IPCC scenario, *P. halepensis* productivity has been simulated to peak in southern France around 2025 (Venetier et al. 2007). *A priori*, the peak of productivity should occur earlier in Mediterranean ecosystems than in temperate ecosystems. In fact, although iWUE has increased in all situations where it has been measured, the productivity peak seems to have already occurred in most forests. Gathering results from 37 cases, Silva and Anand (2013) have reported that tree productivity has decreased especially at latitudes lower than 40°, while mixed responses to CO_2 increase occurred above that latitude, thus agreeing with an earlier occurrence of the peak in the Mediterranean regions. However, Peñuelas et al. (2011), in a study carried out from results obtained in 47 sites in various parts of the world including 8 Mediterranean stands, reported no consequence of CO_2 increases on tree growth. Charru et al. (2010) and Silva et al. (2010) even reported a decrease of forest productivity in temperate and boreal forests. In all these situations, certainly other factors related to climate change, such as drought, may have counterbalanced the potential positive effect of CO_2 increase on tree growth.

28.5.3 *Effect of Climate Change on Tree Growth, Mortalities, and Seed Production*

Although the Mediterranean vegetation including trees is rather well adapted to drought (Timbal and Aussenac 1996; Manes et al. 2006), repeated extreme climatic situations may be a problem, especially when drought return intervals become shorter than the time needed by the trees to fully recover, making drought effects cumulative. Climate change can induce tree mortality directly by drought or heat stress, or indirectly by pest attacks (Sect. 28.6) or various other indirect mechanisms (Allen et al. 2010). Extensive growth reduction and mortalities of dominant tree species, as well as reduced seedlings recruitments, due to effects of climate change (with or without pest attacks) have been reported in almost all forested areas of the world, mainly in the northern hemisphere where Mediterranean areas have been largely concerned [(numerous references in Allen et al. (2010) and Settele et al. (2014)]. According to Lindner et al. (2010), forest productivity in Mediterranean regions is expected to decline due to strongly increased drought and fire risks. Various tree species in all regions of the Mediterranean Basin have already been concerned, especially with the decrease of rainfalls over the whole area since the late 1970s.

On the northern rim, confirming the high risk in the Mediterranean area, in a study carried out in various European latitudes over 1987–2006, Carnicer et al.

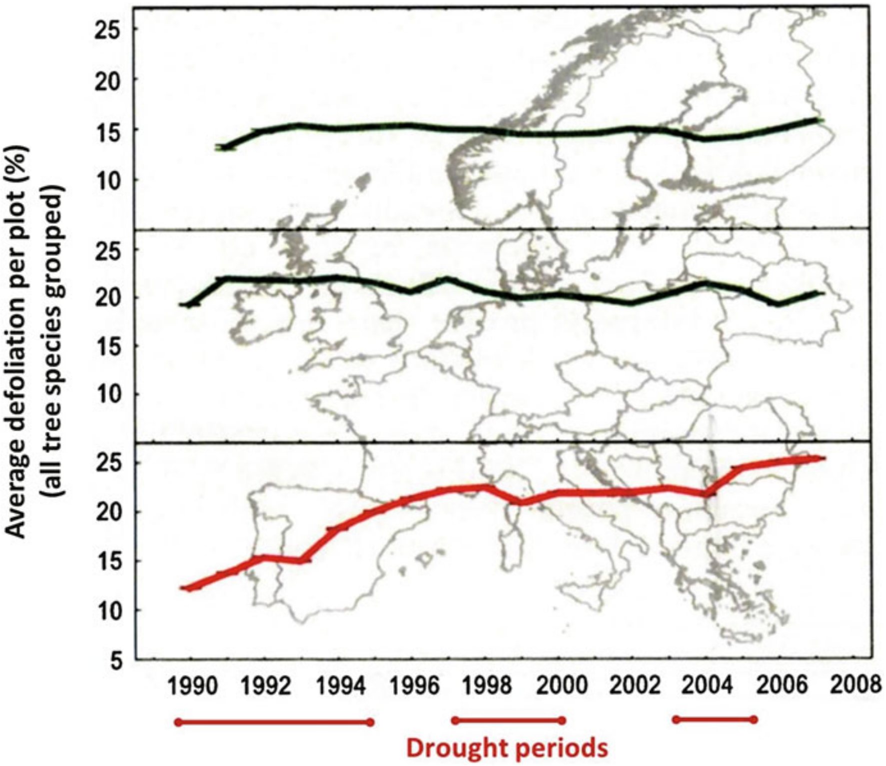

Fig. 28.5 Annual trends in drought-induced crown defoliation, in the forests of southern, central and northern Europe from 1990 to 2007 (From Carnicer et al. (2011), with permission)

(2011) have reported a significant increase of drought-induced crown defoliation rates in the forests of southern Europe but not in those of other latitudes (Fig. 28.5), followed by a significant increase of tree mortality rates. All tree species were affected, even among the typical Mediterranean ones (5 oak and 6 pine species, *Eucalyptus* species and *Juniperus thurifera*), drought effect being particularly important in xeric areas. In Southeastern France, after the heat-wave of 2003 and during the repeated droughts from 2004 to 2007, radial growth, crown development and fruiting of *P. halepensis*, all significantly decreased, and the partial recovery of trees after 2008 will certainly not avoid a delayed dieback (Girard et al. 2012). Stands at the warm edges of their species range are particularly exposed to growth reduction or mortalities. In Northern Spain, with increase of water stress, radial growth of *P. nigra*, *P. sylvestris* and *P. uncinata* has decreased since the mid-twentieth century (Andreu et al. 2007), and a wide-spread mortality of *P. sylvestris* has been predicted at low elevation (Gea-Izquierdo et al. 2014). In the southern sierras, drought effects exacerbated by intra-specific competition, has caused a decrease of the forest cover by *A. pinsapo* since 1991 below 1100 m, while it is still increasing above (Linares et al. 2009, 2010). In Southeastern France, silver fir *A.*

alba is declining and consistent mortalities have been reported as a result of drought, modulated by soil conditions (Cailleret et al. 2013).

On the southern rim, in Morocco, under the joint effects of climate change and human pressure (cutting and grazing), the forested area has already decreased by 48 % between 1939 and 1994. Presently it covers largely less than half of its area of 1940 and, in spite of the planting effort, an additional loss of 45 % of the present area is foreseen at the horizon 2050 (Benziane et al. 2010). For the same reasons but direct human causes being dominant, the “La Mamora” cork oak forest, in the Rabat region, has lost 13 % (50,000 ha) of its area between 1938 and 2000. In Algeria and Morocco, the cedar (*C. atlantica*) forest of the Middle Atlas has decreased by 18–40 % depending on localities, mainly as a result a repeated droughts since 1980 (24 % precipitation decreased in Morocco) (Zine El Abidine 2003; Bentouati 2008; Benziane et al. 2010).

In Eastern Mediterranean, *P. brutia* (the most drought-tolerant among the Mediterranean pines) experienced its lowest growth of the twentieth century and even mortalities, in several Greek islands from 1980 to 2000 (Sarris et al. 2007, 2011). In Samos for example, tree ring width of 40 year-old trees in that period has been half that of trees of the same age in the 1905–1925 period (Körner et al. 2005). Considering the climate scenarios of the IPCC, growth reduction, mortalities and damage by fires are predicted to be even more severe in that region in the future (Sarris et al. 2011).

There is species-specific drought tolerance among trees species under field conditions in the Mediterranean Basin, corresponding to different responses to drought (Hoff and Rambal 2000; Peñuelas et al. 2001; Martinez-Vilalta and Piñol 2002). For example, pines react rather quickly by reducing their water demand, whereas Mediterranean oaks such as *Q. ilex* maintain their physiological activities until water stress become very severe (Hoff and Rambal 2000). Differences among species concerned both the response to severe drought and the capacity to recover (Peñuelas et al. 2001). Nevertheless, as results of increasing drought and climatic disturbance risks, the various scenarios of the IPCC predict a near serious decrease of forest productivity in Southern Europe, contrary to Northern Europe. In the Southern rim after 2050, the xerophytic woodlands with *P. halepensis*, *J. thurifera*, and *Tetraclinis articulata* would disappear (Kovats et al. 2014). Many forest stands of the Southern rim could also disappear because of drought effects being exacerbated by human overexploitation of forest (especially through browsing), which is predicted to continue or even increase.

28.5.4 Effect of Climate Change on Tree Phenology

Shifts in phenology over recent decades as consequence of climate warming have been reported in many parts of the world, with advancement s of spring events and delays of autumn events, for many kinds of organisms among which trees (Parmesan and Yohe 2003; Cleland et al. 2007; Parmesan 2007; Peñuelas et al. 2013). For trees of the northern hemisphere in temperate regions, spring advancement has been estimated at 3–3.3 days/decade during the second half of the twentieth century (Root et al. 2003; Parmesan 2007). For Europe during the period 1971–2000, plant spring advancement would have been 2.4–2.5 days/decade, corresponding to a phenological response to temperature increase of the preceding months estimated at 2.5 days/°C (Menzel et al. 2006). Similarly, for vegetation between 30°N and 80°N, the start of the growing season has been estimated to have advanced by 5.4 days between 1982 and 2008 (Jeong et al. 2011). However, these global estimations, even limited to plants, hide much difference among species, regions and latitudes. Spring advancement is slower in low than in high latitudes. Root et al. (2003), considering a large diversity of organisms (694 species from mollusks to trees) during the last 50 years of the twentieth century, give a mean advanced phenological shift of 4.2 ± 0.2 days/decade for species located from 32° to 49.9° latitude, and 5.5 ± 0.1 days/decade for those located from 50° to 72°. Parmesan (2007), studying 203 species of the Northern hemisphere gathering various plants and animal species, from insects to trees, located between the 30th and the 75th parallel, showed that change in phenology during the twentieth century, was effectively very significantly and negatively correlated with latitude, but latitude explained only less than 4 % of the between species variations (Fig. 28.6). Spring advancement for plants in the Mediterranean Basin is thus, on average, certainly lower than in temperate Europe.

Shifts in tree phenology have already been reported in the Mediterranean Basin revealing large between species differences. In Northeastern Spain, several plant

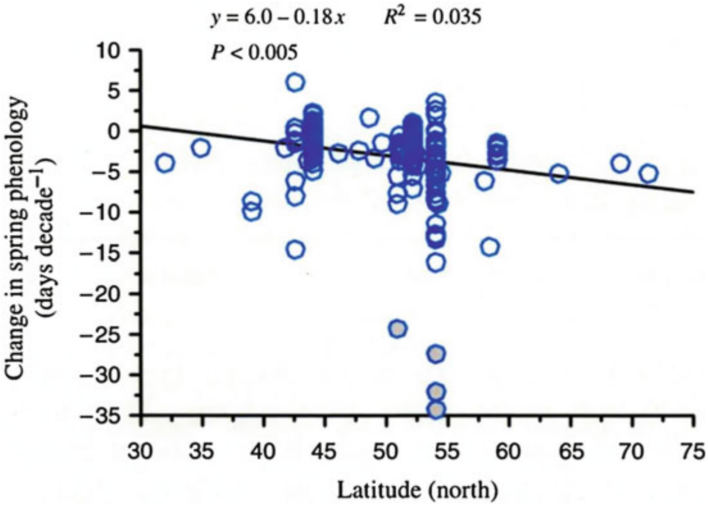

Fig. 28.6 Effect of latitude on change in spring phenology, in response to climate change of 203 plant and animal species. Trend was significant both with and without the four most extreme species (*shaded circles*) (From Parmesan (2007), with permission of "John Wiley and Sons" (CCA licence 3630321005744))

species, among which trees were followed year by year for phenological events (Peñuelas et al. 2002). From 1952 to 2000 depending on species, trees' unfolding phenology was advanced in 18 species by 8.3–37.2 days and one species did not respond. During the same period, leaf fall was delayed in 18 tree species by 7.4–34.8 days and 3 species did not respond. Flowering was advanced in 13 tree species by 6.7–70.1 days, 14 species did not respond and 3 delayed their flowering. From 1974 to 2000, trees' fruiting phenology was advanced by 4.5–42.6 days in 8 tree species, 6 species did not respond and 2 species delayed their fruiting phenology. All phenological changes were correlated with temperature changes, especially with those occurring in the months preceding the phenological events (Peñuelas et al. 2002). These results demonstrate the wide between species variations regarding tree phenological changes in response to temperature changes. For the period 1943–2003 with several plant species among which a large proportion of trees, Gordo and Sanz (2005, 2010) also concluded that, although climate several months before the phenological events interfere, climate conditions during the weeks preceding these events were most important, with temperature explaining most part of the interannual variations. They reported that most spring and summer events showed trends towards advancement, especially since the mid-1970s, but that a large between species variability existed in response to climate warming, including responses in opposite directions. The result of such wide ranges of phenological responses will certainly be modifications in competitive interactions (Peñuelas et al. 2002).

Among Mediterranean tree species, *Cedrus atlantica* has exhibited the most important trend in advancing leaf unfolding, but many other species that are essential components of present Mediterranean forests have changed their leafing phenology very little or not at all, such as *P. pinea* (Gordo and Sanz 2005). During 1952–2000, the flowering phenology of *Q. ilex* advanced by 7.8 days, that of *Q. faginea* and *Q. suber* did not change and that of *Pinus pinea* was delayed by 11.1 days, although flowering phenology advance ranged between 6.7 and 70.1 days for other plants (Peñuelas et al. 2002). According to Cook et al. (2012), a possible explanation for low phenological changes is that response to fall or winter warming and response to spring warming can be of opposite sign. Modifications in competitive interactions may result from these different responses, possibly leading to changes in Mediterranean forest tree communities and in the functioning of Mediterranean forest ecosystems.

Other more complex phenological changes will also certainly contribute in changing interspecific relationships in forest communities. For several Mediterranean plant species including trees, through change in phenology, climate warming can induce uncoupling among different functions in a same tree species. The phenological response to climate change can indeed differ between leaf unfolding, flowering, and fruiting, sometimes even in different directions (Peñuelas et al. 2002). In that manner, from 1952 to 2000, *Tilia cordata* leaf unfolding advanced by 19.0 days but its flowering by 25.3 days, *Acer monspessulanum* and *Platanus hybrida* leaf unfolding advanced by 13.5 and 9.3 days respectively, but their flowering phenology did not changed. From 1952 to 2000, *Quercus ilex* flowering advanced by 7.8 days but its fruiting phenology advanced by 42.6 days from 1974 to 2000. Other

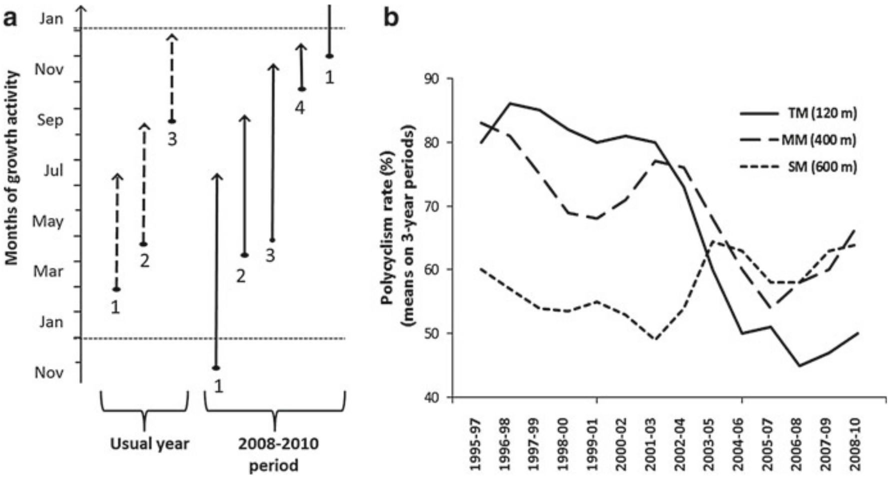

Fig. 28.7 Modification of the number and dates of growth cycles in *Pinus halepensis* in southeastern France. (**a**) Comparison between a usual year and the 2008–2010 period characterized by warm winters and autumns, at 400 m elevation; 1 2 3 4 = cycles of growth activity. (**b**) Evolution of the polycyclism rate from 1995–1997 to 2008–2010 at different elevations; *TM* Thermo-mediterranean level, *MM* Meso-mediterranean level, *SM* Supra-mediterranean level (From Vennetier et al. (2011), modified, with permission)

changes concern tree activity along the year. In southern France, deep modifications of *P. halepensis* polycyclism have been reported, as a result of the combined action, with opposite effects, of temperature and drought (Vennetier et al. 2011). During the 2008–2010 period, at 400 m elevation as a result of temperature increase, *P. halepensis* had a continuous activity all year round due to an advancement of its first growth cycle, a delay of its last growth cycle and an increase in the number of growth cycles (Fig. 28.7a). Between 1995 and 2008 however, increased droughts at low elevation (120–400 m) led polycyclism ratio to decrease, while temperature increase at 600 m led it to increase (Fig. 28.7b). Masting can also be modified under influence of climate change. In a Scots pine forest of Central Spain, hot spring and rainy summer 1997 induced an exceptional cone production in 2000 instead of 2001, leading to an advance of the masting process by 1 year and a permanent alteration in the 3-yearly rhythm of cone production (Martinez-Alonso et al. 2007).

28.5.5 Effect of Climate Change on Tree Species Range

To cope with climate change through displacement, species must be able to track climate change. Recolonization of new areas at the continental scale after glacier ages demonstrates that trees are able to extend their range as a result of climate warming (Cox and Moore 2005). The present velocity of climate warming is however far above that which occurred at the end of the ice ages. It is on average 0.035 °C/year for the world. On average, 1° corresponds to 110 km in flat areas and to 3.8 km in mountainous areas but the real values depend on the degree of altitudinal regional relief (Settele et al. 2014). Expressed in altitudinal variation, 1° corresponds to 180 m. The expression of climate velocity in km/year depends on the regional rate of climate change and on ecosystems (Loarie et al. 2009; Dobrowski et al. 2013), and it depends on the chosen scenario when building predictions. On average, the present climate velocity of 0.035 °C/year corresponds to 3.85 km/year in flat areas and 6.3 m/year in altitudinal variations. In 2085 in flat areas, it would range from 100 m/year under the RCP2.6 (very optimistic) scenario to 7.5 km/year under the RCP8.5 (pessimistic) scenario of CO_2 increase (Settele et al. 2014).

With their slow population turnover, tree species cannot shift rapidly (Lenoir et al. 2008), especially if they are wind-dispersed (Nathan et al. 2011). On average, trees natural dispersal capacities range from few meters to few hundreds of meters per year (Higgins et al. 2003; McLachlan et al. 2005; Meier et al. 2012; Settele et al. 2014). Models built on 30 frequent European tree species predict that the average migration rates of the early successional species, will be less than 200 m/year, with only 271.5 ± 89.5 to 278.2 ± 103.8 m/year for the fastest one *Betula pendula*, depending on IPCC scenarios and model used (Meier et al. 2012). In addition trees' establishment is often more important than their dispersal in limiting displacement rate (Higgins et al. 2003; Meier et al. 2012). Although no typical Mediterranean species were considered in the models by Meier et al. (2012) [Higgins et al. (2003) proposed around 100 m/year (uncertainty 20–230 m/year) for *P. pinaster*], very likely thus trees should lag largely behind climate range shift owing to the present climate velocity, particularly in flat areas. As a result and in the absence of human assisted migrations, they should experience large range contractions, especially at their warm-edge limit. In these conditions, mountains can play the role of climate refuge for trees because of the much lower displacement required to track climate. Moving upward however, contrary to moving northwards, will necessarily cause a decrease of available area and thus of habitat number, which means a decrease of the number of populations and individuals as a result of intra-specific competition. A related extreme situation is that of species which already occupy mountain tops and which are thus at risk of becoming extinct, a rather frequent situation in the Mediterranean Basin, as for *Cedrus atlantica* and *Juniperus thurifera* in North Africa. In the Moroccan High Atlas for example, *J. thurifera* now lives up to the top of several mountains (Fig. 28.8). In mountains, range contractions should thus occur, not only at the species trailing edges as in the case of latitudinal migrations, but also at their front edges.

Migrations have already been demonstrated to occur for a very large diversity of organisms among which forest trees, in accord with climate change predictions in 80 % of the cases (Parmesan and Yohe 2003). Known examples of migration for Mediterranean tree species refer only to altitudinal extension associated with range contractions. In the Moroccan Middle Atlas, *Q. ilex* is already taking the place of *C. atlantica* at its lowest border, while cedar is shifting upwards and invading the distribution area of *J. thurifera* which previously ranged from 2400 to 3300 m in alti-

Fig. 28.8 Extension of *Juniperus thurifera* up to the mountain tops in the Moroccan High Atlas, Oukaïmeden region (Photo F. Lieutier)

tude (Benziane et al. 2010). In Northeastern Spain, as result of a 1.4 °C increase of temperatures during the second half of the twentieth century, *Q. ilex* has progressively replaced *F. sylvatica* at medium altitude, this last species being now refuged above 1300 m (Peñuelas and Boada 2003). Other examples of range contractions at low elevation limits have already been presented above (Sect. 28.5.3) for *P. sylvestris* (Gea-Izquierdo et al. 2014) and *P. pinsapo* (Linares et al. 2009) in Spain. Responses of plants to warming are conditioned not only by changes in temperature, but also by changes in precipitation, land use and species interactions. For the Mediterranean Basin, temperature has been said to be the main factor of range shift on the Northern rim whereas precipitations would be determinant on the southern rim (Quézel and Médail 2003). As specified by Dobrowski et al. (2013), in addition to temperature, a full understanding of changes in multiple climatic factors is needed, such as evapotranspiration and climatic water deficit, to explain all climate-driven species range shifts. According to Cahill et al. (2014), warm-edge limits would be set by both biotic and abiotic factors, but abiotic factors would interfere more frequently.

Various predictions based on climatic envelops have been made regarding the potential distribution of the Mediterranean vegetation, especially of trees, in the context of climate change. It must however be reminded that using climatic envelops to predict potential distribution of trees or any other living species is only a work basis, even if several climate parameters are taken into account. It can help for example in realizing the extent of the climate change effects on living organisms, apprehending modifications of between species relationships, anticipating landscape modifications or future ecosystems, or building scenarios of human assisted migrations, among other uses. In any case, because responses to climate change are species specific, biological communities cannot be considered as fixed entities moving as a whole, forbidding considering ecosystem translation. As results of climate change effects on species ranges, new communities will be built in latitude and altitude, eventually leading to biome changing in some areas. Range changing of trees must thus be considered at the species level. However, even at this scale, climatic envelop must be used carefully. Obviously, tree species will move and their range will extend northwards or upwards anyway but it is difficult to predict the species new distribution areas because several factors others than climate will interfere, among which human action and biological interactions. These factors can be insect pests or pathogens, competition, resistance of flora already present at the new places, obstacles to moving such as fragmented landscapes due to cultivated areas, fires, or biological characteristics of the species (Quézel and Médail 2003; Matthews et al. 2011; Conlisk et al. 2012; Meier et al. 2012; Urban et al. 2012, among others). For example, by modelling migration of temperate trees over Europe during the twenty-first century, Meier et al. (2012) have shown that habitat fragmentation will lead to considerable time lags in range shift, and that inter-specific competition will reduce range shift velocity more than adverse macroclimatic conditions. In California, variations in fecundity (masting), seed predation and increased fire frequency will dramatically compromise the effects of current and even increased dispersal of *Quercus engelmannii*, very probably leading to a dramatic reduction of its abundance as result of climate change, although potential new habitats exist (Conlisk et al. 2012).

In the Mediterranean Basin, potential distributions of forest tree species have been proposed mainly for the Northern rim. A 3 °C increase (corresponding to the year 2100 with the present world climate velocity, but certainly earlier since temperature in the Mediterranean Basin is increasing faster than the world average) would make the sclerophyllous oaks (green, pubescent and cork oaks) to move very significantly in elevation and to the north, and to be replaced in their present localities (except possibly *Q. suber*) by conifers (especially *P. halepensis*, *P. brutia*, *P. pinaster*, *P. pinea*, and juniper) also moving upwards and northwards (Quézel and Médail 2003). Even under an optimistic scenario of climate stabilization in 2100 (RCP2.6 of the IPCC), there would be a 70 to 100 % probability for the French Mediterranean tree species in general (presently limited at the strict Mediterranean area) and to *Eucalyptus*, to potentially shift until the latitudes of Bordeaux and the Burgundy region in 2050, and to the latitude of Orléans in 2100 (Badeau et al. 2004). *Q. ilex* would even reach Southern Britany. Cheaib et al. (2012), in a comparison of models of tree range modifications in France, mentioned that all models agree to foresee a very substantial northward range expansion, especially of *Q. ilex*. In the mountainous areas of Central Spain, Ruiz-Labourdette et al. (2011, 2013) have predicted considerable changes as a result of temperature increase and water deficit (Fig. 28.9). Xeric conifers and sclerophyllous evergreen species (*P. halepensis*, *J. oxycedrus*, *Q. ilex*, *P. pinaster*) would considerably increase their area at the

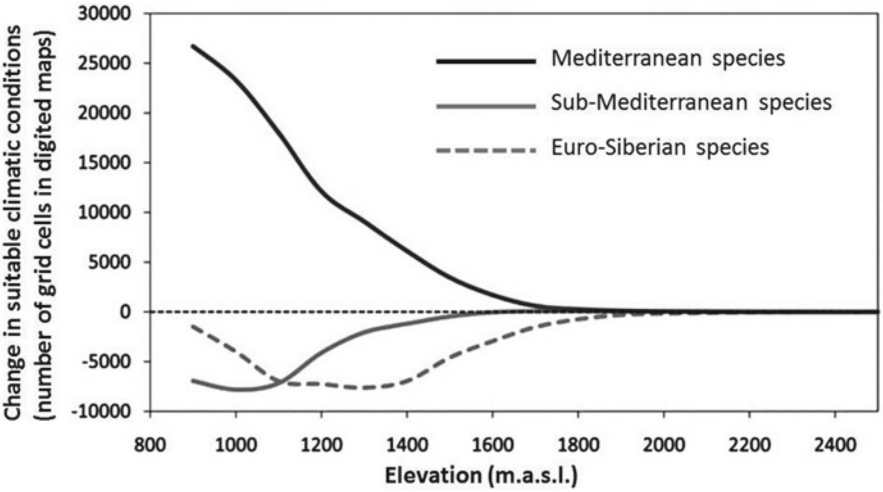

Fig. 28.9 Potential changes in the altitudinal distribution of Mediterranean, sub-Mediterranean and euro-Siberian tree species of Central and Iberian Mountain Ranges under the A2 scenario of CO_2 increase, at the 2071–2100 horizon (From Ruiz-Labourdette et al. (2011), with permission of "John Wiley and Sons" (CCA licence 3630260849671))

expenses of the submediterranean species, while staying at the same elevation. Those ones (*Q. faginea*, *Q. pyrenaica*, *J. thurifera*, *P. nigra salzmannii*) are predicted to slightly shift upward by 25 to 230 m, their area decreasing between 5 % and 70 %, depending on scenarios (RCP2.6 or RCP8.5), taking the place of the Eurosiberian conifers and deciduous species. These later ones (*F. sylvatica*, *P. sylvestris*, *J. communis*) would shift upward by 200–550 m, their range decreasing by 80–99 %, certainly leading the Mediterranean mountains to lose their key-role as refugia for cold-adapted species (Ruiz-Labourdette et al. 2011).

Everywhere consequently, the forest structure will change considerably. For example, under the RCP2.6 scenario, a decrease by up to 30–40 % of the precipitations would lead to the establishment of xerophytic woodlands or to shrublands on the Northern rim by the end of the twenty-first century (Quézel and Médail 2003; Hickler et al. 2012). On the southern rim, according to Quézel and Médail (2003), temperature would not cause significant changes in vegetation structures, except for the bioclimatic belts which will move in elevation. Vegetation modifications would rather be determined by precipitation change. At a long term, thermo- and meso-Mediterranean species would extend in elevation, while cedar stands would locally disappear, possibly for the benefit of *Q. ilex*.

28.5.6 Effect of Climate Change on Fire Disturbance Regime

Fire frequency and extent have already considerably increased since the 1960s in several Mediterranean countries, especially after the 1970s but the burned areas have decreased since 1985 in the Mediterranean Basin as a whole (Shakesby 2011; Pausas and Fernández-Muñoz 2012). Some countries however have been particularly fire-damaged, even after 1985. In Spain from 1960 to 1973, the mean annual burnt area was 50,000 ha and the annual number of fires less than 2000. From 1974 to 1998, the mean annual burnt area increased to 215,000 ha and the annual number of fires to 8550 (Pausas and Vallejo 1999). In Portugal, the annual burnt area, the total number of fires and the number of big fires (above 20,000 ha) have all dramatically increased after 1983, especially during the period 2000–2004 with more than 930,000 ha burnt, of which almost 450,000 ha in the sole year 2003 (Marques et al. 2011). In Greece from 2000 to 2007 and in France from 1976 to 2006, drought related tree mortalities coincided with very severe fire outbreaks (Nageleisen et al. 2010; Sarris et al. 2011). The main factor of increase at the regional scale has been the socio-economic changes that have occurred during the second half of the twentieth century, namely abandoned lands and tourism pressure. However, prolonged drought and hot periods have increased the risk of fires, making climate an efficient contributing factor when temperature is high, air dry and fuel moisture low (Piñol et al. 1998; Pausas and Vallejo 1999; Moriondo et al. 2006; Shakesby 2011). Moreover, trees killed by drought or by pathogens and insects attacks favored by water stress, increase the quantity of fuel.

During the twenty-first century, the socio-economic aspects will still be the main causes of fire, but climate will become increasingly favorable. Under the optimistic (RCP2.6) scenario of CO_2 increase, little change should be observed in forest susceptibility to fires in Southern Europe, but changes are believed to be very substantial under scenario RCP8.5, with both a higher number of fire danger days and a longer fire season, resulting in an increase of the burned areas by a factor of 3 to 5 compared to present (Kovats et al. 2014; Settele et al. 2014). Moreover, the increase of fire frequency could compromise forest natural restoration. In France for example, it has been estimated that the turnover of fires at a given place would change in forest from 72 years (present average) to 62 years in 2100, and from 20 to 16 years in low vegetation. This will make natural restoration of forests impossible in many cases, possibly resulting in a decrease of more than half of the French Mediterranean forested area (Nageleisen et al. 2010). Forest structure on the northern rim will thus depend on fire recurrence (Mouillot et al. 2002; Pausas 1999b) (Fig. 28.10). With a low frequency of fires, forests should be dominated by oaks and pines. Increase in fire frequency should result in decrease of those species for the benefit of fire-tolerant shrubs and, in case of high fire recurrence (frequency less than 20 years), in a very low abundance or even absence of oaks and pines. Such a tendency in fire increase should not be observed in the southern rim of the Mediterranean Sea because traditional land-uses should remain the major socio-economic system (Pausas and Vallejo 1999). Similarly to the Mediterranean Basin, in California, a

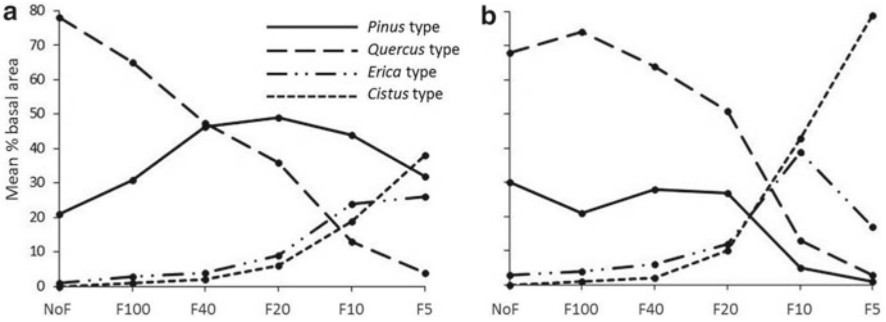

Fig. 28.10 Simulation of the evolution of four woody plant functional types in Mediterranean ecosystems under various regimes of fire frequency, with (**a**) or without (**b**) possible dispersal from the surrounding vegetation (10 replicated simulations for 500-year). *NoF* no fire, *F100* fire every 100 year, *F40* fire every 40 year, *F20* fire every 20 year, *F10* fire every 10 year, *F5* fire every 5 years (From Pausas (1999b), modified, with permission of "John Wiley and Sons" (CCA licence 3630270508920))

doubling of CO_2 would increase fire events by 40–50 % (Fried et al. 2004), leading broad-leaved trees to replace needle-leaved trees and grasses to replace trees (Lenihan et al. 2003).

28.6 Consequences for Forest Insect Communities and Biological Characteristics of Future Pests

28.6.1 General Considerations

As an important component of forest ecosystem functions, insect communities are concerned by disturbances in forest, and there are now large evidences that forest herbivorous insects have already been affected in the various aspects of their population dynamics by climate change (Netherer and Schopf 2010). Insects are ectothermic and are thus highly sensitive to temperature, which makes this factor the dominant climatic parameter affecting insects, but makes also insects able to quickly respond to temperature change (Bale et al. 2002). Insects are also among the species the most susceptible to landscape disturbances and fragmentation (Sanways 1998) accompanying climate change. Consequently, all aspects of their biology will be concerned at both individual and population levels. However, insects have the possibility to phenotypically and genetically put up with temperature change thanks to several particularities of their biology, such as short live cycles (with sometimes several generations per year), high reproductive capacities and high mobility, making them potentially able to profit from climate change (Ayres and Lombardero 2000). Species with currently a wide latitudinal distribution are especially favored because, through their different local populations, they are already submitted to large temperature variations over their natural range, and are thus pre-adapted to cope with temperature change, contrary to localized species (Bale et al. 2002). From this standpoint, Mediterranean species, which generally have a rather limited distribution, seem particularly vulnerable to climate change, especially if they are in mountains.

Since responses to climate change are species-specific for all kind of organisms, there will necessary be important differences between responses of trees and responses of insects, mainly as consequence of different length of life cycle and different mobility. As a result, the relationships between trees and phytophagous insects will be often deeply affected. In addition, the different guilds of phytophagous insects have different strategies to exploit their host trees, which themselves use various strategies of resource allocation. Tree insect relationships are thus expected to be affected in much diversified ways depending on both insect guilds and tree species.

Climate change can affect insect communities directly, especially through temperature change (warmer winter, longer warm season, temperature level moving towards optimum) and extreme events, or indirectly through modifications of their relationships with host trees (phenology, quality and resistance) and associated organisms (competitors, enemies, mutualists, symbionts) (Ayres and Lombardero 2000; Rouault et al. 2006; Hance et al. 2007; Netherer and Schopf 2010, among others). Direct effects as well as indirect effects through changes in host tree phenology and quality (including resistance) are rather well documented. Indirect effects though impacts on predators and parasitoids have also been often considered, but very few attempts have been made to study indirect effects through impact on other associated organisms. Indirect effects on all associated organisms must however be studied if we need to accurately predict climate induced changes in populations of forest insect pests. It is a very complex approach as several trophic levels interfere, each involving both qualitative and quantitative species specific responses to climate change, together with possible adaptations to new hosts (Ayres and Lombardero 2000; Rouault et al. 2006; Hance et al. 2007). Moreover, data and predictions mainly concern temperate and boreal regions, from which it is not easy to extrapolate to the Mediterranean forests because of the particularities of that area (Sects. 28.2 and 28.3). Summer temperatures and droughts for example may cause serious problems to both insects and trees in Mediterranean areas, but not necessarily in temperate and boreal forests, where they could be favorable to insects. In the followings, we shall thus mainly use examples from the Mediterranean areas, while considering direct effects on abundance, phenology and dispersal, and indirect effects through host tree. Then, possible consequences of climate change for the biodiversity of forest insects will be discussed.

28.6.2 Changes in Abundance of Indigenous Insect Species as Direct Effects of Climate Change

Predictions for temperature change in the Mediterranean Basin are warmer winters and warmer and drier summers (Sect. 28.4). In general, temperature is favorable to insects through accelerating larval development and thus increasing voltinism in addition to effect of earlier spring flights (Sect. 28.6.3). All those effects contribute to population increase and eventually to more frequent and heavier damage. This is typically the case of bark beetles, where high population levels are necessary to reach the critical threshold of attack densities above which trees defenses are overcome (Berryman 1976; Raffa and Berryman 1983; Christiansen et al. 1987; Lieutier 2004). In the Mediterranean Basin, such a scenario can occur with several polyvoltine bark beetle species, such as *O. erosus*, but also with the much more dangerous monovoltine species *T. destruens* of which the number of sister broods depends on temperature (Lieutier et al. 2015). However, with a higher number of individuals in a population there is a risk of competition lowering performances such as mean weight and individual fecundity. Moreover, in other species than bark beetles, if warmer winter temperatures can favor insect survival they could also disturb winter diapause possibly resulting in negative effects on populations. In addition, one may wonder about the effect of warmer and drier summers on summer generations in a region already characterized by warm and dry summers (Sect. 28.2.1). Would a strong selection pressure favor establishment of a summer diapause in species which do not already have this adaptation? Even in case of already existing summer diapause, temperature increase may be a problem if the timing is modified. The case of the pine processionary moth *T. pityocampa* can illustrate that situation. Larval feeding and maturation of that insect taking place in winter, increase of winter temperature has accelerated larval development. As a result now, summer pupal diapause takes place earlier and the young larvae hatch earlier than some decades ago, submitting them to important mortalities when, as in 2003 at low elevation in France, summer temperatures are still too high at the time of their hatching, a phenomenon which never occurred some decades ago (Bouhot-Delduc 2005; Robinet et al. 2013). Consequently, accelerating development and increasing generation number does not necessarily mean heavier damage.

There are several examples in the Mediterranean Basin, where forest insect populations have been directly favored by temperature increase, leading to increased damage to forests. In North Africa, attacks on *Cedrus atlantica* by Tortricidae have increased only since the last 30 years (Mouna 2013), possibly as a result of climate change. In Algeria, according to Chakali and Ghelem (2008), repeated droughts during the last decades, in addition to the bad sanitary status of oak stands, have played an important role in population dynamics of *Lymantria dispar*. In France, the number of damage reports involving *C. florentinus* has increased between 1989 and 2013 following droughts, although not limited to the Mediterranean area and possibly related to weakened trees (Sallé et al. 2014 and Fig. 28.11). According to Rouault et al. (2006), the oak leaf roller *Tortrix viridana* could benefit from increased spring temperature. Originally limited to Mediterranean areas, damage by the poplar wooly aphid *Phloeomyzus passerinii* have extended north, mainly due to the emergence of local populations previously contained at low population levels and now benefiting from temperature increase (Lieutier et al. 2014). Similarly, other Mediterranean insect species at endemic population levels and which do not cause any damage presently, could take advantage of temperature increase, eventually combined with tree weakening, arrival of new host trees and modifications of the forest composition, to reach high population levels and become emerging pest species. However,

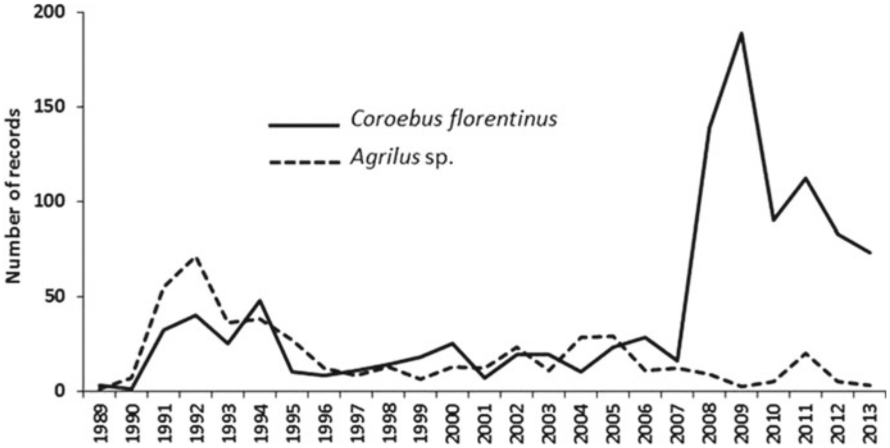

Fig. 28.11 Variation of the number of damage records involving the jewel beetles *Coroebus florentinus* and *Agrilus* sp. (Buprestidae) on oaks from 1989 to 2013 and relation with droughts (From Sallé et al. (2014), modified, with permission of Elsevier)

since their biology has not been studied in details, the factors involved in their population dynamics are completely unknown, making thus impossible to predict which species will become a pest. Leaf miners, defoliators, sap suckers, seed insects, phloem or wood borers are all candidates. Some of these species could even shift from a rare, endangered and even protected status to a pest status. As an example, the longhorn beetle *C. cerdo* living on various broadleaved trees is presently strictly protected everywhere in Europe, although its status varies from rare (northern Europe) to common in some localities of southern Europe (Evans et al. 2004). However, it is considered as a real pest of oaks in North Africa (Bouhraoua et al. 2002). Certainly, temperature increase and water stress on trees, together with change in sylvicultural methods will favor significant increases of its populations on both the southern and the northern rim of the Mediterranean Sea.

Storms, which have become more frequent and should continue to increase (Sect. 28.4), can provide an abundant source of fresh food for bark beetles and other xylophagous insects, favoring the increase of their populations. Depending on their frequency, these extreme events, combined with high beetle voltinism, could allow permanent high levels in bark beetle populations, leading them to overcome tree resistance and to kill healthy trees over large areas, as it has already occurred several times in temperate Europe (Grégoire and Evans 2004, among others). However, storms can also have positive effect on insect biodiversity, by providing large numbers of dead trees and thus offering a diversity of habitats for a number of xylophagous and saproxylic species, among which several endangered and protected ones (Speight et al. 1999; Vallauri et al. 2005).

Fires also are predicted to be more frequent and extended in the Mediterranean areas, at least in the context of a severe scenario of CO_2 increase (Sect. 28.5.6). In the Mediterranean basin, several xylophagous insect species, mostly bark beetles,

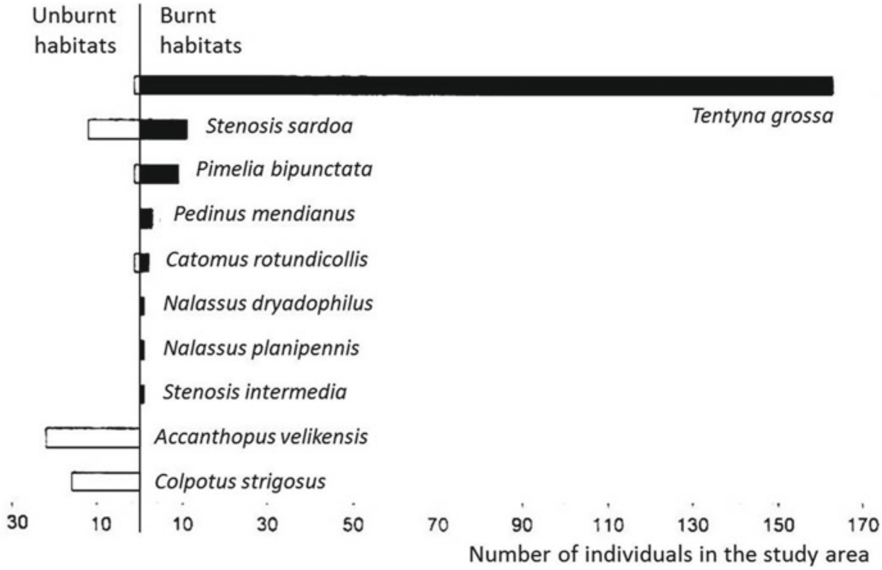

Fig. 28.12 Short term effect of fire on a Tenebrionid community in a *Pinus pinea* stand in central Italy (From Fattorini (2010), modified)

have frequently been observed killing fire damaged pines (Fernandez Fernandez 2006; Santolamazza-carbone et al. 2011) (Sect. 28.3). If fires become more frequent and more extended, one may fear an increase of their populations, possibly leading to damage on trees which survived the fire. In return, tree mortality caused by bark beetles can create higher fuel levels resulting in fires of greater intensity and frequency. However, predators of bark beetles have also been reported to be attracted by fire-damaged trees at about the same ratio as bark beetles, and oleoresin flow also increases in trees with scorched bole (Santoro et al. 2001). A modulation of bark beetle population increase by predators and tree resistance mechanisms may thus interfere, possibly avoiding a permanent high level of bark beetle populations after a fire, but this may depend on fire frequency. The longhorn beetle *Arhopalus rusticus*, reported to cause low damage in Italy and Portugal (Evans et al. 2004), is also known to cause mortality in fire-damaged pines in Sweden (Ehnström et al. 1995). It could thus be favored if fire frequency and intensity increase in the Mediterranean areas. Fires can also result in changing the structure of insect communities. Both positive and negative short term consequences on biodiversity have been reported. In Turkey, a fire in a *P. brutia* forest induced important changes in the structure of the buprestid communities, with immediate increase of species richness and total abundance (Kaynas and Gurkan 2005), in relation to the feeding habits of these insects which live upon weakened trees and branches. These effects decreased along with successional age. Fire effects can however be opposite for communities with different feeding habits. In Central Italy, important short term changes with strong biodiversity decrease have been reported in the structure of tenebrionid communities after a severe fire in *P. pinea* plantations (Fattorini 2010) (Fig. 28.12). Forest can recover from fire and beetle communities can come back to their original structure if fire frequency stays low, but changes can become definitive in case of high fire frequency. Insect communities will also evidently depend on the changes induced by the frequency of fires in the forest structure regarding both the dominant trees and the dominated woody and herbaceous species (Sect. 28.5.6 and Fig. 28.10).

28.6.3 Changes in Insect Phenology as Direct Effects of Climate Change

Phenological coincidence with their host plant is essential for the survival of phytophagous insects, particularly for specialists (Van Asch and Visser 2007). This is especially true when a particular insect stage must feed on a particular type of plant organ at a particular stage of development. A well-documented example among defoliators of the northern rim of the Mediterranean Sea is the green oak leafroller *T. viridana* in oak forests of southeastern France. Overwintering is spent at egg stage and hatching of the young neonate larvae in spring must coincide with budburst to ensure larval survival, leading to large between year variations in population levels, depending if spring temperature allows or does not allow the phenological coincidence (Du Merle 1988, 1993) (Fig. 28.13).

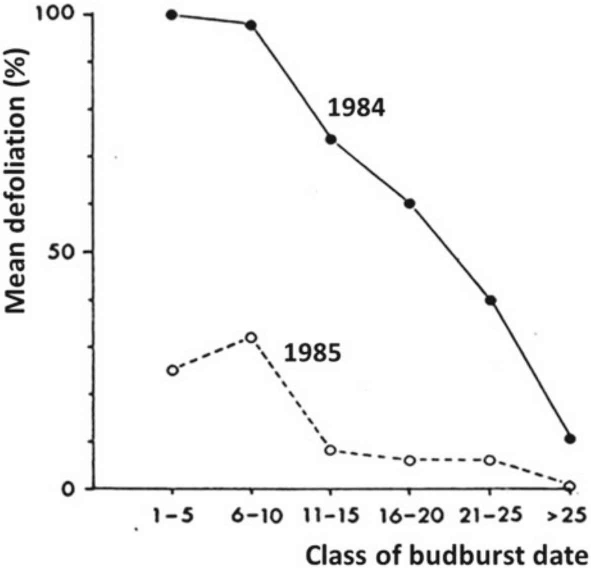

Fig. 28.13 Defoliation of *Quercus ilex* by the green oak leafroller *Tortrix viridana* (Tortricidae) in southeastern France, in relation to phenological coincidence between budburst dates and egg hatching. In 1984, contrary to 1985, a good coincidence led to heavy damage. Whatever the year, early budburst allowed a higher coincidence with egg hatching than late budburst (From Du Merle 1988, modified)

Such disruptions of plant-insect interactions occur when interacting species respond differently to temperature variations (Parmesan 2006). Each species indeed reacts to temperature variations according to the thermal sensitivity of its metabolic rate, that is according to the value of its Q_{10} (Berg et al. 2010). According to Berg et al. (2010), the Q_{10} of plants (herbs and trees together) would average about 1.3 (extreme 1.1–1.6) while that of foliar insects would average 3 (extreme 2.2–4.5), thus contributing to explain the existence of asynchronies in responses to warming. In these conditions, global warming can result in dramatic effects on the populations of specialized phytophagous insects. *A priori*, phenological changes could be negative for the insects if the result is an asynchrony with the usual host trees, possibly leading to regression of indigenous pests, or positive if the result is a phenological coincidence with new hosts, possibly leading to the emergence of new indigenous pests. However, mainly negative effects have been reported. According to Singer and Parmesan (2010), disruptions between phytophagous insects and their host plants could have been the rule for a long time and could have existed already prior the beginning of the industrial period. Considering that possibility, the present climate warming would increase the vulnerability of phytophagous insects. Insect phenological changes may also be considered as adaptations to climate warming, species unable to adjust their phenological behavior through preadapted individuals being negatively affected, especially in highly seasonal habitats. Similarly, changes in plant phenology may allow preadapted phytophagous species (indigenous or exotic) to exploit new empty niches, opening on novel tree-insect relationships and possibly to new pests, especially if similar adaptations of natural enemies are delayed (Harrington et al. 2001).

Many shifts in phenology have already occurred over recent decades for phytophagous insects (Bale et al. 2002; Parmesan 2006; Menéndez 2007; Van Asch and Visser 2007; Robinet and Roques 2010, among others). However, most reports concern temperate and boreal ecosystems, very few the Mediterranean ecosystems, and almost none Mediterranean forest insects. In Mediterranean localities, although phenology of all organisms has advanced since the 1970s, insect phenology has advanced much faster than plant phenology, possibly causing asynchrony in plant-insect interactions (Gordo and Sanz 2005). First appearance and spring flights occur earlier. A study carried out on 35 Spanish butterfly species concluded that their advance was three times more important than the advance of the first flowering of herbs (Parmesan 2007). Another study in the same country showed that all kinds of butterfly species and families were concerned by that earlier activity, univoltine as well as multivoltine, whatever the overwintering stage (Stefanescu et al. 2003). Similar observations have been made in the Central Valley of California, with however more important changes for species overwintering as pupae rather than larvae (Forister and Shapiro 2003). Because each species responds individually to temperature increase (cf. above), large among species differences can occur even in a same locality and in a same insect guild, for both the date of first appearance and the date of flight. For example in 15 years, depending on species, the first appearance of Spanish butterflies has advanced by 2–6.2 weeks and their mean dates of flight by

1.5–4 weeks (Stefanescu et al. 2003). In most studies, insect phenological modifications result directly from effects of the climate parameters, such as for the Californian butterflies where variation in changing dates can be mainly explained by increase of winter and spring temperatures and decrease in winter precipitations. However, indirect effects might also be concerned through food availability, as for seed insects where population fluctuations can be in agreement with the periodicity of seed production through prolonged diapause (Turgeon et al. 1994).

Questions also arise from phenological modifications in trees. Since uncoupling can occur between different tree functions such as unfolding, flowering and fruiting in a same tree species (Peñuelas et al. 2002; Vennetier et al. 2011) (Sect. 28.5.4), one may wonder about the consequences for the associated phytophagous insects. Will they change their phenology the same way as their host tree organ? Unfortunately, no data exist on changes in phenology of phytophagous insects associated with different tree organs. Other questions relate to the possible consequences of climate-induced alteration in masting for the cone and seed insects. In the study reported by Martinez-Alonso et al. (2007), cone production was advanced by 1 year, making it to occur 2 years after the previous cone production instead of 3 years (Sect. 28.5.4). As the incidence of prolonged diapause in seed insects largely vary among insects, cones, trees, and localities (Turgeon et al. 1994), it is very difficult to determine what could have been for them the consequences, positive or negative, of the masting alteration.

28.6.4 Changes in Range and Dispersal of Indigenous Insect Species as Direct Effects of Climate Change

Climatic envelopes based on temperature can be used to foresee the potential insect range shifts as result of climate warming. However, the same restrictions as for trees apply. In addition to climate factors, interspecific relationships such as competition, predation or parasitism, and the presence or absence of possible host plants also interfere in modifications of insect ranges, as well as obstacles to migrations, be they natural or resulting from human actions such as landscape fragmentation. As for trees also, changes in insect ranges are species specific. Moreover, even if changes in temperature seem to be a very important factor for ectothermic terrestrial animals, especially when considered at the regional level, the role of other climate factors such as precipitations may be essential in some situations. Nevertheless, owing to its predominant role among all climate factors affecting insects, temperature has most been often considered in studies related to changes in insect range. The present section is thus developed based on the role of temperature, while taking into account biological interactions through the relationships between phytophagous insects and their host trees. More complex interactions will be presented in Sect. 28.7.

It is well recognized that climate change has led to rapid modifications of the range of many insect species following relatively low temperature variations, and several studies in all continents and latitudes have reported that certain species have already shifted their range by several 10 s of km in latitude or hundreds of meters in elevation over the last decades (Walther et al. 2002, among others). If temperate insect species seem limited in their distribution more by summer heat availability than by lethal extreme temperatures (Bale et al. 2002), certainly for Mediterranean insects, both parameters interfere. Indeed, if as for temperate insects, lethal cold temperatures are not a limiting factor for Mediterranean insects, on the contrary lethal extreme summer temperatures can be reached at low elevation, whereas summer heat availability limits extension in elevation. The pine processionary moth is a demonstrative example of that situation (Sects. 28.3 and 28.6.2). Temperature increase can directly favor insect dispersion though two main complementary ways: reaching the temperature threshold for flight earlier in spring, and allowing flight during a longer period (Menendez 2007). For example, the flight temperature threshold of *T. destruens* and *T. piniperda* is 12 °C and, because the beetles are already mature in their overwintering sites, spring flight dates vary according to the date of reaching this threshold (Lieutier et al. 2015). In the Italian Alps, the summer 2003 heat wave allowed the temperatures to frequently and largely exceed the threshold for nocturnal flight of the pine processionary moth females (14 °C), leading to a considerable upward shift of the range limit (Battisti et al. 2005, 2006, and see below). For polyvoltine species, increasing the number of generations can allow the range limit to efficiently advance through successive “jumps”.

According to Parmesan et al. (1999), a range shift occurs when there is net extinction at the warm boundary or net colonization at the cold boundary. As consequences of the temperature limiting effects presented above for Mediterranean insects, the shifts in distribution of these insects should typically occur through both phenomena, especially in mountains. This is in agreement with the expectations of Netherer and schopf (2010) that forest phytophagous insect populations in Southern Europe should shift northwards together with range contractions on their southern limit. Several such examples are presented below. However, physiological characteristics of the insect can modulate the effect of temperature increase. For example, fast growing, non diapausing species and those which do not depend on low temperature to induce diapause would be able to rapidly shift northwards or upwards at both their leading and trailing edges, whereas slow growing species and those needing low temperature to induce diapause would experience range contraction on their trailing edge (Bale et al. 2002). Both situations can indeed be met in the Mediterranean Basin, even in the same insect genus. The cedar processionary moth *T. bonjeani* with its winter diapause belongs to the second case, making probable a range contraction at its lower range limit although it could extend in altitude as cedar is expected to do. Oppositely, *T. pityocampa* belongs to the first case. It does not have a winter diapause but a summer pupal diapause which usually allows avoiding high summer temperatures (Huchon and Demolin 1970). As a consequence, it has already shown a rapid extension in both latitude and elevation (see below). In fact all situations seem possible, at least according to temperate and boreal observations, with both edges moving northwards/upwards, only the leading edge moving with the trailing edge staying the same, or no moving for the leading edge with contraction at the warm edge (Menendez 2007). Shifting in elevation is a frequent possible response of the Mediterranean insects to climate warming because they often live in rather topographically perturbed regions. But, as for trees, moving upward means decrease and loss of habitats and thus range contraction, possibly leading at term to species extinction (Sect. 28.6.6). For 16 butterfly species in Central Spain, Wilson et al. (2005) have shown that species distribution has risen by 212 ± 60 m in 30 years. Meanwhile however, one third of the habitat area has been lost, and this drastic range contraction is foreseen to continue during the twenty-first century, inducing a loss of habitat of 50–80 %. The situation should become even more dramatic for species already restricted to cool localizations and which have already shown severe range contractions (Parmesan 2006), as it is the case for insects associated with *J. thurifera* in several mountain tops in the Moroccan High Atlas (Fig. 28.8).

Insects generally have high dispersal capacities which should allow them to most often track climate change, even under severe scenarios of CO_2 increase, at least in elevation (Settele et al. 2014). While rising up their lower distribution limit by more than 200 m in 30 years, the 16 butterfly species studied in mountains of Central Spain by Wilson et al. (2005) have exactly followed their isotherm and thus have successfully tracked climate change. Indeed, during the same period, temperature has increased by 1.3 °C, an equivalence of 225 m in elevation. But shifting upward is easier than northward because distances between isotherms in elevation are much shorter than in latitude. In a study on European butterflies over the 1990–2008 period, Devictor et al. (2012) have calculated that the northward climatic debt of butterflies was 135 km behind climate. In both upwards and northwards however, most phytophagous insects disperse much farther than their host plants (Kinlan and Gaines 2003; Berg et al. 2010; Settele et al. 2014) (Fig. 28.14). On the front edge of their extension, the presence of host plants is evidently a decisive factor for phytophagous insects, and thus, while evaluating the range extension of forest insects, the availability of their host trees must be taken into consideration, in addition to distribution of suitable climate space, especially for specialists (Merrill et al. 2008). Although not a forest insect, the case of the butterfly *Aporia crataegi* perfectly illustrates the role of host plant. In Central Spain, the warm range limit of this species has shifted upward since the 1970s, but the leading edge has stayed at the same elevation although suitable space exists and temperatures has become favorable, a situation explained by the absence of host plants at higher elevation (Merrill et al. 2008).

Owing to the differences between the dispersal capacities of trees and those of their phytophagous insects, the situation in which both the warm range margin and the cold range margin of the insect shift upward/northward defines two particular areas: a trailing area where the phytophagous insect has disappeared but where its usual host tree is still present, and a leading area where the insect can have dispersed but where its usual host tree may be present or absent. In the trailing area, one can imagine that damage could decrease as result of the spatial discordance between the original insect and its usual host tree. However, empty niches in trees weakened by climate conditions would rather become rapidly occupied by a local insect species previously limited by interspecific competition or by a new arriving insect species,

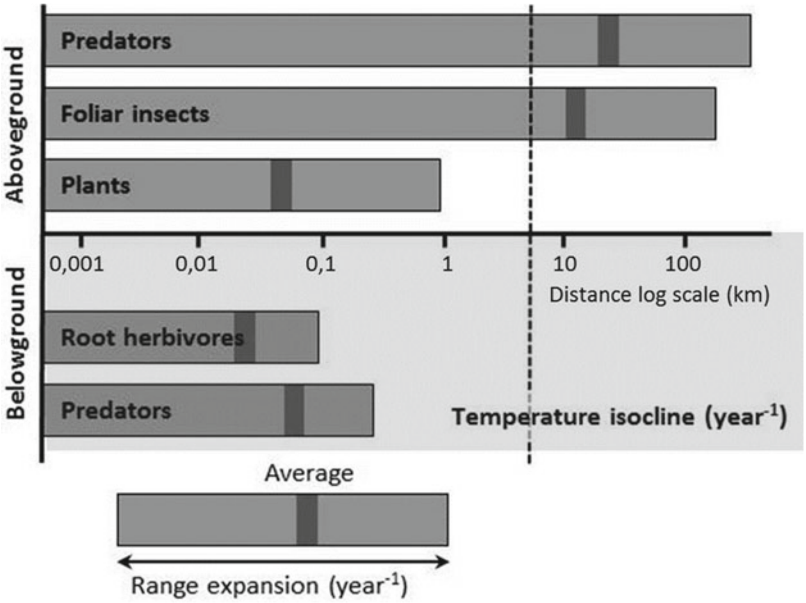

Fig. 28.14 Differential latitudinal dispersal rates in organisms, compared with annual displacement distance of temperature isocline (From Berg et al. (2010), modified, with permission of "John Wiley and Sons" (CCA licence 3630331056146))

causing new kinds of damage which would progressively shift upward/northward with the trailing edge of original insect. In the leading area, the shifting insect may find its normal host if that one has a wide natural distribution or has been planted in programs of human-assisted migration, but may also shift on a new host, especially if its usual host is absent. Shifting on a new host will obviously create new tree-insect interactions. However if the usual host is present and especially if it has been planted, its relationships with the environment will have changed, possibly leading to changes in insect attraction and defense mechanisms (Harrington et al. 2001; and Sect. 28.6.5). In both cases thus, deep modifications of tree-insects relationships will occur, possibly associated with insect genetic differentiation, making climate an indirect factor of speciation. Relationships with other species will also be modified, possibly for the benefit of the shifting insect, especially through escaping natural enemies, as already reported (Menendez et al. 2008). In all cases, new species interactions and new communities will thus be built in the leading area. These possible scenarios in the trailing and the leading areas potentially concern all Mediterranean tree species susceptible to extend northwards or upwards: *P. pinaster*, *P. nigra laricio*, *P. halepensis*, *P. brutia*, the Mediterranean oaks, *Cedrus*, *Tilia*, *Eucalyptus* and other exotic drought resistant species.

There is no known example of the scenarios proposed in the trailing area, but several examples of the scenarios of the leading area have been reported for the Mediterranean Basin, with presence of the usual host as well as with shifting on a

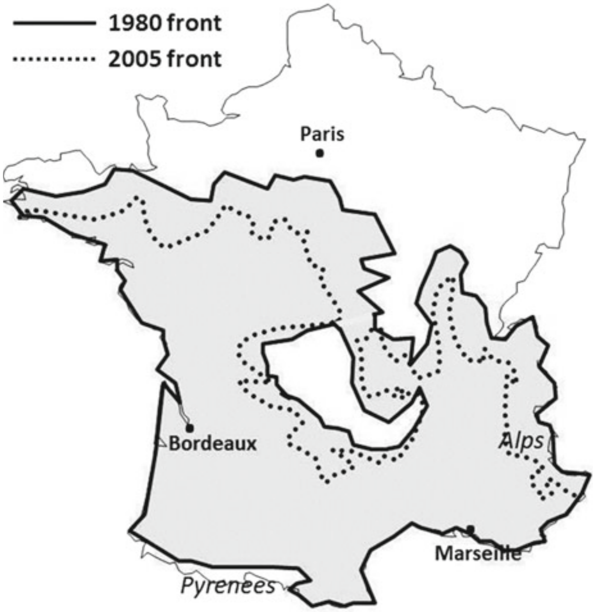

Fig. 28.15 Expansion range of the pine processionary moth *Taumetopoea pithyocampa* in France from 1979 to 2005 (From Robinet et al. (2007), modified, with permission of "John Wiley and Sons" (CCA licence 3630270986817))

new host. In Northern Italy, at the southern border of the European Alps and the southern range margin of spruce forests, *I. typographus* altitudinal outbreak range has significantly shifted upwards in the spruce stands during the last 15 years (Marini et al. 2012). Certainly however, the best known example of climate-induced range shift both in elevation and in latitude of an originally Mediterranean insect, with usual host species already being present in the leading area, is that of the pine processionary moth *T. pityocampa*. This insect has extended in elevation by 110–230 m in Northern Italy from 1975 to 2004, and by 87 km northwards in France from 1979 to 2004, of which 55.6 km during the last 10 years (Battisti et al. 2005; Robinet et al. 2007) (Fig. 28.15).

This rapid expansion is due to increase of winter temperature, both releasing thermal thresholds allowing better larval survival and enhancing feeding activity (Battisti et al. 2005; Robinet and Roques 2010). The altitudinal expansion perfectly illustrates the mechanisms of extension, especially during the 2003 heat wave, with effect of winter temperatures both facilitating the expansion (through temperature increase at lower elevation) and limiting it (through too cold temperatures in higher elevation) (Battisti et al. 2005, 2006). The situation is however different regarding the mechanisms involved in the latitudinal extension at low elevation, where high summer temperatures such as those of 2003 can stop the extension through lethal effects on the young larvae (Bouhot-Delduc 2005; Robinet et al. 2013) (Sect. 28.6.2).

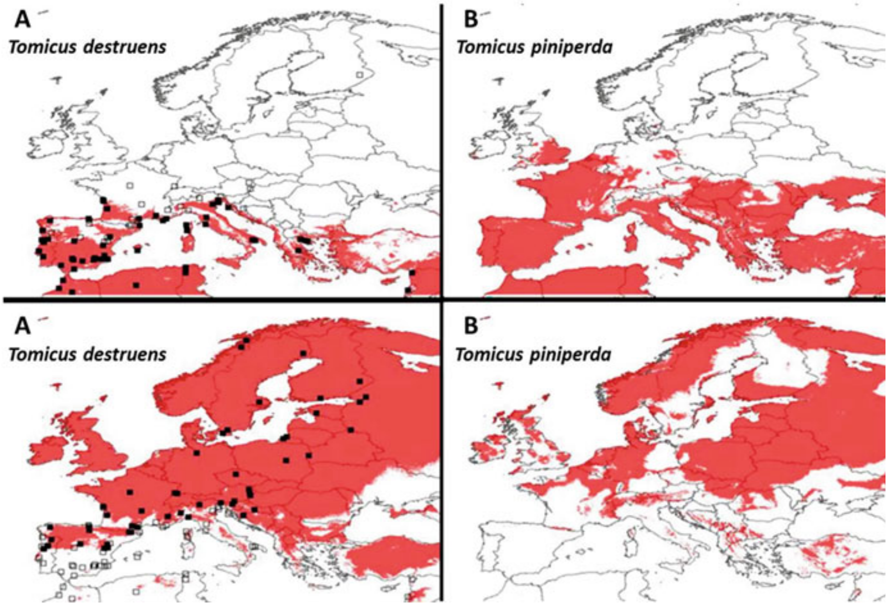

Fig. 28.16 Potential distribution area of the bark beetles *Tomicus destruens* and *Tomicus piniperda*, based on temperature requirements of each species. (**a**) Potential present distribution area; (**b**) potential distribution area in 2080 under the A2 scenario of CO_2 emission of the IPCC (From Horn et al. (2014), with permission)

This example illustrates the necessity to consider the whole insect life cycle and all seasons when estimating the effect of a warmer world on insects, and demonstrates that a same climatic event can have very different effects depending on topographic and local conditions. It also illustrates the necessity of considering not only the average variations of the climatic parameters, but also the extreme events and their frequency (Robinet et al. 2013).

The bark beetle *T. destruens* is an excellent example of possible northward extension with host change. This insect is presently localized mainly in the Mediterranean Basin but, in some localities of the Northern rim, it occurs sympatrically with *T. piniperda* of which the range extends all over the European temperate and boreal areas, these distributions corresponding to the thermic needs of the two species (Horn et al. 2012) (Fig. 28.16a). However, temperature increase is predicted to deeply affect the competition between these species, while making the northern edge of *T. destruens* range to move northward at the expenses of the warmer edge of *T. piniperda* range (Horn et al. 2014) (Fig. 28.16b). This will lead *T. destruens*, presently feeding upon Mediterranean pines, to develop upon new pine species perfectly suitable for it but presently not available because located in region where temperatures are too low for this beetle (Horn et al. 2014). During the last decades as result of temperature rising and probably of host weakening due to decrease in precipitations, *C. florentinus*, a thermophilic insect initially specialized on Mediterranean oak species, has extended its range until south-west Germany where it develops now upon temperate oaks, and is predicted to continue its northward expansion in the future (Buse et al. 2013). Similar observations have been made with *C. undatus* present in warm locations in Germany (Evans et al. 2004). A genetically different population of its usual host can also be found by the expanding insect in its leading area, possibly resulting in damage in case of higher susceptibility. In southern Spain, global warming has allowed *T. pityocampa* to invade the endemic stands of *P. sylvestris* ssp. *nevadensis* located at the trees upper limit (2100 m) in the Sierra Nevada. As a result these stands, uninjured until now because of low winter temperatures limiting larval development, are presently experiencing a significant decrease of trees' growth rate and very low seed production, threatening the survival of this endemic and relic tree subspecies (Hódar et al. 2003).

28.6.5 Indirect Effects of Climate Change Through Modification of Host Tree Quality, Resistance and Attractiveness

Drought and high temperatures can potentially affect any plant process, with consequences for phytophagous insects mainly through tree nutritive quality, resistance and attractiveness (Rouault et al. 2006). Meanwhile, insect will be affected in various ways, depending on the nature and intensity of the stresses and their combination, the plant tissue they feed upon, and their host range (specialists or generalists) (Koricheva et al. 1998a; Zvereva and Kozlov 2006; Jactel et al. 2012). Drought and high temperatures can alter water, carbohydrates and nitrogen content in trees with a possible increase of nutritional value of tree tissues (Rouault et al. 2006; Zverera and Koslov 2006; Jactel et al. 2012). CO_2 and temperature increase can however also stimulate carbon assimilation and tree growth and alter carbon allocation pattern, leading to modification of nutrient balance and concentration of secondary metabolites, with often decrease in nutritional quality of tree tissues and increase in concentration of metabolites involved in tree resistance. The result could be an increase of insect feeding to compensate the decrease of tree nutritional quality, with reduction of their fitness through slow development and small size (Lincoln et al. 1993; Bezemer and Jones 1998). Many studies have considered climate parameters separately, but there are interactions between the various climate factors regarding effects on tree-insect interactions. For example, in a meta-analysis on experimental studies considering only two climate parameters, CO_2 and temperature, Zvereva and Kozlov (2006) have shown that, depending on tree tissues and species responding to CO_2 increase, modifications of compounds involved in tree defenses could be independent of temperature, mitigated by temperature, or could occur only under a combination of both CO_2 increase and temperature increase. In fact, several modified climate parameters interfere in combination, to change tree metabolism through complex processes. Simultaneously, these combined climate parameters directly affect insects (Sects. 28.6.2, 28.6.3 and 28.6.4) that are facing the modifications of their host trees. In addition, both chemical responses of plants to climate parameters and corresponding modifications in insect performances are species specific (Lindroth et al. 1993; Jones and Hartley 1998). The consequences are complex deep modifications of the tree-insect interactions which are thus, not surprisingly, difficult to apprehend, even without taking into account the role of upper trophic levels also affected by climate change.

Water stress effect on tree resistance to insects has been the subject of many studies. It is agreed now that water stress has complex and sometimes opposed effects on tree resistance depending not only on insect guilds but also on its intensity. According to various hypotheses, water stress intensity can modulate plant allocations to secondary metabolites, leading to a diversity of effects on tree resistance (Stamp 2003, and references therein). A mild drought could concentrate nitrogen and thus favor defoliators, whereas intermediate and severe droughts could decrease leaf content and concentration in secondary metabolites and thus negatively affect defoliators (Mattson and Haack 1987; Koricheva et al. 1998b; Rouault et al. 2006; Netherer and Schopf 2010). However, very few examples in these hypotheses concern Mediterranean insects. From meta-analyses on effect of stresses (Koricheva et al. 1998a) and drought (Jactel et al. 2012) on damage to trees, it has been concluded that damage by primary insects living on foliar organs such as chewing and galling insects would be favored, damage by primary insects living on woody organs such as sucking and boring insects would be disfavored, and damage by secondary insects living on woody organs such as bark beetles would be disfavored by a mild stress but favored by an intense stress. However, most studies used in these meta-analyses relate to insects of temperate or boreal forests, where extreme climate situations similar to those frequently occurring in the Mediterranean areas are not necessarily reached. Even, there are several cases where these conclusions seem not to apply to Mediterranean insects.

Among such Mediterranean counter-examples, in southern Europe at the occasion of the severe drought of 1990–1995, a strong and sudden negative correspondence has been observed in 1994–1995 between drought effects on *Q. ilex* and impact of insect defoliations (Carnicer et al. 2011), which has been interpreted as result of chemical modifications in trees (Fig. 28.17). Similarly, in a field comparison of performances of various insects in naturally water stressed and in controlled watered Scots pine in Southeastern France, it has been reported a slower development of the pine processionary larvae and a lower survival of its colony on stressed trees (Roques et al. 2002). Responses of most secondary wood borers such as bark beetles (and their associated fungi) to water stressed trees seem however most often in agreement with the conclusions of the meta-analyses. Moderate water stress increased pine resistance to *Leptographium wingfieldii*, a fungus associated with *T. destruens* and *T. piniperda*, whereas a severe water stress decreased it (Croisé and Lieutier 1993; Croisé et al. 2001; Dreyer et al. 2002; Lieutier 2004). Following the severe drought of 1988 in Greece, the volume of bark beetles killed trees in fir forests in 1989 represented 4.3 % of the existing growing stock and 2.2 times the annual yield for the country (Markalas 1992). Similarly, during the severe 2003

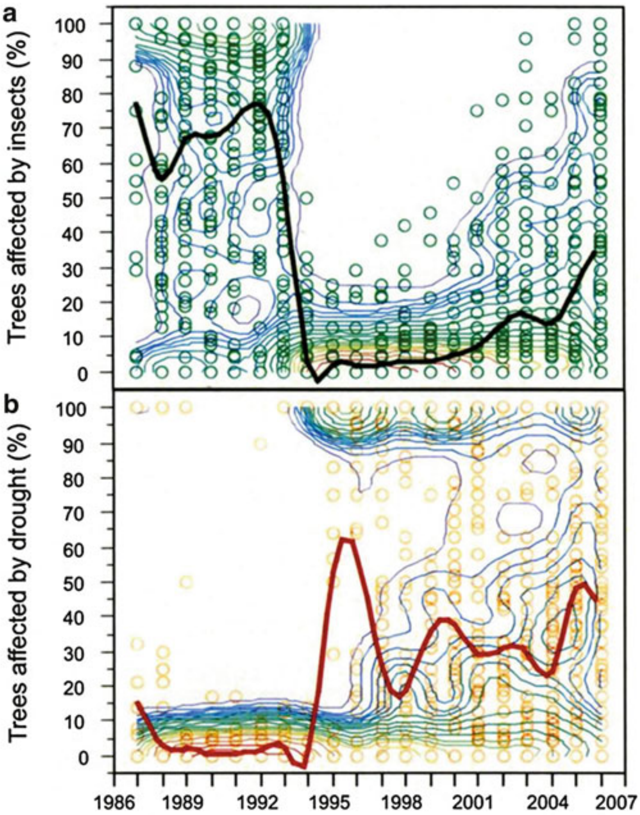

Fig. 28.17 Evolution of the percentage of trees affected by insect defoliations (**a**) and the percentage of trees affected by drought (**b**) in the Iberian Peninsula from 1986 to 2007, for *Quercus ilex*, the most widespread tree species in Southern Europe. *Dots* represent sampled plots. Their density is provided by a smooth surface. Red contour lines indicate maximum point density. Spline fits describe the temporal variation in the percentage of affected trees (From Carnicer et al. (2011), with permission)

drought in France, woodborers were positively influenced by prolonged water stress and the decline of host resistance (Rouault et al. 2006). In North Africa, water stress on Cedar trees benefits to *Phaenops marmottani* (Ghaioule and Lieutier 2009) (Sect. 28.7). Nevertheless, *Phoracantha* species in *Eucalyptus* do not agree with the conclusions of the meta-analyses since both too dried and too moist tree tissues are detrimental to larval success of *P. semipunctata* or *P. recurva* (Hanks et al. 1999; Haddan et al. 2010).

Because tree resistance to secondary wood borers in general and bark beetles in particular can increase or decrease depending on water stress severity, the climatic and topographic heterogeneity of the Mediterranean ecosystems will probably lead to a mosaic of opposite effects of water stress on tree resistance, resulting in a mosaic of beetle populations with different levels. One may however wonder about the stability of such a situation. Moreover, since tree response to water stress is species specific, the threshold of stress severity below which tree resistance increases and above which it decreases is also species specific. Consequently, it is difficult to predict the effect of precipitation change on tree resistance (Sallé et al. 2014). However, with the predicted increasing droughts in the Mediterranean areas (Sect. 28.4), certainly the threshold of stress severity will be reached in most tree species and damage by secondary pest insects are likely to increase. In a global study of drought and heat-induced tree mortality, it has been shown that xylophagous insects are generally associated with tree mortality in Mediterranean ecosystems but that they generally do not have a primary role (Allen et al. 2010). However, outbreaks and future damage can be predicted if repeated drought and heat occur. For example, damage by the buprestids *C. florentinus* (on various oaks and chestnut-trees), *C. undatus* (on holm and cork oaks) and *Melonophila picta* (on poplars and willows), insects that are presently mainly located in the Mediterranean area (Evans et al. 2004), could increase in that region and possibly extend to other European regions. In the same context, damage by *Cerambyx welensii* (= *C. velutinus*), presently located on weakened holm and cork oaks in the Iberian Peninsula (Evans et al. 2004), could also extend.

Water stress and other environmental factors can also affect emissions of volatile organic compounds (VOCs) from trees (Rouault et al. 2006; Yuan et al. 2009). Owing to the basic ecological functions played by these compounds at all level of the tritrophic interactions (plant-plant, insect-insect and plant-insect relationships), climate change could deeply modify the ecosystem functioning (Yuan et al. 2009). Again, most results considering impact of climate change on VOCs refer to temperate or boreal insects and plants, but there is no reason to think that their functions will not be impacted in Mediterranean forest ecosystems. However, effects of climate factors on VOCs emissions seem to largely vary, sometimes even in opposite directions, depending on compounds, tree species and importance of the climate stress for trees, and the consequences for insect behavior and performances have not been tested in the field. Regarding Mediterranean trees, mild water storages have been reported to enhance terpene emissions by leaves of *Q. ilex* and *Q. suber* but drastic storages decreased them (Bertin and Staudt 1996; Staudt et al. 2002, 2008; Plaza et al. 2005). Mono- and sesquiterpene emissions by leaves of young *C. sempervirens* considerably increased during the first 2 months of a 4-month water stress experiment, α-pinene, β-pinene and sabinene being particularly concerned, while limonene was affected to a lesser extent (Yani et al. 1993). Studying under field conditions a diversity of Mediterranean woody species including *Q. coccifera*, *Q. ilex*, *A. unedo* and *P. halepensis*, Llusià and Peñuelas (2000) observed that total terpene emission and that of most individual terpenes (especially α-pinene and β-pinene), were positively correlated with temperature variations (although not for *Q. coccifera*). Interestingly however, no correlation existed between emission of limonene and temperature. Knowing that α-pinene and β-pinene are generally considered insect-attractants whereas limonene is often a deterrent, all these observations may be of particular importance for modifying tree-insect communication systems.

28.6.6 Effects of Climate Change on Forest Insect Biodiversity Through Extinctions and Invasions

Global biodiversity has already considerably decreased as result of the combined effect of climate change and human impacts (Settele et al. 2014). Whatever the considered scenarios, CO_2 increase will not stop before at least several decades and will continue to be accompanied by important other human impacts, partly as result of climate change itself. As a consequence, the twenty-first century is predicted to be characterized by an unprecedented decrease of biodiversity, especially in the Mediterranean areas, where both climate change and human impacts are particularly important (Sala et al. 2000; Bellard et al. 2012; Settele et al. 2014). For a global mean temperature increase of 2–3 °C above pre-industrial levels, approximately 20–30 % of the plant and animal species could disappear (Fischlin et al. 2007) and probably more in the Mediterranean areas. Modifications in land use (especially habitat fragmentation) are the main consequences of the combined impact of climate change and human actions. Especially, fragmentation resulting from range contraction could be the cause of local extinctions by reducing dispersion possibilities (Hill et al. 2011). Landscape modifications deeply change competition and other species interactions, which in general interfere in any extinction process and which would be the main cause of population decline and extinction (Norberg et al. 2012; Cahill et al. 2013). The adaptation of insects of Mediterranean ecosystems to live in small areas may modulate species disappearance (Sanways 1998), but the high level of narrow endemism in these regions may result in the disappearance of species if modifications occur in their locality, a risk conceivable especially if climate modifications are spatially heterogeneous.

Local extinctions are important at low elevation and southern edges (Berg et al. 2010). Searching for causes other than habitat loss in extinction of Italian butterfly and zygaenid populations, Bonelli et al. (2011) concluded that populations at their range edges were particularly exposed to extinctions. In addition, even if they have the possibility to move in altitude, mountain species which cannot adapt locally are particularly exposed to extinction at their upper edge because of reduction in their habitat area (Sect. 28.6.4). Temperature increase may also finally push them out of the limits of their environmental needs and host range, leading them to extinction, as it is at risk for insects of cedar and thurifer juniper in North Africa.

Alien invasive species are predicted to widely change in distribution as a result of climate change which, in general, increases the chance of establishment, growth, spread and survival of invasive species (Walther et al. 2009; Smith et al. 2012). There are several possible explanations of this facilitation of exotic species. Contrary to indigenous species expanding in response to climate change or facing environmental change in their natural area, most invasive species are not necessarily limited by climate conditions (Hill et al. 2011). Temperature increase can positively affect the per-capita reproductive capacity of the populations introduced at a low density, helping them to overcome the Allee effect (Robinet and Roques 2010). Introduced species can also occupy empty niches left by indigenous populations which have moved or disappeared. Climate change can also enable alien insect species to invade new areas, extending from the areas where they had been previously introduced (Walther et al. 2009; Huang et al. 2011; Bradley et al. 2010; Smith et al. 2012). In the Mediterranean Basin, that has been the case for the palm weevil *Rhynchophorus ferrugineus* introduced from Melanesia and which stayed much localized at low population level during many years, before recently expanding over areas (Roques 2010)., Climate change can also allow indigenous species to expand their natural range into new areas, eventually causing extensive damage to trees, as in the case of the bark beetles *D. ponderosae* and *D.rufipennis* in Northern America (Raffa et al. 2008; Bentz et al. 2010).

28.7 Conclusions: Forest Insect Communities and Insects' Damage as Result from Complex Interactions

For practical reasons, climate factors have been most often analyzed separately for their effects on insects, but climate change effects on insects and their interactions with other organisms result from several climate parameters varying simultaneously and not always in the same direction. For example, Zverera and Kozlov (2006) have indicated that temperature can modulate CO_2 effects in one direction or another (Sect. 28.6.5). Interactive effects of temperature and drought are especially important but have been rarely studied (Jamieson et al. 2012). In addition, variability of climatic factors and their extremes are also important, especially for tree and insect phenology as well as insect abundance and range extensions. The case of the pine processionary moth presented in Sect. 28.6.2 is particularly demonstrative of that situation. Acceleration of larval development allowed by mild winter led to stopping the species northwards expansion at low elevation because of too high summer temperatures in 2003, while the same heat wave had positive effects in the Alps, with important altitudinal expansion due to increased flight possibilities of adults (Battisti et al. 2005, 2006; Robinet et al. 2010).

In most cases, several parameters related not only to climate but also to human actions, as well as biotic factors interfere in complex biological systems. The dieback of *C. atlantica* in the Middle Atlas of North Africa is a first example which gives an idea of the complex interactions interfering between climate change, tree resistance, tree competition for water, and insect population increase. After several years of controversial theories, it seems now clear that the primary causal factor of that dieback is a long term precipitation deficit that has occurred since the beginning of the 1980s although the first tree mortalities were observed in 1994–1995 (Et-Tobi 2008; Benziane et al. 2010). This water deficit has created a permanent water stress in cedars, exacerbated by competition for water among cedars as well as between cedars and the green oak *Q. ilex*, which most often cohabit in the same stands (Mokrim 2009; Et-Tobi et al. 2009; Chouraichi 2009; Zine El Abidine and Aadel 2009; Ghailoule et al. 2014). The final result has been a dramatic weakening of *C. atlantica*, at the benefit of green oaks, leading to cedar death, often accelerated by the successful establishment of the secondary jewel beetle *Phaenops marmottani* (Ghaioule and Lieutier 2009; Benziane et al. 2010). In complement to temperature increase, this has led the populations of that insect to increase, allowing it to successfully attack a large number of trees, and making it to be sometimes wrongly considered as the main dieback factor, the more as the first stages of cedar dieback are very difficult to observe (Mouna 2013). In the dieback of the cork-oak *Q. suber*, climate change interferes together with several human factors in a complex insect system. The dieback began in the 1980s in the whole Mediterranean area. *S*everal factors among which modifications of climate and water cycle, fires, pollution, and inadequate forest management are involved, allowing *Platypus cylindrus*, a secondary Platypodidae, to take advantage of the deterioration of the physiological status of its host tree *Q. suber*, often accompanied by phytopathogenic fungi (Sousa and Debouzie 2002; Sousa et al. 2008). The dieback is especially important in many stands located in semi-arid areas (Bouhraoua et al. 2002), which proves the role of climate, but human factors are also decisive. The case of bark beetle outbreaks represents a third situation in which climate change can interfere in a complex community of organisms. Most bark beetle species are associated with a diversity of fungal and mite species which form a community of organisms of which all members play a particular role from the beginning of tree attack to tree death (Klepzig and Six 2004; Lieutier et al. 2009). Mainly through temperature, climate can affect growth and assemblage composition of this associated fauna and microflora, and hence beetle aggressiveness. In the Mediterranean Basin, *T. destruens* and *O. erosus* are associated with several Ophiostomatoid species (Lieutier et al. 2002; Ben Jamâa et al. 2007), and each of them has specific thermal requirements (Lieutier and Yart 1989). Consequently, temperature increase will certainly affect fungal species differently, causing modifications of species assemblages, as already demonstrated for the fungal flora and mite fauna associated with *D. frontalis* (Hofstetter et al. 2007; Six and Bentz 2007). Owing to the essential role played by fungal complexes in beetle-tree interactions (Klepzig and Six 2004; Lieutier et al. 2009), modifications in nutrition and aggressiveness of bark beetles must follow.

More generally, climate change induces modifications at the community and ecosystem levels. The responses of organisms to each of the climate parameters differ among guilds and species. These species specific non coordinated responses in survival, development, phenology and expansion are responsible for deep modifications in species interactions involving all trophic levels (competition, parasitism, predation, mutualism, symbioses), which in turn also cause modifications in population ecology. The conjunction of such direct and indirect effects of climate change makes any coevolution impossible and makes the bases of the ecosystem functioning to be drastically disturbed, leading to new species interactions and thus to building of new ecosystems. As constituents and actors of ecosystem functioning, insects are basically concerned by these changes. Many recent papers have detailed and emphasized the importance of these mechanisms as general consequences of climate change for ecosystems structure and functioning (Ayres and Lombardero 2000; Bale et al. 2002; Thomas and Blanford 2003; Rouault et al. 2006; Hance et al. 2007; Parmesan 2007; Tylianakis et al. 2008; Netherer and Schopf 2010; Gilman et al. 2010; Berg et al. 2010; Montoya and Raffaelli 2010; Jamieson et al. 2012; Cahill et al. 2013; among others). The concepts developed in those papers are mainly based on examples from temperate and boreal ecosystems but their generality makes the conclusions to fully apply to Mediterranean forest ecosystems.

As discussed in Sect. 28.6, some possible consequences of climate change for insect ecology and damage in Mediterranean forest ecosystems can be foreseen, based on the existence of the present forest pests. However, the predicted overthrow in ecosystems functioning will certainly lead to the involvement of new factors in the population dynamics of forest insects. This new control will probably allow the emergence of new forest pests of which we cannot even suspected the nature presently. Even if relatively few data are available on climate impact on forest insects in Mediterranean ecosystems compared to temperate and boreal ecosystems, only research conducted at the community level could open on predictions in that field.

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References

Allen CD, Macalady AK, Chenchouni H et al (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manage 259:660–684

Andreu L, Guttierez E, Macias M et al (2007) Climate increases regional tree-growth variability in Iberian pine forests. Glob Chang Biol 13:804–805

Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci Total Environ 262:263–286

Badeau V, Dupouey JL, Cluzeau C et al (2004) Modélisation et cartographie de l'aire climatique potentielle des grandes essences forestières françaises. In: Projet CARBOFOR Séquestration de carbone dans les grands écosystèmes forestiers en France, Rapport final tâche D1, 49 pp

Bale JS, Masters GJ, Hodkinson ID et al (2002) Herbivory in global change climate research: direct effects of rising temperature on insect herbivores. Glob Chang Biol 8:1–16

Barbero M, Loisel R, Quézel P (1995) Les essences arborées des iles méditerranéennes: leur rôle écologique et paysager. Ecol Medit 21:53–59

Battisti A, Stastny M, Netherer S et al (2005) Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecol Appl 15:2084–2096

Battisti A, Stastny M, Bufo E et al (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. Glob Chang Biol 12:662–671

Bellard C, Bertelsmeier C, Leadley P et al (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377

Ben Jamâa ML, Lieutier F, Yart A et al (2007) The virulence of phytopathogenic fungi associated with the bark beetles *Tomicus piniperda* and *Orthotomicus erosus* in Tunisia. For Pathol 37:51–63

Bentouati A (2008) La situation du Cèdre de l'Atlas dans les Aurès (Algérie). Forêt Médit 24:203–208

Bentz BJ, Régnière J, Fettig CJ et al (2010) Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. Bioscience 60:602–613

Benziane M, Aafi A, Sbay H et al (2010) Les écosystèmes naturels marocains et les changements climatiques: la résilience écologique à l'épreuve. Centre de Recherche Forestière, Rabat

Berg MP, Kiers ET, Driessen G et al (2010) Adapt or disperse: understanding species persistence in a changing world. Glob Chang Biol 16:587–598

Berryman AA (1976) Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. Environ Entomol 5:1225–1233

Bertin N, Staudt M (1996) Effect of water stress on monoterpene emissions from young potted holm oak (*Quercus ilex* L.) trees. Oecologia 107:456–462

Bezemer TM, Jones TH (1998) Plant-insect herbivore interactions in elevated atmospheric CO_2: quantitative analyses and guild effects. Oikos 82:212–222

Bonelli S, Cerrato C, Loglisci N et al (2011) Population extinctions in the Italian diurnal Lepidoptera: an analysis of possible causes. J Insect Conserv 15:879–890

Bouhot-Delduc L (2005) La gradation de la chenille processionnaire du pin a culminé sur la façade atlantique lors de l'hiver 2003–2004. Bilan de la santé des forêts en 2004, Ministère de l'Agriculture, Paris, 7 pp

Bouhraoua RT, Villemant C, Khelil MA et al (2002) Situation sanitaire de quelques subéraies de l'ouest algérien: impact des xylophages. IOBC/WPRS Bull 25:85–92

Boydak M, Dogru M (1997) The exchange of experience and state of the art in sustainable forest management by ecoregion: Mediterranean forests. XIth World Forestry Congress report, Antalya, pp 179–205

Bradley BA, Blumenthal DM, Wilcove DS et al (2010) Predicting plant invasions in an era of global change. Trends Ecol Evol 25:310–318

Buse J, Griebeler EM, Niehuis M (2013) Rising temperatures explain past immigration of the thermophilic oak-inhabiting beetle *Coroebus florentinus* (Coleoptera: Buprestidae) in southwest Germany. Biodivers Conserv 22:1115–1131

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC et al (2013) How does climate change cause extinction? Proc R Soc B Biol Sci 280:20121890

Cahill AE, Aiello-Lammens ME, Fisher-Reid MC et al (2014) Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. J Biogeogr 41:429–442

Cailleret M, Nourtier M, Amm A et al (2013) Drought-induced decline and mortality of slver fir differ among three sites in Southern France. Ann For Sci 71:643–657, doi: 10.100713595-013-0265-0

California Mediterranean Research Learning Center (2010) National Park Service, US Department of the Interior. http://www.researchlearningcenter.com/pages/about.html

Cardenas AM, Gallardo P (2012) The effect of temperature on the preimaginal development of the Jewel beetle, *Coraebus florentinus* (Coleoptera: Buprestidae). Eur J Entomol 109:21–28

Carle P (1975) Problèmes posés par les ravageurs xylophages des conifères en forêt méditerranéenne. Rev For Fr 27:283–296

Carnicer J, Coll M, Ninyerola M et al (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proc Natl Acad Sci U S A 108:1474–1478

Chakali G, Ghelem M (2008) Etat sanitaire des subéraies en Algérie. Ann Rech For Maroc 39:93–99

Charru M, Seynave I, Morneau F et al (2010) Recent changes in forest productivity: an analysis of national forest inventory data for common beech (*Fagus sylvatica* L.) in north-eastern France. For Ecol Manage 260:864–874

Cheaib A, Badeau V, Boe J et al (2012) Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty. Ecol Lett 15:533–544

Chouraichi M (2009) Evaluation de la relation entre les paramètres physiques, chimiques et hydriques du sol et le dépérissement du Cèdre dans la région du Moyen Atlas et élaboration de l'indice de sensibilité du Cèdre au dépérissement. Ann Rech For Maroc 41:78–94

Christiansen E, Waring RH, Berryman AA (1987) Resistance of conifers to bark beetle attack: searching for general relationships. For Ecol Manage 22:89–106

Cleland EE, Chuine I, Menzel A et al (2007) Shifting plant phenology in response to global change. Trends Ecol Evol 22:357–365

Conlisk E, Lawson D, Syphard AD et al (2012) The roles of dispersal, fecundity, and predation in the population persistence of an oak (*Quercus engelmannii*) under global change. PLoS One 7:e36391

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Cook BI, Wolkovich EM, Parmesan C (2012) Divergent responses to spring and winter warming drive community level flowering trends. Proc Natl Acad Sci U S A 109:9000–9005

Cox CB, Moore PD (2005) Biogeography. An ecological and evolutionary approach, 7th edn. Blackwell, Malden

Croisé L, Lieutier F (1993) Effect of drought on the induced defence reaction of Scots pine to bark beetle associated fungi. Ann Sci For 50:91–97

Croisé L, Lieutier F, Cochard H et al (2001) Interactive effect of drought stress, and high density stem-inoculations with *Leptographium wingfieldii*, on hydraulic properties of young Scots pine trees. Tree Physiol 21:427–436

Dale VH, Joyce LA, McNulty S et al (2001) Climate change and forest disturbances. BioScience 51:723–734

Della-Marta PM, Haylock MR, Luterbacher J et al (2007) Doubled length of western European summer heat waves since 1880. J Geophys Res 112:D15103

Devictor V, van Swaay C, Brereton T et al (2012) Differences in the climatic debts of birds and butterflies at a continental scale. Nat Clim Chang 2:121–124

Dobrowski SZ, Abatzoglou J, Swanson AK et al (2013) The climate velocity of the contiguous United States during the 20th century. Glob Chang Biol 19:241–251

Dreyer E, Guérard N, Lieutier F et al (2002) Interactions between nutrient and water supply to potted *Pinus sylvestris* trees and their susceptibility to several pests and pathogens. In: Lieutier F (ed) Effects of water and nutrient stress on pine susceptibility to various pest and disease guilds, Final scientific report of the EU project FAIR 3 CT96-1854, Manuscript sent to the European Commission, Brussels, pp 63–81

Du Merle P (1988) Phenological resistance of oaks to the green oak leafroller, *Tortrix viridana* (Lepidoptera: Tortricidae). In: Mattson WJ, Lévieux J, Bernard-Dagan C (eds) Mechanisms of woody plant defenses against insects: search for pattern. Springer, New York, pp 215–226

Du Merle P (1993) Peuplements forestiers et insectes ravageurs. In: Oswald H (ed) Rencontres Forestiers-Chercheurs en Forêt Méditerranéenne, Les Colloques, vol 63. INRA Editions, Versailles, pp 75–87

Du Merle P, Attié M (1992) *Coroebus undatus* (Coleoptera: Buprestidae) sur chêne liège dans le Sud-Est de la France: estimation des dégâts, relations entre ceux-ci et certains facteurs du milieu. Ann Sci For 49:571–588

Du Merle P, Brunet S, Cornic JF (1992) Polyphagous potentialities of *Choristoneura murinana* (Hb.) (Lept. Tortricidae): a monophagous folivore extending its host range. J Appl Entomol 113:18–40

Edenhofer O, Pichs-Madruga R, Sokona Y et al (2014) Technical summary. In: Edenhofer O, Pichs-Madruga R, Sokona Y et al (eds) Climate change 2014: mitigation of climate change: contribution of Working Group III to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge/New York

Ehnström B, Långström B, Hellqvist C (1995) Insects in burned forests – forest protection and faunal conservation (preliminary results). Entomol Fenn 6:109–117

Espírito-Santo MM, Fernandes GW (2007) How many species of gall-inducing insects are there on earth, and where are they? Ann Entomol Soc Am 100:95–99

Et-Tobi M (2008) Inventaire dendrométrique et phytosanitaire des cédraies d'Azrou et Ait Youssi Lamekla. In: Etude des causes du dépérissement de la cédraie du Moyen Atlas (Ifrane), Convention FAO/UTF/MOR028 – HCEFLCD, Maroc

Et-Tobi M, Mhirit O, Benziane M (2009) Changements climatiques, dégradations et dépérissements: arguments et nouveaux outils pour une réforme de la sylviculture des cédraies au Maroc. Ann Rech For Maroc 41:27–47

Evans HF, Moraal LG, Pajares JA (2004) Biology, ecology and economic importance of Buprestidae and Cerambycidae. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer, Dordrecht, pp 447–474

Fabre JP, Mouna M, Du Merle P et al (1999) Le point sur certains ravageurs du Cèdre de l'Atlas en Afrique du Nord, en France et en Europe. Forêt Médit 20:203–218

Fattorini S (2010) Effects of fire on tenebrionid communities of a *Pinus pinea* plantation: a case study in a Mediterranean site. Biodiv Conserv 19:1237–1250

Fernandes GW, Price PW (1992) The adaptive significance of insect gall distribution: survivorship of species in xeric and mesic habitats. Oecologia 90:14–20

Fernandez Fernandez MM (2006) Colonization of fire-damaged trees by *Ips sexdentatus* (Boerner) as related to the percentage of burnt crown. Entomologica Fenn 17:381–386

Ferreira MC, Ferreira GS (1987) Impacte de fogo nos escolitídeos associados com Pinheiro bravo. Floresta 4–5:12–14

Fischlin A, Midgley GF, Price JT et al (2007) Ecosystems, their properties, goods, and services. In: Parry ML, Canziani OF, Palutikof JP et al (eds) Climate change 2007: impacts, adaptation and vulnerability, Contribution of Working Group II to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 211–272

Forister ML, Shapiro AM (2003) Climatic trends and advancing spring flight of butterflies in lowland California. Glob Chang Biol 9:1130–1135

Fried JS, Torn MS, Mills E (2004) The impact of climate change on wildfire severity: a regional forecast for Northern California. Clim Change 64:169–191

Gea-Izquierdo G, Viguera B, Cabrera M et al (2014) Drought induced decline could portend widespread pine mortality in the xeric ecotone in managed Mediterranean pine-oak woodlands. For Ecol Manage 320:70–82

Ghailoule D, Rossi JP, Lieutier F (2014) Spatio-temporal characterization of cedar (*edrus atlantica* Manetti) dieback in two stands of the Moroccan Middle Atlas: preliminary results. Ann INRGREF 17:145–156

Ghaioule D, Lieutier F (2009) Dépérissement du Cèdre et relations avec les facteurs biologiques dans le Moyen Atlas. Ann Rech For Maroc 41:69–77

Gilman SE, Urban MC, Tewksbury J et al (2010) A framework for community interactions under climate change. Trends Ecol Evol 25:325–331

Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. Glob Planet Chang 63:90–104

Girard F, Vennetier M, Guibal F et al (2012) *Pinus halepensis* Mill. Crown development and fruiting declined with repeated drought in Mediterranean France. Eur J For Res 131:919–931

Gordo O, Sanz JJ (2005) Phenology and climate change: a long-term study in a Mediterranean locality. Oecologia 146:484–495

Gordo O, Sanz JJ (2010) Impact of climate change on plant phenology in Mediterranean ecosystems. Glob Chang Biol 16:1082–1106

Grégoire JC, Evans HF (2004) Damage and control of BAWBILT organisms, an overview. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer, Dordrecht, pp 19–37

Haddan M, Sauvard D, Lieutier F (2010) Tree factors in relation to success of artificial introductions of *Phoracantha recurva* larvae in various *Eucalyptus* species in Morocco. Redia 93:19–30

Hance T, van Baaren J, Vernon P et al (2007) Impact of extreme temperatures on parasitoids in a climate change perspective. Annu Rev Entomol 52:107–126

Hanks LM, Paine TD, Millar JG et al (1999) Water relations of host trees and resistance to the phloem-boring beetle *Phoracantha semipunctata* F. (Coleoptera: Cerambycidae). Oecologia 119:400–407

Harrington R, Fleming RA, Wolwod I (2001) Climate change impacts on insect management and conservation in temperate regions: can they be predicted? Agric For Entomol 3:233–240

Hickler T, Vohland K, Feehan J et al (2012) Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Glob Ecol Biogeogr 21:50–63

Higgins SI, Clark JS, Nathan R et al (2003) Forecasting plant migration rates: managing uncertainty for risk assessment. J Ecol 91:341–347

Hill JK, Griffiths HM, Thomas CD (2011) Climate change and evolutionary adaptations at species' range margins. Annu Rev Entomol 56:143–159

Hódar JA, Castro J, Zamora R (2003) Pine processionary caterpillar *Thaumetopoea pityocampa* as new threat for relict Mediterranean Scots pine forests under climatic warming. Biol Conserv 110:123–129

Hoff C, Rambal S (2000) Les écosystèmes forestiers méditerranéens. CEFE, Montpellier

Hofstetter RW, Dempsey TD, Klepzig KD et al (2007) Temperature-dependent effects on mutualistic, antagonistic, and commensalistic interactions among insects, fungi and mites. Community Ecol 8:47–56

Horn A, Kerdelhué C, Lieutier F et al (2012) Predicting the distribution of the two bark beetles *Tomicus piniperda* and *T. destruens* in Europe and the Mediterranean region. Agric For Entomol 14:358–366

Horn A, Kerdelhué C, Lieutier F et al (2014) Modelling the geographic distributions of the two bark beetles *Tomicus destruens* and *Tomicus piniperda* in Europe and in the Mediterranean region. Ann INRGREF 17:157–171

Huang D, Haack RA, Zhang R (2011) Does global warming increase establishment rates of invasive alien species? A centurial time series analysis. PLoS One 6:1–5

Huchon H, Demolin G (1970) La bioécologie de la processionnaire du Pin. dispersion potentielle – dispersion actuelle. Rev For Fr 22:220–234

Hulme M, Doherty R, Ngara T et al (2001) African climate change: 1900–2100. Climate Res 17:145–168

Jactel H, Petit J, Desprez-Loustau ML et al (2012) Drought effects on damage by forest insects and pathogens: a meta-analysis. Glob Chang Biol 18:267–276

Jamieson MA, Trowbridge AM, Raffa KF et al (2012) Consequences of climate warming and altered precipitation patterns for plant-insect and multitrophic interactions. Plant Physiol 160:1719–1727

Jeong SJ, Ho CH, Gim HJ et al (2011) Phenology shifts at start vs. end of growing season in temperate vegetation over the Northern Hemisphere for the period 1982–2008. Glob Chang Biol 17:2385–2399

Jimenez A, Gallardo A, Antonietty CA et al (2012) Distribution of *Coraebus undatus* (Coleoptera: Buprestidae) in cork oak forests of southern Spain. Int J Pest Manag 58:281–288

Jones CG, Hartley SE (1998) Global change and plant phenolic concentrations: species level predictions using the protein competition model. In: De Kok LJ, Stulen I (eds) Respônses of plant metabolism to air pollution and global change. Backhuys, Leiden, pp 23–50

Kaynas BY, Gurkan B (2005) Changes in Buprestidae (Coleoptera) community with successional age after fire in a *Pinus brutia* forest. J Pest Sci 78:53–55

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proc Natl Acad Sci U S A 105:11823–11826

Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007–2020

Klepzig KD, Six DL (2004) Bark beetle–fungal symbiosis: context dependency in complex associations. Symbiosis 37:189–205

Koricheva J, Larsson S, Haukioja E (1998a) Insect performance on experimentally stressed woody plants: a meta-analysis. Annu Rev Entomol 43:195–216

Koricheva J, Larsson S, Haukioja E et al (1998b) Regulation of woody plant secondary metabolism by resource availability: hypothesis testing by means of meta-analysis. Oikos 83:212–226

Körner C, Sarris D, Christodoulakis D (2005) Long-term increase in climatic dryness in the East-Mediterranean as evidenced for the island of Samos. Reg Environ Chang 5:27–36

Kovats RS, Valentini R, Bouwer LM et al (2014) Europe. In: Barros VR, Field CB, Dokken DJ et al (eds) Climate change 2014: impacts, adaptation, and vulnerability. Part B: regional aspects, Contribution of Working Group II to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge/New York, pp 1267–1326

Långström B, Hellqvist C, Ehnström B (1999) Susceptibility of fire damaged Scots pine (*Pinus sylvestris* L.) to attack by *Tomicus piniperda* L. In: Lieutier F, Mattson WJ, Wagner MR (eds) Physiology and genetics of tree-phytophage interactions. INRA Editions, Versailles, pp 299–311

Lavorel S (1999) Ecological diversity and resilience of Mediterranean vegetation to disturbance. Divers Distrib 5:3–13

Lenihan JM, Drapek R, Bachelet D et al (2003) Climate change effects on vegetation distribution, carbon, and fire in California. Ecol Appl 13:1667

Lenoir J, Gegout JC, Marquet PA et al (2008) A significant upward shift in plant species optimum elevation during the 20th century. Science 320:1768–1771

Lieutier F (2004) Host resistance to bark beetles and its variations. In: Lieutier F, Day KR, Battisti A et al (eds) Bark and wood boring insects in living trees in Europe, a synthesis. Kluwer, Dordrecht, pp 135–180

Lieutier F (2006) Changing forest communities: role of tree resistance to insects in insect invasions and tree introductions. In: Paine TD (ed) Invasive forest insects, introduced forest trees, and altered ecosystems. Springer, Dordrecht, pp 15–51

Lieutier F, Yart A (1989) Preferenda thermiques des champignons associés à *Ips sexdentatus* et *Tomicus piniperda* (Coleoptera Scolytidae). Ann Sci For 46:411–415

Lieutier F, Ghaioule D, Yart A et al (2002) Attack behavior of pine bark beetles in Morocco and association with phytopathogenic fungi. Ann Rech For Maroc 35:96–109

Lieutier F, Yart A, Sallé A (2009) Stimulation of tree defenses by Ophiostomatoid fungi can explain attack success of bark beetles on conifers. Ann For Sci 66:801, 22 p

Lieutier F, Pointeau S, Dardeau F et al (2014) Le puceron lanigère: les avancées de la recherché. Rev For Fr 66:25–40

Lieutier F, Långström B, Faccoli M (2015) The genus *Tomicus*. In: Vega FE, Hofstetter RW (eds) Bark beetles: biology and ecology of native and invasive species. Elsevier, Oxford, pp 371–426

Linares JC, Camarero JJ, Carreira JA (2009) Interacting effects of changes in climate and forest cover on mortality and growth of the southernmost European fir forests. Glob Ecol Biogeogr 18:485–497

Linares JC, Camarero JJ, Carreira JA (2010) Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. J Ecol 98:592–603

Lincoln DE, Fajer ED, Johnson RH (1993) Plant-insect herbivore interactions in elevated CO_2 environments. Trends Ecol Evol 8:64–68

Lindner M, Maroschek M, Netherer S et al (2010) Climate change impacts, adaptive capacity, and vulnerability of European forests ecosystems. For Ecol Manage 259:698–709

Lindroth RL, Kinney KK, Platz CL (1993) Response of deciduous trees to elevated atmospheric CO_2: productivity, phytochemistry, and insect performance. Ecology 74:763–777

Llusià J, Peñuelas J (2000) Seasonal patterns of terpene content and emission from seven Mediterranean woody species in field conditions. Am J Bot 87:133–140

Loarie SR, Duffy PB, Hamilton H et al (2009) The velocity of climate change. Nature 462:1052–1055

Lombardero MJ, Ayres MP (2011) Factors influencing bark beetle outbreaks after forest fires on the Iberian Peninsula. Environ Entomol 40:1007–1018

Lumaret JP, Ghaioule D, Maatouf N et al (2005) Initial data on the biology of *Sphodroxia maroccana* Ley (Coleoptera: Melolonthidae) and an estimation of the damage due to this new pest on cork-oak seedlings in the Mamora Forest (Morocco). In: Lieutier F, Ghaioule D (eds) Entomological research in Mediterranean forest ecosystems. INRA Editions, Paris, pp 139–145

Manes F, Vitale M, Donato E et al (2006) Different ability of three Mediterranean oak species to tolerate progressive water stress. Photosynthetica 44:387–393

Marini L, Ayres M, Battisti A et al (2012) Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. Clim Change 115:327–341

Mariotti A (2010) Recent changes in the Mediterranean water cycle: a pathway towards long term regional hydrological change? J Clim 23:1513–1525

Markalas S (1992) Site and stand factors related to mortality rate in a fir forest after a combined incidence of drought and insect attack. For Ecol Manage 47:367–374

Markalas S (1997) Frequency and distribution of insect species on trunks in burnt pine forests of Greece. Mitteil Schweizerischen Entomo Gesel 70:57–61

Marques S, Borges JG, Garcia-Gonzalo J et al (2011) Characterization of wildfires in Portugal. Eur J For Res 130:775–784

Martinez-Alonso C, Valladares F, Julio Camarero J et al (2007) The uncoupling of secondary growth, cone and litter production by intradecadal climatic variability in a Mediterranean Scots pine forest. For Ecol Manage 253:19–29

Martinez-Vilalta J, Piñol J (2002) Drought-indiuced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. For Ecol Manage 161:247–256

Matthews SN, Iverson LR, Prasad AM et al (2011) Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history-factors. For Ecol Manage 262:1460–1472

Mattson WJ, Haack RA (1987) The role of drought in outbreaks of plant-eating insects. Bioscience 37:110–118

McLachlan JS, Clark JS, Manos PS (2005) Molecular indicators of tree migration capacity under rapid climate change. Ecology 86:2088–2098

Meier ES, Lischke H, Schmatz DR et al (2012) Climate, competition and connectivity affect future migration and ranges of European trees. Glob Ecol Biogeogr 21:164–178

Mendel Z (1992) Occurrence of *Matsucoccus josephi* in Cyprus and Turkey and its relation to decline of Aleppo pine (Homoptera: Matsucoccidae). Entomol Gener 17:299–306

Mendel Z, Madar Z, Golan Y (1985) Comparison of the seasonal occurrence and behavior of seven pine bark beetles (Coleoptera: Scolytidae) in Israel. Phytoparasitica 13:21–32

Menendez R (2007) How are insects responding to global warming? Tijdschrift Entomol 150:355–365

Menéndez R, Gonzalez-Megias A, Lewis OT et al (2008) Escape from natural enemies during climate-driven range expansion: a case study. Ecol Entomol 33:413–421

Menzel A, Sparks TH, Estrella N et al (2006) European phenological response to climate change matches the warming pattern. Glob Chang Biol 12:1969–1976

Merrill RM, Gutiérrez D, Lewis OT et al (2008) Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. J Anim Ecol 77:145–155

Météo-France (2015) http://www.meteofrance.fr/climat-passe-et-futur/changement-climatique/simulateur-climatique

Mokrim A (2009) Dépérissement du Cèdre de l'Atlas: Ambiance climatique et bilan de la croissance radiale. Ann Rech For Maroc 41:48–68

Montoya JM, Raffaelli D (2010) Climate change, biotic interactions and ecosystem services. Philos Trans R Soc B 365:2013–2018

Moriondo M, Good P, Durao R et al (2006) Potential impact of climate change on fire risk in the Mediterranean area. Clim Res 31:85–95

Mouillot F, Ranbal S, Joffre R (2002) Simulating climate change impacts on fire frequency and vegetation dynamics in a Mediterranean-type ecosystem. Glob Chang Biol 8:423–437

Mouna M (2013) Les insectes du Cèdre de l'Atlas (*Cedrus atlantica* Manetti) dans le nord de l'Afrique, vol 48, Série zoologie. Travaux de l'Institut scientifique, Rabat

Munz PA, Keck DA (1968) A California flora. University of California Press, Berkeley, 1681 pp

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nageleisen LM, Piou D, Saintonge FX et al (2010) La santé des forêts. CNPF/IDF, Paris

Nathan R, Horvitz N, He YP et al (2011) Spread of North American wind-dispersed trees in future environments. Ecol Lett 14:211–219

Netherer S, Schopf A (2010) Potential effects of climate change on insect herbivores in European forests – general aspects and the pine processionary moth as specific example. For Ecol Manage 259:831–838

Norberg J, Urban MC, Vellend M et al (2012) Eco-evolutionary response of biodiversity to climate change. Nat Clim Chang 2:747–751

Paine TD, Steinbauer MJ, Lawson SA (2011) Native and exotic pests of *Eucalyptus*: a worldwide perspective. Annu Rev Entomol 56:181–201

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Syst 37:637–669

Parmesan C (2007) Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Glob Chang Biol 13:1860–1872

Parmesan C, Yohe G (2003) A globally coherent finger-print of climate change impacts across natural systems. Nature 421:37–42

Parmesan C, Ryrholm N, Stefanescu C et al (1999) Poleward shifts in geographical ranges of butterfly species associates with regional warming. Nature 399:579–583

Paula S, Arianoutsou M, Kazanis D et al (2009) Fire–related traits for plant species in the Mediterranean Basin. Ecology 90:1420, 20 p

Pauli H, Gottfried M, Dullinger S et al (2012) Recent plant diversity changes on Europe's mountain summits. Science 336:353–355

Pausas JG (1999a) Mediterranean vegetation dynamics: modelling problems and functional types. Plant Ecol 140:27–39

Pausas JG (1999b) Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: a simulation approach. J Veg Sci 10:717–722

Pausas JG, Fernández-Muñoz S (2012) Fire regime changes in the western Mediterranean Basin: from fuel-limited to drought-driven fire regime. Clim Change 110:215–226

Pausas JG, Vallejo VR (1999) The role of fire in Mediterranean ecosystems. In: Chuvieco E (ed) Remote sensing of large wildfires in the European Mediterranean Basin. Springer, New York, pp 3–16

Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). Glob Chang Biol 9:131–140

Peñuelas J, Lloret F, Montoya R (2001) Severe drought effects on Mediterranean woody flora in Spain. For Sci 47:214–218

Peñuelas J, Filella J, Comas P (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. Glob Chang Biol 8:531–544

Peñuelas J, Canadell JG, Ogaya R (2011) Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. Glob Ecol Biogeogr 20:597–608

Peñuelas J, Sardans J, Estiarte M et al (2013) Evidence of current impact of climate change on life: a walk from genes to the biosphere. Glob Chang Biol 19:2303–2338

Piñol J, Terradas J, Lloret F (1998) Climate warming, wild fire hazard, and wildfire occurrence in coastal eastern Spain. Climatic change 38:345–357

Plaza J, Nunez L, Pujadas M et al (2005) Field monoterpene emission of Mediterranean oak (*Quercus ilex*) in the central Iberian Peninsula measured by enclosure and micrometeorological techniques: observation of drought stress effect. J Geophys Res 110:1105

Price PW, Fernandes GW, Lara ACF et al (1998) Global patterns in local number of insect galling species. J Biogeogr 25:581–591

Quézel P, Barbero M (1989) Zonation altitudinale des strctures forestières de végétation en Californie méditerranéenne. Leur interprétation en fonction des méthodes utilisées sur le pourtour méditerranéen. Ann Sci For 46:233–250

Quézel P, Médail F (2003) Ecologie et biogéographie des forêts du bassin méditerranéen, Environmental series. Elsevier, Paris

Raffa KF, Berryman AA (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecol Monogr 53:27–49

Raffa KF, Aukema BH, Bentz BJ et al (2008) Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58:501–517

Rathgeber C, Guiot J, Roche P et al (1999) Augmentation de productivité du chêne pubescent en région méditerranéenne française. Ann For Sci 56:211–219

Robinet C, Roques A (2010) Direct impacts of recent climate warming on insect populations. Integr Zool 5:132–142

Robinet C, Baier P, Pennerstorfer J et al (2007) Modelling the effects of climate change on the potential feeding activity of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Notodontidae) in France. Glob Ecol Biogeogr 16:460–471

Robinet C, Rousselet J, Goussard F et al (2010) Modelling the range expansion of an urticating moth with global warming: a case study from France. In: Settele J (ed) Atlas of biodiversity risks – from Europe to the globe, from stories to the maps. Pensoft, Sofia, pp 82–83

Robinet C, Rousselet J, Pineau P et al (2013) Are heat waves susceptible to mitigate the expansion of a species progressing with global warming? Ecol Evol 3:2947–2957. doi:10.1002/ece3.690

Root TL, Price JT, Hall KR et al (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

Roques A (2010) Alien forest insects in a warmer world and a globalized economy: impacts of changes in trade, tourism and climate on forest biosecurity. N Z J For 40:77–94

Roques A, El Alaoui El Fels MA (2005) Overview of the arthropod fauna that colonises seed cones in the Mediterranean Basin. In: Lieutier F, Ghaioule D (eds) Entomological research in Mediterranean forest ecosystems. INRA Editions, Versailles, pp 59–78

Roques A, Raimbault JP, Garcia J et al (2002) Improvement of soil water and nutrient conditions in a dry and poor site of Scots pines and susceptibility to insects and pathogens. In: Lieutier F (ed) Effects of water and nutrient stress on pine susceptibility to various pest and disease guilds, Final scientific report of the EU project FAIR 3 CT96-1854, Manuscript sent to the European Commission, Brussels, pp 81–97

Rouault G, Candau JN, Lieutier F et al (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. Ann For Sci 63:613–624

Ruiz-Labourdette D, Nogués-Bravo D, Ollero HS et al (2011) Forest composition in Mediterranean mountains is projected to shift along the entire elevational gradient under climate change. J Biogeogr 35:1–15

Ruiz-Labourdette D, Schmitz MF, Pineda FD (2013) Changes in tree species composition in Mediterranean mountains under climate change: indicators for conservation planning. Ecol Indic 24:310–323

Rundel PW (1998) Landscpe disturbance in Mediterranean-type ecosystems: an overview. In: Rundel PW, Montenegro G, Jaksic FM (eds) Landscape disturbance and biodiversity in Mediterranean-type ecosystems, Ecological Studies Vol. 136, Springer, Berlin, pp 3–22

Sala OE, Chapin IFS, Armesto JJ et al (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774

Sallé A, Nageleisen LM, Lieutier F (2014) Bark and wood boring insects involved in oak decline in Europe: current knowledge and future prospects in the context of climate change. For Ecol Manage 328:79–93

Sanchez-Osorio I, Tapias R, Dominguez I et al (2007) Characterization of the electroantennographic response by *Cerambyx welensii* Küster and *Prinobius germari* Germar (Coleoptera: Cerambycidae) to olfactory stimuly. Invest Agrar-Sist R 16:95–106

Santolamazza Carbone S, Pestaña M, Vega JA (2011) Post-fire attractiveness of maritime pine (*Pinus pinaster* Ait.) to xylophagous insects. J Pest Sci 84:343–353

Santoro AE, Lombardero MJ, Ayres MP et al (2001) Interactions between fire and bark beetles in an old grown pine forest. For Ecol Manage 144:245–254

Sanways MJ (1998) Insect population changes and conservation in the disturbed landscapes of Mediterranean-type ecosystems. In: Rundel PW, Montenegro G, Jaksic FM (eds) Landscape disturbance and biodiversity in Mediterranean-type ecosystems, Ecological Studies Vol. 136, Springer, Berlin, pp 313–348

Sarris D, Christodoulakis D, Körner C (2007) Recent decline in precipitation and tree growth in the eastern Mediterranean. Glob Chang Biol 13:1187–1200

Sarris D, Christodoulakis D, Körner C (2011) Impact of recent climatic change on growth of low elevation eastern Mediterranean forest trees. Clim Change 106:203–223

Saugier B, Roy J, Mooney HA (2001) Estimations of global terrestrial productivity: converging toward a single number? In: Roy J, Saugier B, Mooney HA (eds) Terrestrial global productivity. Academic Press, San Diego

Scarascia-Mugnozza G, Oswald H, Piussi P et al (2000) Forests in the Mediterranean region: gaps in knowledge and research needs. For Ecol Manage 132:97–109

Schvester D (1971) *Matsucoccus feytaudi* Duc. et "dépérissement" du Pin maritime. In: Annales de Zoologie – Ecologie Animale, hors série, INRA, Versailles, pp 139–151

Settele J, Scholes R, Betts R et al (2014) Terrestrial and inland water systems. In: Field CB, Barros VR, Dokken DJ et al (eds) Climate change 2014. Impacts, adaptation and vulnerability. Part A: global and sectorial aspects, Contribution of Working Group II to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge/New York, pp 271–359

Shakesby RA (2011) Post-wildfire soil erosion in the Mediterranean: review and future research directions. Earth Sci Rev 105:71–100

Silva LCR, Anand M (2013) Probing for the influence of atmospheric CO_2 and climate change on forest ecosystems across biomes. Glob Ecol Biogeogr 22:83–92

Silva LCR, Anand M, Leithead MD (2010) Recent widespread tree growth decline despite increasing atmospheric CO_2. PLoS One 5:e11543

Singer MC, Parmesan C (2010) Phenological asynchrony between herbivorous insects and their hosts: signal of climate change or pre-existing adaptive strategy? Philos Trans R Soc Lond B 365:3161–3176

Six DL, Bentz BJ (2007) Temperature determines symbiont abundance in a multipartite bark beetle-fungus ectosymbiosis. Microb Ecol 54:112–118

Smith AL, Hewit N, Klenk N et al (2012) Effects of climate change on the distribution of invasive alien species in Canada: a knowledge synthesis of range change projections in a warming world. Environ Rev 20:1–16

Soria FJ, Ocete M (1993) Estudios poblacionales sobre *Coroebus florentinus* (Herbst) (Col., Buprestidae) en alcornocales andaluces. Bol San Veg Plagas 19:27–35

Sousa E, Debouzie D (2002) Contribution à la bioécologie de *Platypus cylindrus* F. au Portugal. IOBC/WPRS Bull 25:75–83

Sousa E, El Antry S, Atay Kadiri Z et al (2008) Problématique des subéraies dans le bassin méditerranéen. Ann Rech For Maroc 39:63–73

Speight MR, Hunter MD, Watt AD (1999) Ecology of insects: concepts and applications. Blackwell, Oxford

Stamp N (2003) Out of the quagmire of plant defense hypotheses. Q Rev Biol 78:23–55

Staudt M, Rambal S, Joffre R et al (2002) Impact of drought on seasonal monoterpene emissions from *Quercus ilex* in southern France. J Geophys Res 107:4602–4608

Staudt M, Ennajah A, Mouillot F et al (2008) Do volatile organic compound emissions of Tunisian cork oak populations originating from contrasting climatic conditions differ in their responses to summer drought? Can J For Res 38:2965–2975

Stefanescu C, Peñuelas J, Filella I (2003) Effects of climatic change on the phenology of butterflies in the northwestern Mediterranean Basin. Glob Chang Biol 9:1494–1506

Stuart Chapin F III, Matson PA, Mooney HA (2002) Principles of terrestrial ecosystem ecology. Springer, New York

Thomas MB, Blanford S (2003) Thermal biology of insect-parasite interactions. Trends Ecol Evol 18:344–350

Timbal J, Aussenac G (1996) An overview of ecology and silviculture of indigenous oaks in France. Ann Sci For 53:649–661

Touchan R, Anchukaitis KJ, Meko DM et al (2008) Long term context for recent drought in northwestern Africa. Geophys Res Lett 35, L13705. doi:10.1029/2008GL034264, 5p

Turgeon JJ, Roques A, de Groot P (1994) Insect fauna of coniferous seed cones: diversity, host plant interactions, and management. Annu Rev Entomol 39:179–212

Tylianakis JM, Didham RK, Bascompte J et al (2008) Global change and species interactions in terrestrial ecosystems. Ecol Lett 11:1351–1363

Urban MC, Tewksbury JJ, Sheldon KS (2012) On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. Proc R Soc B 279:2072–2080

Vallauri D, André J, Dodelin B et al (eds) (2005) Bois mort et à cavités: une clé pour les forêts vivantes. Lavoisier, Paris

Van Asch M, Visser ME (2007) Phenology of forest caterpillars and their host trees: the importance of synchrony. Annu Rev Entomol 52:37–55

Venetier M, Vilà B, Liang E et al (2007) Impact of climate change on pines forest productivity and on the shift of a bioclimatic limit in Mediterranean area. In: Leone V, Lovreglio R (eds) Proceedings of the international workshop MEDPINE 3: conservation, regeneration and restoration of Mediterranean pines in their ecosystems, Options Méditerranéennes: Série A, Séminaires Méditerranéens, vol 75. CIHEAM, Montpellier, pp 189–197

Vennetier M, Girard F, Didier C et al (2011) Adaptation phénologique du Pin d'Alep au changement climatique. Forêt Médit 32:151–167

Vindel B, Seller A (2005) La sensibilité des écosystèmes méditerranéens aux changements globaux, Les notes d'alerte du CIHEAM 3, CIHEAM, Montpellier, pp 1–3

Walther GR, Post E, Convey P et al (2002) Ecological responses to recent climate change. Nature 416:389–395

Walther GR, Roques A, Hulme PE et al (2009) Alien species in a warmer world: risks and opportunities. Trends Ecol Evol 24:686–693

Wilson RJ, Gutierrez D, Gutierrez J et al (2005) Changes in the elevation limits and extent of species ranges associated with climate change. Ecol Lett 8:1138–1146

Yani A, Pauly G, Faye M et al (1993) The effect of a long-term water stress on the metabolism and emission of terpenes of the foliage of *Cupressus sempervirens*. Plant Cell Environ 16:975–981

Yuan JS, Himanen SJ, Holopainen JK et al (2009) Smelling global climate change: mitigation of function for plant volatile organic compounds. Trends Ecol Evol 24:323–331

Zine El Abidine A, Aadel T (2009) Etude écophysiologique du dépérissement du Cèdre de l'Atlas (*Cedrus atlantica* M.) dans le Moyen Atlas tabulaire. Ann Rech For Maroc 41:110–122

Zine El Abidine A (2003) Le dépérissement des forêts au Maroc: analyses des causes et stratégie de lutte. Sécheresse 14:209–218

Zverera E, Kozlov V (2006) Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a metaanalysis. Glob Chang Biol 12:27–41

Chapter 29
Follow the Water: Extreme Drought and the Conifer Forest Pandemic of 2002–2003 Along the California Borderland

Richard A. Minnich, Brett R. Goforth, and Timothy D. Paine

Abstract California conifer forests suffer chronic low levels of bark beetle-caused tree mortality, but are subject to periodic episodes of widespread bark beetle outbreaks and extensive tree death. The extent and severity of the outbreaks are strongly influenced by precipitation, slope and aspect, stand density and stocking levels, fire, and soil characteristics as environmental factors. In addition, anthropogenic factors including fire suppression and stand management practices can also influence the susceptibility of forest stands to bark beetle activity. The mountains of southern California in the USA and Baja California Norte in Mexico were subject to a severe drought during 2002–2003. A major bark beetle outbreak accompanied the period of drought. Tree cover death was highest in *Pinus coulteri* (57.8 %), intermediate in *Pseudotsuga macrocarpa* (24.7 %) and mixed conifer forest (26.0–33.6 %), and lowest in subalpine forest (2.0 %) in Southern California mountains. The tree mortality in the adjacent mountains in Baja California was five times lower than what was observed north of the international border. The differences in forest management, particularly historical practices of fire suppression that resulted in stand densification and intense competition for available moisture in California may be the underlying mechanism driving the differences in severity of the bark beetle outbreaks on either side of the border.

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29.1 Introduction

In California's montane conifer forests, drought invariably amplifies tree mortality from bark beetles. But protracted summer drought is the hallmark of the region's Mediterranean climate. Winter precipitation is followed in summer by rainless episodes lasting for months, and one wonders why California conifer forests are not decimated by insect attacks every year. The correlation between beetle attacks and climate can be diffuse across time and space because bark beetles may delay or prolong the timing of tree mortality episodes (Taylor 1973). Conifer survival depends upon reliable access to water by deep rooting into the regolith. History has recorded mass forest dieback only rarely. In recent times, elevated mortality occurred in southern California conifer forests in 1975–1977 and 1988–1991 (Savage 1994, 1997). The unprecedented pandemic of 2002–2003 in extreme drought, triggered by the driest year in southern California since records began in 1850, brought a unique "teaching moment" on long-term forest dynamics, insects and hydrology. While tree death appears inexplicably random in minor droughts, the sweeping pandemic of 2002–2003 across the mountains uniquely revealed spatial patterns of tree death that helps explain plant response to extreme water deficits and insect attack. This dieback episode occurred in a 4-year drought that culminated with nearly a "rainless" winter, i.e., the lack of precipitation necessary for deep percolation of meteoric water. During the event "drought beat insects to the punch" i.e., hydrologic tree death preceded and superseded bark beetle attack in 2002, but forest insects eventually prevailed in 2003 before dieback ceased the following year.

Relationships between drought, bark beetles, and forest tree mortality are influenced by atmospheric climatology, soil-water balance and conifer physiology, wildfire and bark beetles. How these variables influence tree death can be teased out by examining the California borderland and broad scales. This investigation compares forest mortality patterns observed in three mountain ranges: the San Bernardino Mountains (SBM) and San Jacinto Mountains (SJM) in southern California USA (SCA), where fire suppression has been systematically practiced since ca. 1900, and the Sierra San Pedro Mártir (SPM) in Baja California Mexico (BCA), where the fire regime is unmanaged (free-burning) (Fig. 29.1). The tree mortality pandemic was investigated in three steps: (1) roadside repeat photography during the epidemic; (2) production of maps of whole-stand mortality using repeat aerial photography, and (3) high resolution census of dead trees visible on aerial photograph sample 1.0 ha plots. The latter two tasks were accomplished using Google Earth™ digital aerial photo color imagery from 2003 to 2005.

Following the water, several important themes emerge that require future investigation. Coniferous trees root deeply, not only into shallow rocky soils, but also down through a pedogenically weathered parent material of porous regolith that provides secure root extractible water in summer drought (see Graham et al. 2010). Protracted drought occurs because the region lies on the equatorward margin of rain-bearing storms of the jet stream leading, to multi-

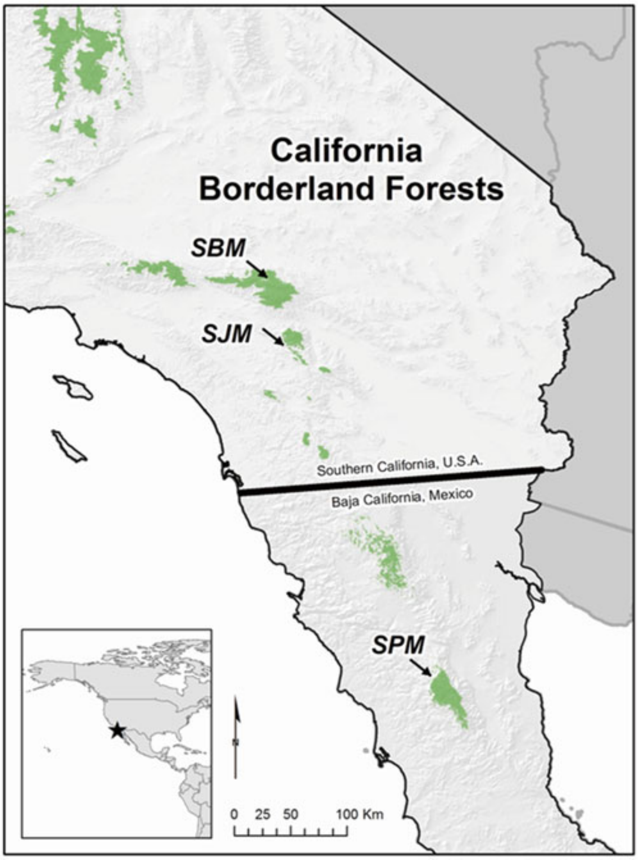

Fig. 29.1 Location map of the California borderland, San Bernardino Mountains (SBM), San Jacinto Mountains (SJM), and Sierra San Pedro Mártir (SPM)

year drought and "rainless" winters. Nevertheless, a single major storm in a dry year can saturate soils to bedrock. How much precipitation is needed to saturate soils to field capacity and provide deep percolation to regolith storage? Rates of soil moisture loss vary in vegetation successions with time-since-fire? Severe soil water depletion may cause mass hydrologic tree death before bark beetle tree death, i.e., mortality proliferates ahead of beetle reproduction and dispersal. Hydrologic tree death correlates with terrain gradients as factors of drought stress (e.g., slope, aspect, and elevation) while insect attack tree deaths are predicted to be patchy and randomly distributed related to intrinsic demographic factors like reproduction, dispersal and pheromone behavior of insects. Another issue in this moment of global change research, is whether upslope forest retreat from the pandemic in SCA is a "recalibration of tree limits," or a symptom of changing climate.

29.2 Conifer Forests Along the California Borderland

Conifer forests are similar in distribution in all three mountain ranges (Minnich and Franco Vizcaino 1998; Minnich 2001; Minnich and Everett 2001; Minnich 2007a; Minnich et al. 2011). In southern California (SCA), coastal escarpments below 1400–1900 m have extensive chaparral with patches of closed cone conifer forest (*Pinus attenuata, Pinus coulteri*), and mixed evergreen forests (*Quercus chrysolepis, Pseudotsuga macrocarpa)* in canyons, cliffs and north facing slopes. At higher elevations, chaparral gives place to mixed conifer forest (*Pinus ponderosa*, *P. jeffreyi*, *P. lambertiana*, *Abies concolor*, *Calocedrus decurrens*) which gives place to subalpine forest >2500 (e.g., *Pinus contorta*, *P. flexilis*) (vegetation typology after Barbour et al. 2007). Forest assemblages in the SPM are ca. 100–200 m higher than in SBM and SJM. The SPM forests lack *P. ponderosa, P. flexilis,* and *Pseudotsuga macrocarpa* but contain *Cupressus montana*.

29.3 Insect Pathogens in Conifer Forest

Tree diseases are viewed as landscape mediators to biological and geophysical features that predispose forest patches to disease (Holdenrieder et al. 2004). The focus here will be bark beetles that were significant in the 2002 pandemic. Drought reduces the photosynthetic capacity of trees and the levels of carbohydrates used for growth and tissue repair (Grulke et al. 2009). While the stress incurred by the dry conditions may kill trees directly, the reduction in resin pressure also predisposes these trees to attack by bark beetles and pathogens, and increases fire hazard (McBride and Miller 1999). Deficient precipitation can reduce tree vigor and predispose trees to anomalous disease or insect attack. Mortality tends to increase in multi-year droughts, particularly in highly resource competitive dense stands, or stands with pre-existing damage or stresses (Taylor 1973; Pronos et al. 1999; Fenn et al. 2003).

Native insect herbivores and pathogens, including bark beetles, mistletoes and root diseases, perform an important function in conifer forests by killing moribund trees and nutrient cycling (Pronos et al. 1999). Pine beetles are either host specific or generalists. Among those that kill trees in southern California, the *Dendroctonus jeffreyi* breeds almost exclusively in Jeffrey pine, the *Dendroctonus pseudotsugae* is exclusive to Douglas firs, *Dendroctonus brevicomis* attacks ponderosa and Coulter pine, and *Scolytus ventralis* attack white fir. *Dendroctonus ponderosae* breeds in many pine species (Wood et al. 2003).

Beetles and engravers are opportunists that attack trees in a weakened or dying state due to root erosion, snow breakage, advanced age, lightning strikes, drought and other factors that compromise tree vigor. With only a few rare exceptions, either the host tree is killed by the colonizing bark beetles or the host resistance of the tree kills the attacking adults. To kill a tree, large numbers must successfully colonize in a relatively short period of time (Paine et al. 1984; Paine et al. 1997). Adults emerge from the larval host tree and search for susceptible hosts. Healthy pines and firs respond by exuding pitch, which either "pitches out" the adults or blocks its progress. In weak trees with reduced resin pressure, the adults are able to initiate colonization and produce aggregation pheromones that attract other colonizing adults. Pheromone production ceases when the host tree ceases resin flow (Raffa and Berryman 1983) signaling the death of the tree. Eggs are laid in the inner bark and the larvae excavate galleries in directions generally perpendicular to the adult galleries. Pupation occurs either in the inner bark or in the outer bark, depending on the species of beetle. Western pine beetle can produce up to four generations in a year in southern California due to the mild thermoclimate permitting the populations to expand rapidly when there is an abundance of susceptible host material available for colonization.

There is a threshold of attacking beetles required to kill trees, and that threshold is a function of the vigor of the host; a smaller number of beetles is necessary to kill stressed trees than vigorously growing trees (Paine et al. 1984). Under normal conditions when background populations of beetles are low, tree mortality is usually at low levels when stands have a few weak trees. However, under drought conditions when there are large numbers of highly stressed trees, a relatively small population of beetles can kill many trees. As a result, the population of beetles will increase in those drought stressed trees, and many more trees will be at high risk because more vigorous trees can be killed by the larger number of adults that respond to the aggregation pheromones (Paine et al. 1984).

In forests of the California borderland, bark beetles, needle miners, scales, engravers, and other insects attack and kill trees at any time, in wet or dry years. With roots tapped deep into moisture stored within the porous fractured regolith, trees more commonly perish for reasons other than drought. Mortality tends to increase in multi-year droughts (Taylor 1973). Bark beetles are ever present to cull individual weakened trees, the cooperative pheromone behavior of these insects concentrates mortality within discrete clusters, often randomly distributed across forests. Hence, insects tend to prevail over water deficits in cause of tree death. Mortality rates in SPM seldom exceed 1–3 tree ha^{-1} (Minnich et al. 2000; Stephens et al. 2003).

29.4 Atmospheric Climatology

Conifer forests cover high mountains of the California borderland where relatively few storms produce annual rainfall totals of 50–100 cm by orographic lift on the windward escarpments. High rainfall results despite air mass stability in the storm precipitation period ahead of passing cold fronts due to efficient orographic lift in air flow up transverse aligned slopes (summary in Minnich 2007b). The region's position along the equatorward margin of the jet stream also makes possible the prospect of entire precipitation seasons without wetting storms.

In winter strong latitudinal temperature gradients focus the polar-front jet stream and onshore flow of moist surface westerlies around surface low pressure in the

Gulf of Alaska into northern California and the Pacific Northwest. The distribution of conifer forests of the California borderland correlates with mechanical lift of stable cold frontal storm air masses of extratropical cyclones of the jet stream. The frontal zone that brings most precipitation is strongly affected by the cold, upwelling Pacific Ocean, the cold lower air layers from the south and southwest stabilizing air masses. Relatively low precipitating cloud layers (typically 3–4 km msl), fast-moving wind fields and associated high vapor flux couple mechanical lift in laminar flow (high standing precipitation) with local physiography along windward slopes and descent (low precipitation) on leeward slopes. It is uncommon to have unstable air and deep convection. In the SCA east-west oriented Transverse Ranges, annual precipitation is highest (80–100 cm) on the steep southern escarpment of SBM that lies at right angles to storm winds. In the north-south Peninsular Ranges, annual precipitation in SJM ranges is 40–70 cm because storm winds more frequently parallel the windward escarpment. The SJM is also rain shadowed by the Santa Ana Mountains and Palomar Mountain along the coast. Annual precipitation also ranges from 40 to 70 cm in SPM, despite its lower latitude, because there are no upwind mountain rain shadows. Interannual precipitation is exceptionally variable due to the region's position along the southern margin of the jet stream and Mediterranean climate along the North American Pacific coast. Mean annual temperatures and potential evapotranspiration do not significantly differ among the three mountains within overlapping elevation zones providing forest habitat (Minnich 2001; Franco-Vizcaino et al. 2002).

In summer, reduced latitudinal temperature gradients weaken the jet stream which shifts poleward to western Canada. Gulf of Alaska low pressure is replaced by surface high pressure covering the northeast Pacific Ocean. A vital component of the Mediterranean climate is the coastal "marine layer," a steady-state feature associated with the cooling and moistening of the tropospheric boundary layer overlying the cold, upwelling California Current. It is capped by a strong thermal inversion that divides the "marine layer" from warm and dry subsiding air masses aloft. The "marine layer" air mass stability precludes convective precipitation from May to September. Average monthly rainfall is near zero from May to October except in mountains subject to infrequent North American monsoon thunderstorms.

29.5 Evergreen Forest Physiology and Hydrology

In chaparral, stomatal closure diminishes water loss and reduces CO_2 uptake with photosynthetic rates in summer drought, but this is compensated by efficient canopy maintenance (Keeley and Davis 2007). It is doubtful that plants "conserve" water in view of leaf-air water vapor diffusion physics. Plants exploit water rapidly in competition with neighbors until forced to stomatal closure (Poole and Miller 1975). Evergreen assemblages in the California borderlands, including chaparral, *Quercus chrysolepis* woodland, and conifer forest, dominate mountainous terrain with shallow rocky soils. The environmental stress all conifers tolerate is that the season of growth and plant water demand is also the dry season. During winter, a water surplus and saturation of pores in weathered regolith can span all elevations, but the surplus lasts later into spring and early summer at higher altitudes (Pronos et al. 1999; Royce and Barbour 2000, 2001; Franco-Vizcaino et al. 2002). Available water in soil is virtually depleted by the end of September (Arkley 1981), but deep rooting extracts water from fractured weathered regolith through late summer and fall (Jones and Graham 1993; Hubber et al. 2001; Witty et al. 2003; Graham and Hubbert 2012). Ironically, shallow soils with low field capacities assure deep percolation of meteoric water even in modest drought. One or two soaking storms per year may be sufficient to maintain regolith water storage. On bedrock slopes, percolation can be concentrated in weathered fractures by runoff from surrounding impermeable rock surfaces, even in small storms. Impervious surfaces also retard evaporation of moisture stored in the porous weathered regolith below.

More broadly in the California borderlands, the critical importance of weathered regolith as a surrogate source of soil moisture is implied where woody evergreen assemblages reach their limits of growth precisely at the terminus of slopes underlain by bedrock. While alluvial plains adjoining the slopes tend to have greater water holding capacity, the substrate is also more porous and can readily drain to depths beyond the rooting zones of evergreen sclerophyllous vegetation. Alluvial fans, floodplains, stream terraces and deeply weathered hills are dominated by shallow-rooted mesophyllous deciduous oak woodlands (e.g., *Quercus lobata*, *Q. douglasii*, *Aesculus californica*) with drought response through leaf fall, and/or rooting to groundwater (*Q. lobata*, White 1966; Allen Diaz et al. 2007; Rempe and Dietrich 2014).

29.6 Fire Ecology

Periodic wildfire synchronizes forest-stand dynamics by removing biomass, reducing plant water demand and competition for water, and stimulating recruitment. The role of fire history in the 2002–2003 pandemic is illustrated in a “natural experiment” in which burning in conifer forest in SCA has been altered by fire suppression for more than a century while free-burning continues in BCA.

In the California borderland, a discrete shift in the pattern of fire occurs along the international boundary between the USA and Mexico (Minnich 1983; Minnich et al. 1995; Minnich and Chou 1997). In BCA chaparral and conifer forest free burning produces a fine-grained mosaic of small burn patches and discrete local-scale heterogeneity of fuels, with site-specific fire return intervals of ca. two to three per century. These mosaics are an outcome of time-dependent fuel accumulation giving the landscape a self-organized of patches that have burned at different times. Fire is constrained in early successions because young vegetation constitute little fuel (i.e., low biomass energy) and high fuel moisture content because of small canopy leaf area and transpiration demand (Minnich and Franco Vizcaíno 2009). Broadscale flammability of vegetation occurs when a combustion threshold is attained after decades of growth, where calorie output from pyrolysis of fuel exceeds latent heat input needed to desiccate fuels and sustain fire spread. Carbohydrate energy eventually surpasses the latent heat sink of vegetation due to cumulative fuel build-up, increasing dead fuel content, and diminished live fuel moisture with greater canopy transpiration in time-since-fire succession of growth.

Under free burning, fires occur by chance in modal weather conditions of the climate, mostly in summer. In SCA, suppression has reduced the number of fires, while increasing the size of old-growth burn scars and thus the spatial extent of subsequent fires. Fire enlargement is further encouraged by the selection of fire "starts" (ignitions) to escape in more extreme weather than by chance. Fuel accumulation over broad areas is coupled with increasing probability of failure by fire fighting forces to extinguish ignitions during extreme weather conditions, notably in autumnal dry warm "Santa Ana" winds when fire spread rates are most rapid (Minnich and Chou 1997). Fire suppression management has significantly altered mixed conifer forest since ca. 1900 by eliminating the stand-thinning effect of recurrent understory fires. In SPM free burning has maintained open forests similar to that recorded in photographs and written reports in southern California before the onset of fire control ca. 1900 (Minnich 1988).

Conifer forest assemblages have characteristic physical and population structure, subcanopy of chaparral and oak woodlands, as well as accumulation patterns of combustible biomass (summary in Minnich 2007a). This reflects selection pressures of fire that covary with gradients in climate, productivity and rates of fuel accumulation. On coastal escarpments and mountain crests, fires burn chaparral and mixed conifer forest two to three times per century, then increase to multi-century intervals in slow-growing subalpine forest. In chaparral, short-lived *Pinus attenuata* and *P. coulteri* are usually fire-killed because of their small stature and integration of crowns with the high biomass shrub layer. Fires are followed by vigorous pulsed cohort regeneration from dormant seed dispersed from serotinous cones. *Pseudotsuga macrocarpa* occurs in compact groves of long-lived trees in canyons, cliffs and shady slopes in association with solid mid-story of canyon live oak. Chaparral fires shift to litter fires, the flames scorching the canyon live oak layer and leaving taller long-lived *P. macrocarpa* undamaged (Minnich 1999). Steep terrain, erosion of organic matter, and scarce chaparral subcanopy reinforce fire resistance. After intense defoliating fires, *P. macrocarpa* survives by epicormic resprouting along the upper bole and primary branches. Above the chaparral, mixed-conifer forest experience recurrent surface fires that selectively remove saplings to polesize trees, leaving residual, mixed-aged parks of mature trees. In SPM forests form an umbrella-like canopy with live crown bases 5–15 m above ground. Tree densities (dbh > 10.0 cm) average ≈50 ha^{-1} in monotypic *Pinus jeffreyi*, ≈100 ha^{-1} in mixed conifer forest (*P. jeffreyi-Abies concolor*) and 150 ha^{-1} in *Abies concolor-P. lambertiana* forest (Savage 1997; Minnich et al. 2000; Maloney and Rizzo 2002; Stephens et al. 2003). The SPM forest densities, species composition, and tree diameter frequency distributions broadly overlap with those recorded in the 1929–1934 Vegetation Type Map Survey (VTM) in SBM (Minnich et al. 1995). Forest densities in SBM have since increased by a factor of 1.5–2.0 in the absence of fire as a result of ingrowth of sapling to pole-size stems (10–29.9 cm DBH) with dominance in the subcanopy shifting from shade-intolerant *Pinus ponderosa* and *P. jeffreyi* to shade-tolerant *Abies concolor* and *Calocedrus decurrens* (Minnich et al. 1995). In subalpine forest, stand-replacement fires periodically denude stands at intervals of centuries due to low primary productivity rates (Minnich 1988). The removal of the tree layer discourages short-term fire recurrences. Even low intensity burns are often fatal to *Pinus contorta* and *P. flexilis* because the thin bark of these species does not prevent fatal damage to cambium. Fires leave discrete patches of different age that fade with the development of stand cohorts that attain canopy closure by ca. 100 years.

29.7 The 2002–2003 Pandemic

The winter of 2001–2002 in southern California was the driest year since instrumental records began in 1850 at San Diego (National Centers for Environmental Information 2015). Only 17 cm was recorded at Big Bear Dam or 22 % of normal (Fig. 29.2), and the drought was severe throughout the California borderland with percent of normal precipitation ranging from 14 % to 32 % (Table 29.1). There were no deep wetting storms that winter which followed 3 dry years in association with strong La Niña conditions in the Pacific Ocean beginning in the spring of 1998. Conifer forests of the California borderland experienced unprecedented die-off including extensive areas of whole-stand mortality. The previous pandemic of comparable magnitude may have occurred long before 1850. In open forest of *Pinus jeffreyi* forests on semiarid leeward slopes of SBM, whole stands of large diameter overstory dominant old-growth trees experienced hydrologic death in 2002. Tree-rings were cored from 26 old-growth trees at 3 sites in July 2003 (Heart Bar, Cienaga Seca, Sugarloaf Mt.). Trunk DBH averaged 82.1 cm (range: 67.8–114.0 cm). Annual-ring counts indicate that 69 % of sampled trees established between year 1700 and 1800 (Fig. 29.3). The median age was 265 years, with earliest tree ring

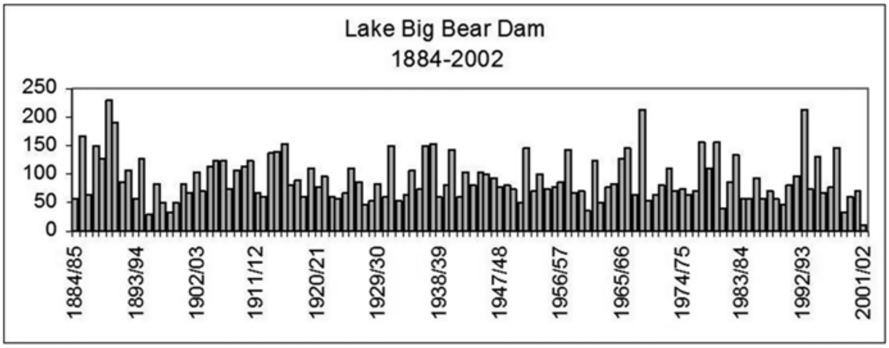

Fig. 29.2 Annual precipitation at Big Bear Lake Dam (cm). Only 17.0 cm fell in the winter of 2001–2002 or 22 % of normal (79.1 cm)

Table 29.1 Annual precipitation (cm) and percent of normal (PON) in the drought of 1999–2002

		Year							
Station	Latitude	1999	PON	2000	PON	2001	PON	2002	PON
Los Angeles	34.02	23.1	61	29.4	78	45.6	121	11.2	30
Riverside	33.97	14.1	56	14.5	57	21.3	84	8.1	32
San Diego	32.73	16.5	66	14.6	58	21.8	80	8.4	31
Ensenada	31.88	17.4	67	12.7	49	27.5	105	8.9	39
Santo Tomás	31.55	13.5	50	13.9	52	26.6	99	3.8	14
Nuevo Baja California	30.51	9.9	55	9.3	52	18.6	105	5.2	29

Sources: U.S Climatological Data, California. http://www.ncdc.noaa.gov/IPS/cd/cd.html
Mexico U.S National Climatic Data Center http://gis.ncdc.noaa.gov/
PON Percent of Normal

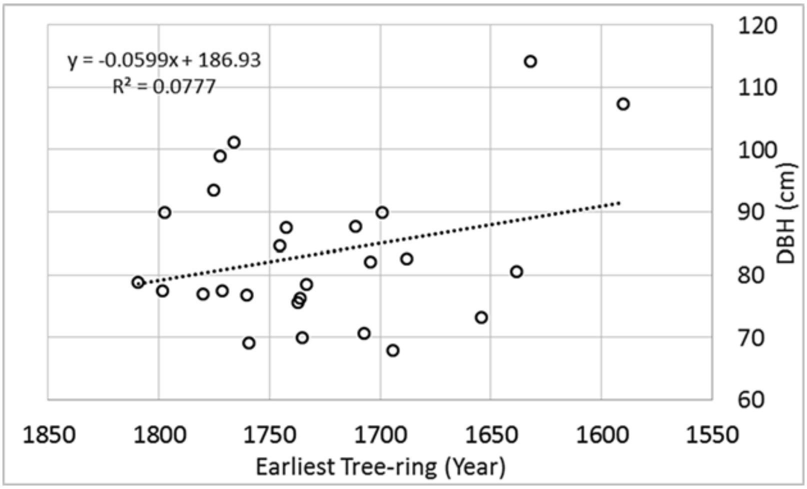

Fig. 29.3 Establishment date and diameter of dead trees in whole-stand mortality stands at Heart Bar, Cienaga Seca, and Sugarloaf Mountain

dating to 1590. These data suggest that the last drought to trigger a die-off on these slopes occurred in the Little Ice Age, perhaps in the eighteenth century, and that drought severity in 2002 was unmatched since that time.

Because extreme events cannot be predicted, we scrambled to record the rapid advance of the pandemic. In SBM and SJM, site-specific, repeat ground photo point surveys were monitored from 2002 to the end of the dieback episode in November 2003. The pandemic proliferated in the summer of 2002 and continued into 2003 despite heavy rains the intervening winter (125 % of normal). The progression of tree mortality in SPM could not be documented because we could visit the area only once at the end of the pandemic in July 2003. There is no Google Earth coverage during the pandemic.

Extreme drought caused anomalous phenological response of vegetation. By spring 2002, leaf shed and crown dieback occurred in evergreen *Quercus chrysolepis* and chaparral taxa such as *Q. berberidifolia*, *Cercocarpus betuloides*, *Arctostaphylos* spp., *Ceanothus*, spp. and *Adenostoma fasciculatum.* Conifers and broadleaf trees exhibited failure in leader growth, crown thinning, and aborted cones and fruits. The defoliation of stems led to tree death because coniferous species are obligate non-sprouters, except for *Pseudotsuga macrocarpa*. These symptoms suggest that regolith stored water became depleted in 2002, triggering conifer die-off before insect attack.

Tree death affected all species throughout SBM and SJM, but the progression of mortality varied over time and by species (Figs. 29.4 and 29.5). *Calocedrus decurrens* and *Pseudotsuga macrocarpa* suffered hydrologic mortality almost entirely in 2002. *C. decurrens* does not host pathogenic insects, and we did not observe evidence of *Dendroctonus pseudotsugae* attack in *P. macrocarpa. C. decurrens* attrition occurred locally along streams and springs that disappeared. Crown defoliation of *P. macrocarpa* was first observed in September 2002, and became extensive by December. It was accompanied by leaf death in associated evergreen *Quercus chrysolepis*, turning the tree crowns golden (Fig. 29.4b). Although *P. macrocarpa* is capable of epicormic resprouting after wildfire, the emergence of new growth from the bole and large branches was uncommon, leading to mortality. Post-drought resprouting of bigcone Douglas fir was limited compared to post-fire resprouting (Minnich 1999). It appears that carbohydrate reserves are more depleted by the gradual defoliation of canopy over months than from "instant" defoliation by fires. Fires denuding nearby chaparral watersheds increase available soil water for resprouting trees, while high water demand persists in old-growth chaparral in drought (Loáiciga et al. 2001). Air pollution may have influenced drought attrition of *P. macrocarpa*. Arbaugh et al. (1999) showed that more than 80 % of Bigcone Douglas fir have reduced recent growth, with trees with high-ozone exposure having larger growth decreases than sites with low ozone, especially in western SBM (Watson et al. 1999). Trees retaining any green canopy recovered after the drought.

In forest dominated by *Pinus coulteri* and *P. jeffreyi*, trees perished primarily from hydrologic death in 2002 and insect mortality in 2003. Evidence of hydrologic death was the absence of frass, bark tunnels, pitch extrusions, other evidence of bark beetle activity in dead trees. Trees perished synchronously in uniform distribution linked to terrain and slope. By fall 2002, mortality in *P. coulteri* was massive even to whole stand levels (Fig. 29.6a). In 2003 mortality was patchy in both species, with new patches developing sequentially, as would be expected from bark beetle infestations. In *P. jeffreyi*, bark beetle attrition continued into early summer 2003, despite heavy rains the previous winter. The most extensive insect activity in the species was observed in alluvial basins such as Garner Valley in SJM. Conspicuous patches of mortality emerged through the dry season in *P. coulteri*.

Mortality in *Pinus ponderosa* forest was largely insect-driven both years (Fig. 29.5). Tree death was consistently patchy at places such as Lake Arrowhead and Idyllwild but was far more extensive in 2003, even after the wet winter of 2002–2003 (Figs. 29.4c and 29.5). We propose that second year tree death increased because of exponential

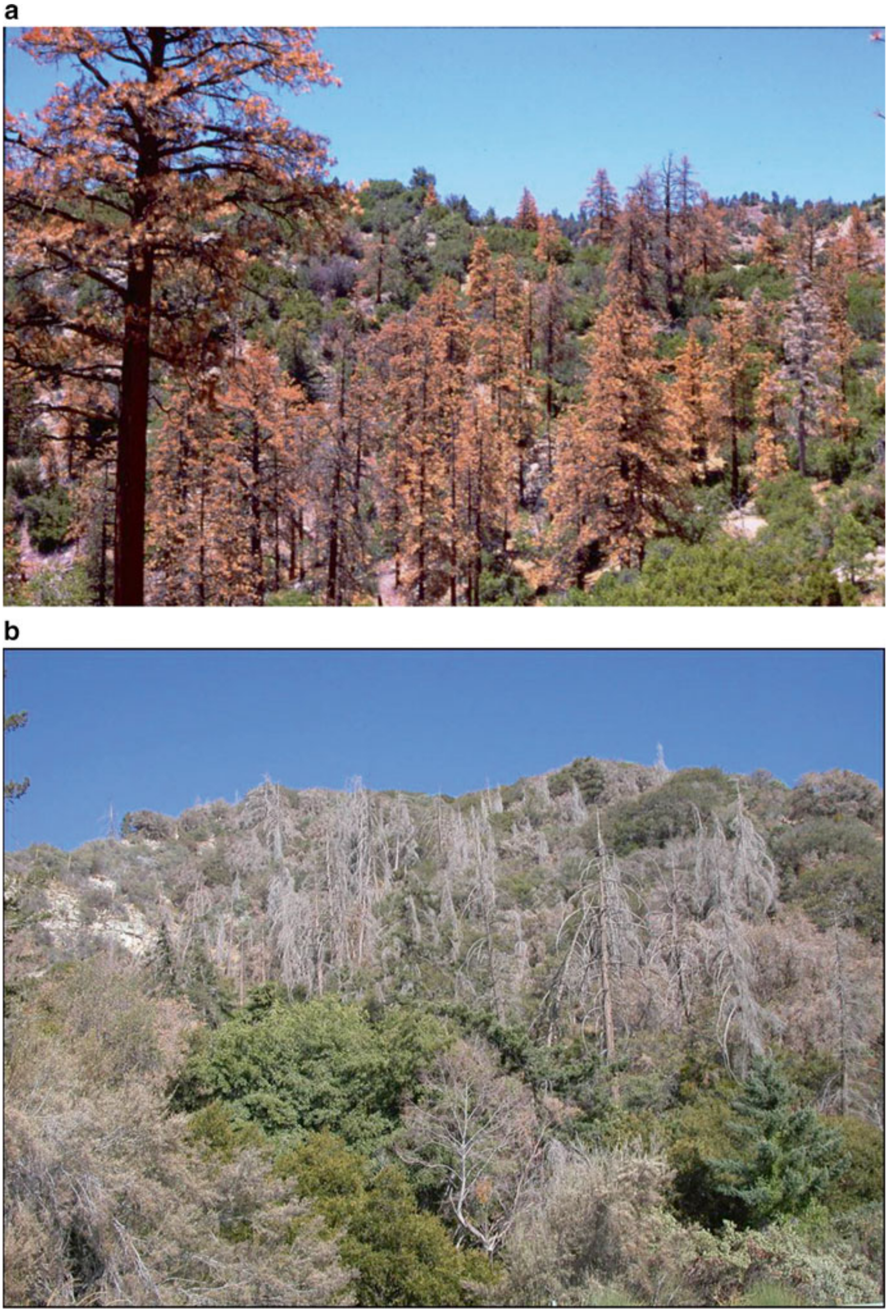

Fig. 29.4 Forest mortality during the 2002–2003 pandemic. (**a**) Dead *Pinus jeffreyi* in 2002, the trees perishing simultaneously that summer. Associated *Juniperus grandis*, *Pinus monophylla*, *Quercus chrysolepis*, *Arctostaphylos* spp. and *Cercocarpus ledifolius* were unaffected. (**b**) *Pseudotsuga macrocarpa* stand in a ravine. Most trees failed to resprout after defoliation (Photo courtesy of Victoria Minnich). (**c**) Dead *Pinus ponderosa* at Lake Arrowhead in 2003. The species sustained the greatest die-off after a wet winter in 2003 from bark beetle infestation. (**d**) Pandemic mortality in *Pinus jeffreyi*, *P. lambertiana*, and *Abies concolor* on Tahquitz Peak, San Jacinto

Fig. 29.4 (continued) Mountains. Die-off decreases above 2300 m near the summit. (**e**) Dead *Abies concolor* surrounded by *green Quercus chrysolepis*. (**f**) Light mortality in open mixed conifer forest of the Sierra San Pedro Mártir, Baja California in July 2003. Scattered *Pinus jeffreyi* perished on a south facing slope (*middle*) (Photo by Brett Goforth)

Fig. 29.4 (continued)

Fig. 29.5 Tree loss in *Pinus ponderosa* at Idyllwild in the San Jacinto Mountains. (**a**) November 2002. (**b**) September 2003

reproduction of subsequent generations of bark beetles. The beetle populations were sufficiently high to overcome tree resistance mechanisms. However, with the return to adequate moisture conditions and restoration of tree defenses following rehydration of the stems, insect mortality would have increased either through failed attacks on resistant trees or during prolonged dispersal flights by beetles searching for a much smaller number of susceptible trees. *Abies concolor* exhibited gradually increasing damage, canopy loss, and mortality over the entire 2-year period. Mortality rates were less than for pines in 2002, but tree loss increased to levels seen in pines the following year. The importance of *A. concolor* mortality from drought versus insects is ambiguous due to continual tree loss through the pandemic (Fig. 29.4e).

Mortality had decreased to background levels in all species by 2004. Heavy rains in the winter of 2002–2003 (PON 125 %) was followed by a dry year in 2003–2004 (PON 65 %) but several soaking rains did occur during that year. In 2004 surviving trees had improved growth flushes and resistance to insect predators compared to 2003 which suggest soil moisture had recharged allowing for rehydration of trees.

29.8 Distribution of Whole-Stand Mortality

Google Earth imagery provides a comprehensive record of tree death in coverages to 2003–2005, at a time when it was still possible to inventory dead trees that retained canopy foliage (Fig. 29.6). Ideally, a goal would be to produce a spatially explicit map of tree loss, but precise mapping is frustrated by the intrinsic variability in tree densities and percent dead. Instead, a map is produced showing whole-stand mortality which represents an unequivocal interpretation, i.e., each polygon signifies total mortality of canopy level trees. Distributions of total mortality would also be expected to reflect broader regional pattern in dieback. In this survey, dead forests in SBM, SJM, and SPM were mapped directly onto Google Earth imagery. The kml polygon files in Google Earth were transferred to ARC GIS to create files of polygon size and cumulative distribution. These were transferred to Excel for analysis of size frequency distributions and area of dead forest.

In SCA, whole-stand mortality exhibits repetitious spatial pattern at watershed scales with respect to terrain elevation, slope, and aspect that indicate hydrologic death (Fig. 29.7). At local scales trees perished on well-drained convex ridgelines and south aspect (equator facing) slopes with high insolation, but survived in canyons and north-facing slopes where convergent water flow and shade reduces temperature and water demand. These trends suggest that depletion of regolith moisture sufficient to kill trees fluctuated with PET and pore water drainage across terrain. In both SBM and SJM, patches of total mortality were absent only at highest altitudes where subalpine forest grows on Mt. San Gorgonio and Mt. San Jacinto. Mortality from bark beetle infestations occurred in patchy random distributions. The most extensive insect mortality occurred in *Pinus ponderosa* dominated forest at Lake Arrowhead. Hydrologic death was most extensive in *P. jeffreyi* forest on south facing slopes. These include the southern escarpments of Mt. San Gorgonio, Mill Creek Ridge, and lee-

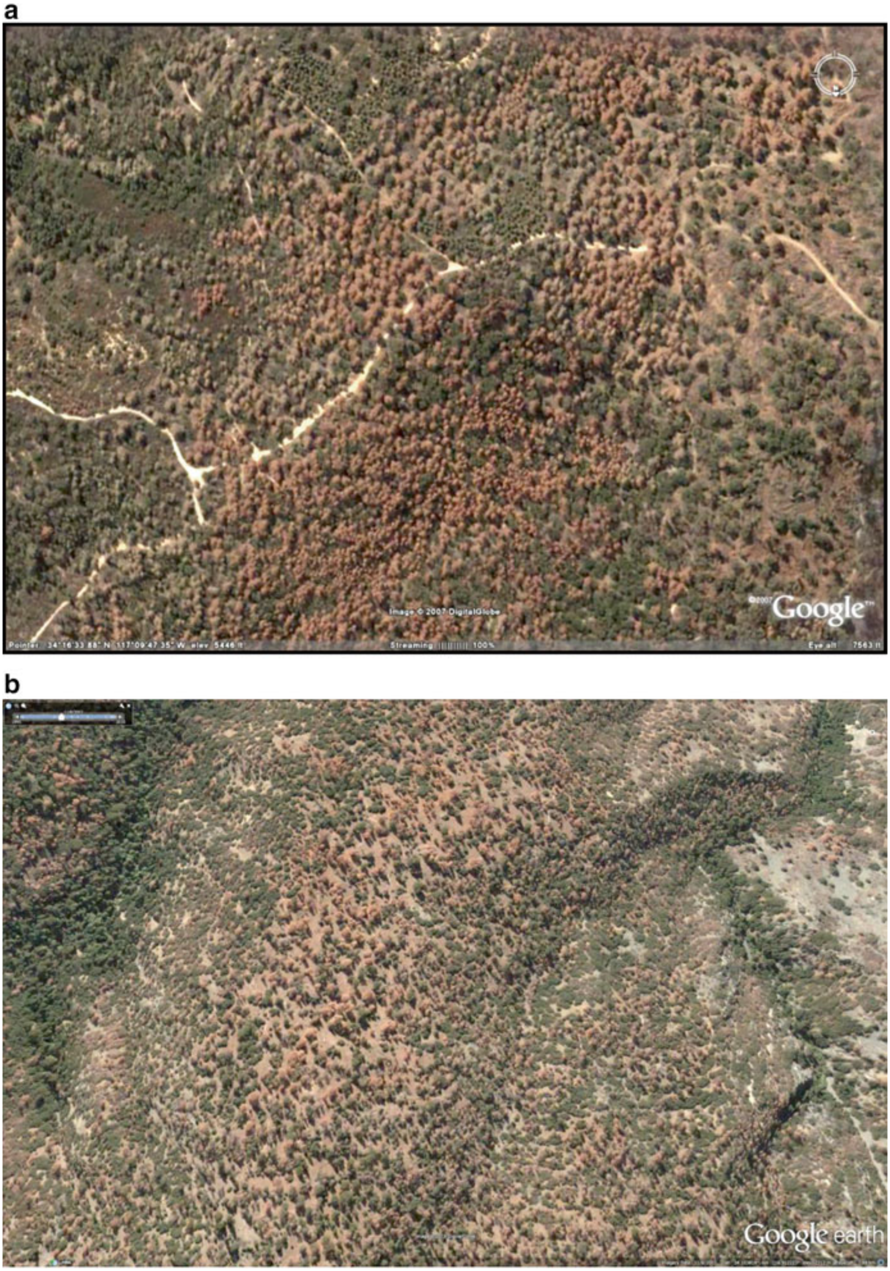

Fig. 29.6 Google Earth imagery of the pandemic. (**a**) Whole-stand mortality in *Pinus coulteri forest* near Lake Arrowhead. (**b**) Mostly dead forest of *P. jeffreyi* on a south facing slope

ward desert slopes in SBM and leeward escarpment of SJM including the Palm Springs Aerial Tramway and Santa Rosa Mountain. Light mortality occurred in monotypic *P. jeffreyi* forest on basin floors, including Big Bear Valley and Holcomb valley in SBM and Garner Valley in SJM. Heaviest mortality in *Abies concolor* forest materialized on the northern escarpment of San Gorgonio Mountain and Palm Divide in SJM. *P. coulteri* sustained widespread whole-stand mortality throughout SBM and SJM.

Whole stand mortality was rare throughout SPM. Tree loss was absent or at background levels in the northern plateau (Vallecitos, 2300–2500 m), but increased in lower plateau surfaces in the south (2100–1800 m). Tree death was greater in long unburned patches at these lower elevations than in recently burned areas (Fig. 29.4f).

The size frequency distribution of dead forest patches (Table 29.2) shows that conifer forest in SCA was extirpated to scales of 100 ha with cumulative area peaking from 4 to 100 ha. A 743 ha patch of ponderosa pine die-off occurred at Lake Arrowhead. In SPM most patches were <1.0 ha. Total whole-stand mortality loss was 6.4 % of forest in SBM, 2.8 % in SJM, and 0.6 % in SPM.

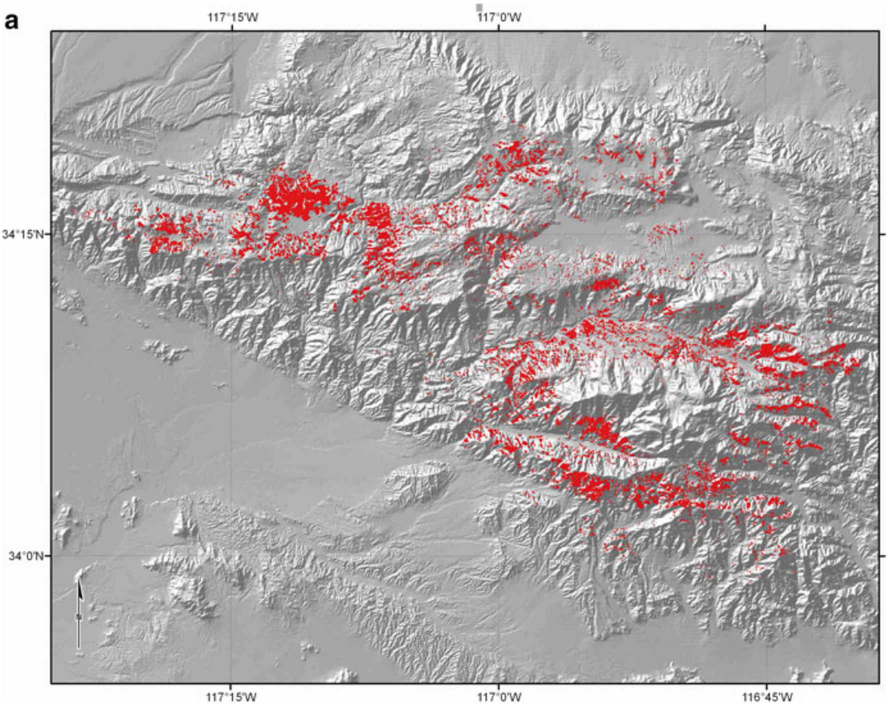

Fig. 29.7 Whole-stand mortality (*red*) in the 2002–2003 drought, mapped from Google Earth imagery in 2003–2005 before canopy leaf drop: (**a**) San Bernardino Mountains; (**b**) San Jacinto Mountains; and (**c**) Sierra San Pedro Mártir

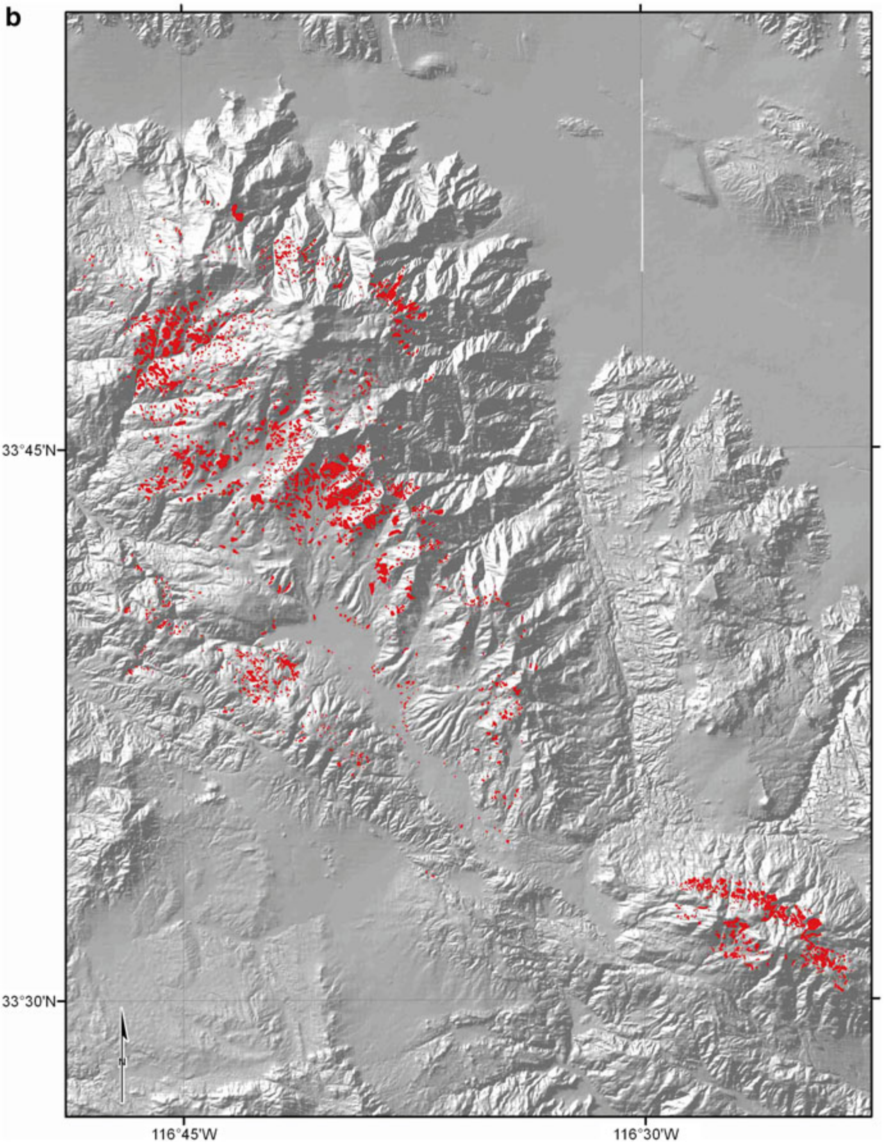

Fig. 29.7 (continued)

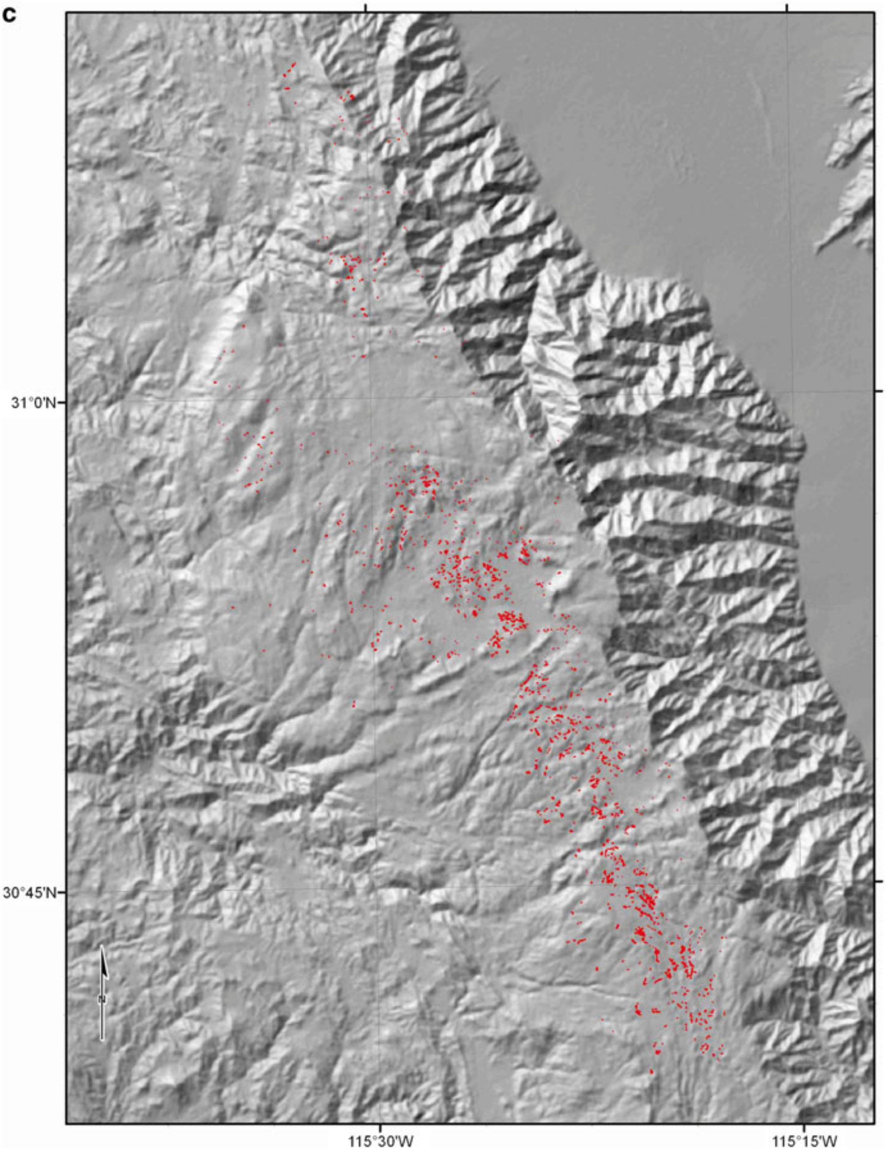

Fig. 29.7 (continued)

29.9 High Resolution Forest Sampling Using Google Earth

One-ha forest samples were taken on Google Earth, using imagery from 2003 to 2005 when dead trees retained foliar canopy at 4162 sites in SBM and SJM, and 1758 sites in SPM. To assure comprehensive uniform coverage, the area was

Table 29.2 Area size frequency distribution of whole stand mortality (frequency and cumulative area)[a]

Region[b]		<1	1–2	2–4	4–8	8–16	16–50	50–100	400–800	Total	Forest area (ha)	Percent loss
SBM	Freq	5279	416	248	130	61	36	8	1	6179		
	Area	1298	581	685	734	637	1014	544	743	6236	97,042	6.4
SJM	Freq	669	51	23	13	5	2			2483		
	Area	176	69	65	72	56	45			1763	63,350	2.8
SPM	Freq	443	33	12	4	1				493		
	Area	123	43	31	24	10				230	35,194	0.6

Data derived from polygon files using ARC GIS

[a] Derived from polygon data files shown in Fig. 27.

[b] *SBM* San Bernardino Mountains, *SJM* San Jacinto Mountains, *SPM* Sierra San Pedro Mártir

sampled in a matrix following an east-west "flight paths," adjusting for scale change with terrain elevation and "eye altitude" using the zoom function on Google Earth. At each site the following was recorded: Location, elevation (m), slope (deg.), vegetation type, living (green) tree cover (%), dead (yellow/brown) tree cover (%), the sum of "live" and "dead" cover representing total tree cover at the onset of the drought, and time-since-fire based on FRAP fire perimeter records in SCA and SPM (Minnich et al. 2000). Pre-suppression burns from 1878 to 1909 were reconstructed from 1938 aerial photographs, ground photographs dating to 1880, and records of fire in the Los Angeles *Times*. Fires were delimited using burn scars on 1938 aerial photograph and georeferenced for transfer onto Google Earth imagery. Slope was estimated using the difference between the highest and lowest elevations in each sample. Aspect was dichotomously fixed hemispherically as "north" or "south" based on the orientation of local contours on topographic sheets.

29.9.1 Species-Specific Death Rates

Forest assemblages exhibit discrete species-specific differences in mortality rate related to species longevity, intrinsic life traits and their corresponding habitats. Mortality rates are inversely related to species longevity. Tree cover death is highest in *Pinus coulteri* (57.8 %), intermediate in *Pseudotsuga macrocarpa* (24.7 %) and mixed conifer forest (26.0–33.6 %), and lowest in subalpine forest (2.0 %). This outcome should be expected, purely on statistical grounds, because long-lived species have the greatest probability of experiencing previous pandemics comparable to 2002. The longevity of trees translates into greater environmental space from which to obtain resources, i.e., stems integrated into the habitat over long time scales have a large proportion of resources carried over long time scales, which may buffer them from environmental variability (Grulke 1999, 2003). Short-lived, closed-cone *Pinus coulteri* is killed in stand-replacement fire cycles. Hence, life spans are defined by fire cycle with intervals of decades but recovery to reproductive maturity develops by 20 years (reviewed in Minnich 2007a). Perhaps selection for rapid growth results in the production of soft wood that offers less resistance insect attack and disease, as well as possible deficient stomatal water regulation in drought. *P. coulteri* sustained the highest mortality among coniferous species in the drought of 1988–1991 (50 ha^{-1} in SJM; Savage 1994). *Pseudotsuga macrocarpa* stems may persist for centuries through survival of recurrent subcanopy burns at intervals of ca. 50 years in shady and fire-resistant canyons subject to convergent water flow (Minnich 2007a). Subalpine forests growing at highest altitudes have the shortest growing seasons, lowest productivity and multi-century fire intervals (Table 29.3).

In BCA tree cover death is 5 times below those in SCA, with all forest assemblages experiencing lower attrition than their counterparts in SCA. Mixed conifer forest assemblages sustained mortality rates of 2.4–9.9 %. *Pinus coulteri* had a general attrition rate of only 8.3 % compared to 57.8 % in SCA. Virtually no trees perished in subalpine *P. contorta* forest. Clearly, other factors transcend species life traits. Mean annual precipitation in SPM is similar to SJM and less than SBM. Since precipitation departures in the 4-year drought were comparable across the California borderland, precipitation alone cannot explain the difference. At climatic time scales, available soil water is not as large as the precipitation gradient because of increases in the ratio of runoff to ET with increasing latitude (Franco-Vizcaino et al. 2002), i.e., differences in available plant water are minimized by low field capacities of shallow soils and regolith. In SCA, a larger portion of annual precipitation is lost in overland flow to the Pacific than in BCA where virtually all water is consumed by transpiration of vegetation, i.e., the relationship between P and ET increasingly stronger as water deficit increases. Hence, the amount of recharge and ET is proportional to the amount of biomass as expressed in canopy leaf area (Franco-Vizcaino et al. 2002). Grulke et al. (2009) showed that *P. ponderosa* mortality was directly related to pre-pandemic forest cover (Fig. 29.8).

29.9.2 Elevation

In SCA forest mortality decreases with altitude, but the trend is not symmetrical. Tree cover death is uniformly high from 1200 to 2300 m before decreasing rapidly to <1 % at 2800 m (Table 29.3). In BCA mortality is greatest at base of the forest 1800–2000 m, then decreases gradually to 2 % at 2500 m. It can be argued that lower mortality in BCA can be attributed to higher elevation forest limits (1700 m vs. 1400 m) but tree loss at fixed altitudes is consistently higher in SCA than BCA. Closed cone forests had anomalously low mortality rates at elevations <1300 m in SCA.

The decrease in forest loss with altitude is related to climatic gradients in which increasing precipitation upslope is phased with decreasing temperature and ET with altitude. Tree mortality profiles suggest that soils and rock mantle depletion extended to as high as 2300 m in SCA and the lower limit of forests (1800 m) in BCA. Low tree loss >2300 m in SCA is related to increasing growing season soil water from snowmelt with elevation. In 2002, snowpack in SBM and SJM was observed at

Table 29.3 Tree cover mortality (percent) in the 2002–2003 drought. Forest types arranged with increasing elevation from the left

A. Elev. (m^3)	Knob-cone[a]	Coulter pine	BCDF	MCF Ppond	Jeffrey pine	MCF Jef P	MCF Wfir	Lodge-pole	Total loss all forests
<1.0	8.4		23.3						13.1
1.0–1.1									16.2
1.1–1.2	1.2		27.9						19.0[b]
1.2–1.3	1.5	17.4	27.0	33.9					17.4
1.3–1.4	2.0	47.4	19.0	28.3	18.3	16.4			22.6
1.4–1.5	2.3	52.7	22.1	28.2	15.7	15.0			28.9
1.5–1.6		66.2	25.3	36.0	28.4	16.5			41.7
1.6–1.7		56.3	27.8	36.8	18.1	15.8	12.4		39.2
1.7–1.8		60.9	25.8	43.6	30.2	26.0	31.0		43.3
1.8–1.9		59.5	8.2	24.2	33.4	32.9	37.0		36.6
1.9–2.0		50.8	16.3	19.7	37.3	33.6	36.6		34.7
2.0–2.1		61.9		20.7	25.7	30.5	36.4		32.9
2.1–2.2		57.3		28.1	36.8	32.6	34.4		33.5
2.2–2.3					26.3	28.3	28.4		28.6
2.3–2.4					40.3	25.9	20.1		25.9
2.4–2.5					25.9	16.5	16.5		16.5
2.5–2.6					20.6	12.2	9.7	11.5	11.4
2.6–2.7						11.8	9.0	4.0	8.7
2.7–2.8						6.8		0.2	3.6
2.8–2.9								0.9	0.9
2.9–3.0								0.1	0.1
3.0–3.1								0	0
3.1–3.2								0	0
3.2–3.3								0	0
N	107	750	56	414	694	2167	534	218	4162
Mean	5.3	57.8	24.7	33.6	28.0	26.0	27.0	2.0	
Mean Tree Cover	36.1 ±23.2	22.3 ±12.1	23.3 ±11.4	47.0 ±23.0	23.6 ±10.0	28.8 ±13.6	34.5 ±15.8	23.5 ±7.1	

B. Elev.(m^3)	Coulter pine	Jef pine	MCF Jef P	MCF W fir	Lodge-pole	Total loss all forest
<1.0						
1.0–1.1						
1.1–1.2						
1.2–1.3						
1.3–1.4						
1.4–1.5						
1.5–1.6						
1.6–1.7						
1.7–1.8	10.5	10.9	10.9			9.7[c]
1.8–1.9	7.0	17.2	15.8			16.7

(continued)

Table 29.3 (continued)

B. Elev.(m^3)	Coulter pine	Jef pine	MCF Jef P	MCF W fir	Lodge-pole	Total loss all forest
1.9–2.0		20.5	17.9			13.1
2.0–2.1		9.5	9.2			9.4
2.1–2.2		13.1	12.0			11.8
2.2–2.3		6.8	6.1			6.1
2.3–2.4		4.0	4.6	8.0		4.4
2.4–2.5		0.3	2.8	2.8	0.1	2.4
2.5–2.6			2.4	2.4		2.4
2.6–2.7			1.5	1.8		1.5
2.7–2.8			0.4	0.5		0.3
2.8–2.9						0
2.9–3.0						
3.0–3.1						
3.1–3.2						
3.2–3.3						
N	55	653	1657	218	64	1758
Mean	8.3	9.9	5.2	2.4	0.1	
Mean Tree Cover	24.1 ±14.9	18.8 ±6.5	21.7 ±7.8	26.2 ±9.6	23.5 ±7.1	

Living and death tree cover measured from Google Earth imagery in 2003–2005 before canopy leaf drop. Sample data on minor forest types (*Juniperus grandis*, *Calocedrus decurrens*, and *Cupressus montana* are included in summary column on right: (A) San Bernardino and San Jacinto Mountains of southern California, USA. (B) Sierra San Pedro Mártir of Baja California, Mexico

[a] Forest types. Knobcone, *Pinus attenuata*; Coulter pine, *Pinus coulteri*; BCDF, *Pseudotsuga macrocarpa*; MCF Ppond, Mixed conifer forest, *Pinus ponderosa*; Jeffrey pine, monotypic *Pinus jeffreyi*; MCF Jef P, Mixed conifer forest, *Pinus jeffreyi*; MCF Wfir, Mixed conifer forest, *Abies concolor-Pinus lambertiana*; Lodgepole, *Pinus contorta-Pinus flexilis* forest. *P. flexilis* occurs only in California

[b] Values for elevations <1300 includes statistically small samples of several types occurring in isolated stands including, Pinus attenuata, Pinus coulteri, Pseudotsuga macrocarpa, and Pinus ponderosa

[c] Includes isolated forests below 1700 m, mostly *Pinus jeffreyi*

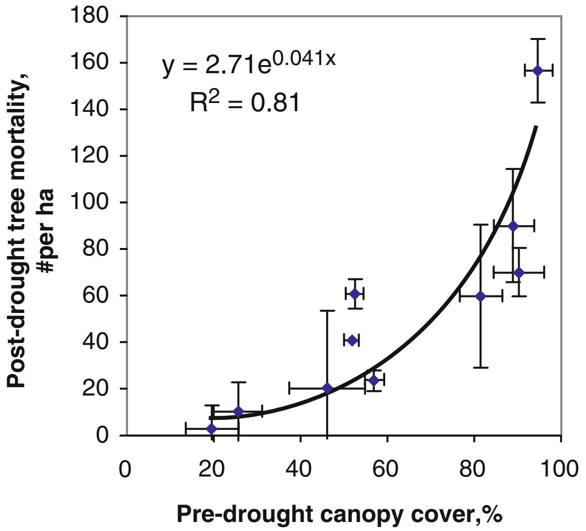

Fig. 29.8 Post-drought tree mortality versus pre-drought canopy cover (%) in ponderosa pine forest of the San Bernardino Mountains (From Gruelke et al. 2009)

3000 m into early May, despite the deficit winter seasonal total precipitation. Soil moisture recharge in rain-dominated climates at lower elevations is linked to the seasonal distribution of storms. With increasing elevation replenishment is postponed to the snowmelt season in spring or early summer when most of the winter's cumulative precipitation in the snowpack is released in a period of weeks. The ratio of frozen precipitation to average annual precipitation in the California borderland decreases uniformly with altitude reflecting atmospheric lapse rates (Minnich 1986). The lower limit of reliable snowfall of 1000–1200 m approximates the moist adiabatic lapse rate from mean sea surface temperatures. Snow/mean annual precipitation ratios in the California borderland increase to 25 % at 1750 m, 75 % at 2750 m and 100 % at 3000 m. Snowmelt is dependent primarily on solar and infrared radiant loading (Miller 1981) in high sun beginning in April. Climatic snowfall data does not exist in BCA but MODIS imagery since 2002 records earlier terminal snow melt in SPM than SCA by ca. 1 month.

The ordinal ranking of species mortality rates in SCA persists at all elevations. For example, *Pinus coulteri* consistently sustained higher mortality than other species at all elevations. This trend lends additional support for species-specific response to extreme drought.

29.9.3 Slope and Aspect

The relationship between pandemic tree loss with slope and aspect exhibits species-specific trends, but does not account for broadscale differences in SCA and BCA. Mortality increases with slope in *Pinus coulteri*, *Pseudotsuga macrocarpa*, and *P. jeffreyi* mixed conifer forest. In these species habitats, regolith appears to desiccate faster at steep, exposed well drained topographic positions such as ridgelines than in sheltered canyon bottoms having convergent water accumulation. Mortality was highest on south-facing slopes in monotypic and mixed *Pinus jeffreyi* forest, *Pinus coulteri* forest, and on steep slopes with *P. ponderosa* forest. Tree loss was greatest on north-facing (poleward) slopes in *Pseudotsuga macrocarpa* and *Abies concolor*, but this trend is biased by the scarcity of these assemblages on south-facing exposures. *Abies concolor* fir attrition was slope neutral. Forest die-off *P. ponderosa* mixed conifer forest was most severe on level surfaces that support deep soils and high forest densities which, in turn, contribute to increased competition for water and mortality (Grulke et al. 2009). In BCA, mortality was largely indifferent to slope (Table 29.4).

29.9.4 Time-Since-Fire

Repeat aerial photography show tree death increases with time-since-fire (TSF) in all forest types in SCA. Mortality was greater in SCA than in BCA. We conclude that die-off was exacerbated in SCA by forest densification in fire suppression,

Table 29.4 Tree cover mortality (percent) by slope and exposure

A. Slope/Asp. (deg. N/S)[a]	Knob-cone[a]	Coulter pine	BCDF	MCF pond	Jeffrey pine	MCF Jef P	MCF Wfir	Lodge-pole	All forest
North <10	–	61.4	–	33.6	19.1	17.8	19.4	8.9	
10–20	5.2	54.8	10.8	35.3	32.6	23.8	22.3	12.8	
20–30	7.1	38.7	26.7	29.1	30.7	31.5	29.6	1.9	
30–40	4.2	31.8	31.6	–	46.2	33.7	31.5	–	
>40	–	70.9	33.1	–	–	21.8	20.6	–	
South<10		67.1	–	32.6	27.2	21.7	16.7	9.9	
10–20		56.9	6.2	31.8	53.1	31.2	38.5	17.8	
20–30		47.6	3.7	50.8	48.9	33.7	–	2.3	
30–40		–	5.1	–	–	40.0	–	–	
>40		–	–	–	–	40.2	–	–	

B. Slope/Asp (deg. N/S)	Coulter pine	Jef pine	MCF Jef P	MCF W fir	Lodge pole	All forest
North <10	5.1	8.9	4.9	2.4	0.1	
10–20	3.5	12.8	4.9	3.4	–	
20–30	11.0	1.9	2.9	2.4	–	
30–40	–	–	1.8	0.3	–	
>40	–	–	–	–		
South <10	–	9.9	6.2	2.7	–	
10–20	–	17.8	5.0	1.7	–	
20–30	–	2.3	0.5	0	–	
30–40	–	–	2.1	1.6	–	
>40	–	–	–	–	–	

(A) San Bernardino and San Jacinto Mountains of southern California, USA. (B) Sierra San Pedro Mártir

[a] Forest types: Knobcone, *Pinus attenuata*; Coulter pine, *Pinus coulteri*; BCDF, *Pseudotsuga macrocarpa*; MCF Ppond, Mixed conifer forest, *Pinus ponderosa*; Jeffrey pine, monotypic *Pinus jeffreyi*; MCF Jef P, Mixed conifer forest, *Pinus jeffreyi*; MCF Wfir, Mixed conifer forest, *Abies concolor-Pinus lambertiana*; Lodgepole, *Pinus contorta-Pinus flexilis* forest. *P. flexilis* occurs only in California

while free burning limits attrition in BCA. The SCA conifer forests have longer fire intervals than BCA despite the similarity of climate and forest vegetation. At the scale of watersheds, evapotranspiration increases with post-fire successional regrowth of vegetation (Loáiciga et al. 2001). Drought stress is predicted to augment tree mortality with increasing TSF. Competition for soil moisture is enhanced by conifer ingrowth increasing tree population susceptibility to attack in drought stress, i.e., reproductive success increases water demand (Pronos et al. 1999). In *Pinus ponderosa* post-drought mortality was directly related to pre-drought canopy cover (Fig. 29.8; Gruelke et al. 2009) (Table 29.5).

In SPM, fire intervals based on spatially explicit maps from repeat aerial photographs are ca. 50 years (Minnich et al. 2000). Based on field TSF chronosequences, it is hypothesized that long interval, free-burning in SPM mixed conifer forest is dependent on the gradual development and vertical integration of conifer in growth with overstory sufficient for flame line convection and consumption of needlecast.

Table 29.5 Tree cover mortality (percent) by time-since-fire (TSF)

A. TSF (years)	Knob-cone[a]	Coulter pine	BCDF	MCF Ppond	Jeffrey pine	MCF Jef P	MCF Wfir	Lodge-pole
<20	–	11.3	5.5	–	16.4	14.6	–	–
20–40	5.9	15.1	16.8	9.9	21.5	17.4	19.2	–
40–60	3.9	46.3	28.0	28.1	25.0	26.1	24.0	–
60–80	–	51.4	8.6	4.8	26.2	31.9	42.8	–
80–100	–	71.6	13.2	32.3	48.1	23.8	29.1	0.1
100–120	–	74.8	84.6	37.8	30.2	23.8	21.9	–
>120	–	73.9	25.6	36.8	28.0	27.3	29.6	–

B. TSF. (years)	Coulter pine	Jef pine	MCF Jef P	MCF Wfir	Lodge-pole
<20	–	12.8	9.8	1.8	–
20–40	3.2	9.2	6.8	4.7	–
40–60	12.3	17.2	3.3	2.7	–
60–80	–	6.1	5.1	1.3	–
80–100	–	12.7	4.5	3.0	–
>100	–	8.3	–	–	0.1

(A) San Bernardino and San Jacinto Mountains of southern California, USA. (B) Sierra San Pedro Mártir of Baja California, Mexico

[a] Forest types. Knobcone, *Pinus attenuata*; Coulter pine, *Pinus coulteri*; BCDF, *Pseudotsuga macrocarpa*; MCF Ppond, Mixed conifer forest, *Pinus ponderosa*; Jeffrey pine, monotypic *Pinus jeffreyi*; MCF Jef P, Mixed conifer forest, *Pinus jeffreyi*; MCF Wfir, Mixed conifer forest, *Abies concolor-Pinus lambertiana*; Lodgepole, *Pinus contorta-Pinus flexilis* forest. *P. flexilis* occurs only in California

Fire starts in open "umbrella" forest parks with vertical detachment of subcanopy and overstory fuels in early succession quickly dissipate as microburns. In *Pinus coulteri,* cohort regeneration limits forest densification. Water demand is enhanced with TSF by the cumulative growth of chaparral and *Quercus chrysolepis* woodlands.

In SPM cumulative TSF patch distributions increase to 57.7 % after 50–60 years (Table 29.6) with few patches exceeding 90 years. In SCA, cumulative distributions increase to 23.4 % at 50 years and 32.8 % at 90 years. More than half of forests had not burned since the nineteenth century. Forest cover at the onset of the pandemic forest cover ranged from 30% to 50 % in SCA and 19–26 % in BCA (Table 29.3). Differences are consistent with the replication of Vegetation Type Map Survey (VTM) survey plots in SBM that show increasing forest density in SBM by a factor 1.5–2.0 over a 60 year period (Minnich et al. 1995).

We suggest that a hypothetical cumulative TSF distribution similar to SPM would have mitigated forest losses in SCA. In SCA forest loss increases with TSF in all forest types (Table 29.5). Modest losses were limited to uncommon stands with TSF <40 years. *P. attenuata* attrition was surprisingly low (5.3 %) but all stands had TSF <60 years. Tree cover losses in BCA were uniform in all age classes ranging from 1.3 to 12.7 % because most forests had burning in the past 60 years. Maximum tree loss occurred in monotypic *Pinus jeffreyi* with TSF of 40–60 years in southern forests at elevations of 1800 m, most exposed to ET stress.

Table 29.6 Decadal time-since-fire (TSF) by percent forest area and cumulative distribution at the onset of extreme drought in 2002[a]

TSF (years)	SCA TSF (%)	Cumulative (percent)	BCA TSF (%)	Cumulative (%)
<10	1.3	1.3	7.9	7.9
10–20	0.2	1.5	5.7	13.6
20–30	4.5	6.0	6.5	19.1
30–40	9.5	15.5	7.3	26.4
40–50	4.3	19.8	9.6	36.0
50–60	4.6	23.4	21.7	57.7
60–70	2.2	25.6	14.0	71.7
70–80	2.4	28.0	4.2	75.9
80–90	4.8	32.8	19.2	94.1
90–100	4.5	37.3	0	94.1
100–110	11.3	48.6	5.9	100.0
110–120	9.0	57.6	–	–
>120	42.4	100.0	–	–

[a] Data obtained from fire perimeter maps in Minnich et al. (2000), FRAP, and historical (pre-suppression) fire history reconstructed from aerial photographs in 1938, ground photographs in 1880–1910, and reported in the Los Angeles Times (unpublished)

29.10 Climate Variability and Future Pandemics

We propose that mixed conifer forest in SCA has enhanced susceptibility to tree pandemics because the past century of fire suppression management has resulted in forest-stand densification which amplifies drought stress among trees competing for soil moisture. When and where pandemics occur is expected to be randomized by local coincidence of multi-year drought punctuated by a “rainless” winter. Previous droughts lacking a “rainless winter” triggered comparatively modest die-back (e.g., 1976–1977, 1988–1991), and a single hydrologic year of extreme drought in 2006–2007 failed to trigger die-off beyond background mortality rates. It appears that depletion of moisture stored deep in a fractured weathered porous regolith requires protracted drought of several years. Increased competition for soil moisture in forests where tree-densities have multiplied over the past century of fire suppression management may lower the drought stress threshold required to sustain pandemics. Dense forests susceptible to pandemics are becoming increasingly widespread in California. Another forest collapse is presently taking hold in the Frazier Mountain-Mt. Pinos region of Ventura and Santa Barbara Counties, 100 km northwest of Los Angeles, is under similar drought conditions to the 2002–2003 pandemic. The area presently has 4-year drought (2011–2015) and precipitation was ca. 35 % of normal in the winter of 2014–2015 (Western Regional Climate Center 2015: http://www.wrcc.dri.edu). The affected area comprises anomalous dense forests with TSF >100 years.

Recent studies have attributed extensive deforestation by drought and fire in the western United States as effects of climate change, overlooking a complicated legacy of fire suppression management. Westerling et al. (2006) posit that global warming has contributed to a substantial increase in large wildfires in the western US beginning in the mid-1980s, with longer wildfire durations and wildfire seasons due to increasing spring/summer temperatures and earlier spring snow melt. The study did not account for fire suppression effects including longer fire intervals, homogenization of fuels across landscapes, and selection for large fires to coincide with extreme weather states (Minnich and Chou 1997; Minnich and Franco-Vizcaino 2009)). Low tree loss under free-burning in BCA compared to SCA indicates such massive disparities in dead fuel build-up from the 2002–2003 pandemic, that megafires are to be expected north of the border regardless of global warming trends. The SPM region is dominated by small to moderate sized fires that have maintained open forests to this day. In SCA open forests were photographed in the late nineteenth century (Minnich 1988). Early twentieth century VTM Survey forest densities and diameter frequency distributions in SBM are similar to those presently in SPM (Minnich et al. 1995). SCA forests now have legacy of massive dead fuel build-up from the 2002–2003 pandemic in surviving dense living forests that have not seen fire for >100 years. BCA forests survived the drought with limited attrition.

Kelly and Goulden (2008) interpreted hydrologic tree death of lower elevation forest in the Santa Rosa Mountains at the south end of SJM as the upslope migration of species predicted in global warming. A central unaddressed question is whether the remnant surviving forest represents a "retreat" as long-term permanent change or "recalibration" to forest boundaries set in the last great pre-historical drought? The recent pandemic is the most extreme event in least 150 years, possibly since eighteenth century Little Ice Age climate. Long-term change assumes that trees will no longer recolonize the dead zone in the coming centuries. Alternatively, the "recalibration" model proposes that drought reversed downward recolonizing forests since the last great pandemic. In the future, lower altitudes gradually recolonize before the next future pandemic under secure regolith water. The zonal pattern of mortality on Santa Rosa Mountain coincides with anomalously old TSF patches having high water demand. SPM forests did not experience upslope retreat in the 2002–2003 pandemic.

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References

Allen-Diaz B, Standiford R, Jackson RD (2007) Oak woodlands and forest. In: Barbour MG, Keeler-Wolf T, Schoenherr AS (eds) Terrestrial vegetation of California, 3rd edn. University of California Press, Berkeley, pp 314–338

Arbaugh MJ, Peterson DL, Miller PR (1999) Air pollution effects on growth of Ponderosa pine, Jeffrey pine, and bigcone Douglas-fir. In: Miller PR, McBride JR (eds) Oxidant air pollution impacts in the Montane Forests of southern California: a case study of the San Bernardino Mountains, vol 134, Ecological studies. Springer, New York

Arkley RJ (1981) Soil moisture use by a mixed conifer forest in a summer-dry climate. Soil Sci Soc Am J 45:423–427

Barbour MG, Keeler-Wolf T, Schoenherr AS (eds) (2007) Terrestrial vegetation of California, 3rd edn. University of California Press, Berkeley

Fenn ME, Poth MA, Bytnerowicz A et al (2003) Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems of the Sierra Nevada. In: Bytnerowicz A, Arbaugh JJ, Alonso R (eds) Ozone air pollution in the Sierra Nevada: distribution and effects on forests, vol 2, Developments in environmental science. Elsevier, Amsterdam/Boston

Franco-Vizcaino E, Escoto-Rodriguez M, Sosa-Ramirez J et al (2002) Water balance at the southern limit of the Californian mixed-conifer forest and implications for extreme-deficit watersheds. Arid Land Res Manage 16:133–147

Graham RC, Hubbert KR (2012) Comment on "Soil moisture response to snowmelt and rainfall in a Sierra Nevada mixed-conifer forest". Vadose Zone J 11(4). doi:10.2136/vzj2012.0004

Graham RC, Rossi AM, Hubbert KR (2010) Rock to regolith conversion: producing hospitable substrates for terrestrial ecosystems. GSA Today 20(2):4–9. doi:10.1130/GSAT57A.1

Grulke NE (1999) Physiological responses of Ponderosa pine to gradients of environmental stressors. In: Miller PR, McBride JR (eds) Oxidant air pollution impacts in the Montane Forests of southern California: a case study of the San Bernardino Mountains, vol 134, Ecological studies. Springer, New York, pp 126–163

Grulke NE (2003) The physiological basis of ozone injury assessment attributes in Sierran conifers. In: Bytnerowicz A, Arbaugh MJ, Alonso R (eds) Ozone air pollution in the Sierra Nevada: distribution and effects on forests, vol 2, Developments in environmental science. Elsevier, Amsterdam/Boston, pp 55–81

Grulke NE, Minnich RA, Paine TD et al (2009) Air pollution increases forest susceptibility to wildfires: a case study in the San Bernardino Mountains in southern California. In: Bytnerowicz A, Arbaugh M, Riebau A, Andersen C (eds) Wildfires and air pollution. Developments in environmental science, vol 8. Elsevier, Amsterdam, pp 365–403

Holdenrieder O, Pautasso M, Weisberg PJ et al (2004) Tree diseases and landscape processes: the challenge of landscape pathology. Trends Ecol Evol 19:446–452

Hubber KR, Beyers JL, Graham RC (2001) Roles of weathered bedrock and soil in seasonal water relations of *Pinus Jeffreyi* and *Arctostaphylos patula*. Can J For Res 31:1947–1957

Jones DP, Graham RC (1993) Water-holding characteristics of weathered granitic rock in chaparral and forest ecosystems. Soil Sci Soc Am J 57:256–261

Keeley JE, Davis FW (2007) Chaparral. In: Barbour MG, Keeler-Wolf T, Schoenherr AA (eds) Terrestrial vegetation of California, 3rd edn. University of California Press, Berkeley, pp 339–366

Kelly AE, Goulden ML (2008) Rapid shifts in plant distribution with recent climate change. Proc Natl Acad Sci USA 105:11823–11826

Loáiciga H, Pedreros D, Roberts D (2001) Wildfire-streamflow interactions in a chaparral watershed. Adv Environ Res 5:295–395

Maloney PE, Rizzo DM (2002) Pathogens and insects in a pristine forest ecosystem: the Sierra San Pedro Martir, Baja, Mexico. Can J For Res 32:448–457

McBride JR, Miller PR (1999) Implications of chronic air pollution in the San Bernardino Mountains for forest management and future research. In: Miller PR, McBride JR (eds) Oxidant air pollution impacts in the Montane Forests of southern California: a case study of the San Bernardino Mountains, vol 134, Ecological studies. Springer, New York, pp 405–416

Miller DH (1981) Energy at the surface of the Earth: a introduction to the energetics of ecosystems, vol 27, International geophysics series. Academic Press, New York

Minnich RA (1983) Fire mosaics in southern California and northern Baja California. Science 219:1287–1294

Minnich RA (1986) Snow levels and amounts in the mountains of southern California. J Hydrol 89:37–58

Minnich RA (1988) The biogeography of fire in the San Bernardino Mountains of California: a historical study. University of California publication in geography, vol 28. Berkeley: University of California Press, pp 1–120

Minnich RA (1999) Vegetation, fire regimes, and forest dynamics in the San Bernardino Mountains. In: Miller PR, McBride JR (eds) Oxidant air pollution impacts in the Montane Forests of southern California: the San Bernardino Mountains case study. Springer, New York, pp 44–78

Minnich RA (2001) Fire and elevational zonation of chaparral and conifer forests in the Peninsular Ranges of La Frontera. In: Webster GL, Bahre CJ (eds) Plant life in La Frontera: observations on vegetation in the United States/Mexico Borderlands. University of New Mexico Press, Albuquerque, pp 120–142

Minnich RA (2007a) Southern California coniferous forest. In: Barbour MG, Keeler-Wolf T, Schoenherr AS (eds) Terrestrial vegetation of California, 3rd edn. University of California Press, Berkeley, pp 502–538

Minnich RA (2007b) California climate, paleoclimate and paleovegetation. In: Barbour MG, Keeler-Wolf T, Schoenherr AS (eds) Terrestrial vegetation of California, 3rd edn. University of California Press, Berkeley, pp 43–70

Minnich RA, Chou YH (1997) Wildland fire patch dynamics in the chaparral of southern California. Int J Wildland Fire 7:221–248

Minnich RA, Everett RG (2001) Conifer tree distributions in southern California. Madroño 48:177–197

Minnich RA, Franco-Vizcaino E (1998) Land of chamise and pines: historical descriptions of northern Baja California. University of California publications in botany, vol 80. Berkeley: University of California Press, pp 1–166

Minnich RA, Franco-Vizcaino E (2009) A probabilistic view of chaparral and forest fire regimes in southern California and northern Baja California. In: Bytnerowicz A, Arbaugh M, Riebau A, Andersen C (eds) Wildland fires and air pollution, vol 8, Developments in environmental sciences. Elsevier, Amsterdam, pp 339–364

Minnich RA, Barbour MG, Burk JH et al (1995) Sixty years of change in Californian conifer forests of the San Bernardino Mountains. Conserv Biol 9:902–914

Minnich RA, Barbour MG, Burk JH et al (2000) California mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Martir, Baja California, Mexico. J Biogeogr 27:105–129

Minnich RA, Franco-Vizcaino E, Goforth BR (2011) Tree species distributions in northern Baja California interpreted from Google Earth imagery. In: Proceedings of the CNPS conservation conference. California Native Plant Society, pp 186–202

National Centers for Environmental Information (2015) National Oceanic and Atmospheric Administration. www.ncei.noaa.gov. Accessed 28 Dec 2015

Paine TD, Stephen FM, Taha HA (1984) Conceptual model of infestation probability based on bark beetle abundance and host tree susceptibility. Environ Entomol 13:619–624

Paine TD, Raffa KF, Harrington TC (1997) Interactions among scolytid bark beetles, their associated fungi and live host conifers. Annu Rev Entomol 42:179–206

Poole DK, Miller PC (1975) Water relations of selected species of chaparral and coastal sage species. Ecology 56:1118–1128

Pronos J, Merrill L, Dahlsten DL (1999) Insects and pathogens in a pollution-stressed forest. In: Miller PR, McBride JR (eds) Oxidant air pollution in the Montane Forests of southern California: a case study of the San Bernardino Mountains, vol 134, Ecological studies. Springer, New York, pp 317–337

Raffa KF, Berryman AA (1983) The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecol Monogr 53:27–49

Rempe DM, Dietrich WE (2014) A bottom-up control on fresh-bedrock topography under landscape. Proc Natl Acad Sci USA 111:6576–6581

Royce EB, Barbour MG (2000) Mediterranean climate effects. II Conifer growth phenology across a Sierra Nevada ecotone. Am J Bot 88:919–932

Royce EB, Barbour MG (2001) Mediterranean climate effects. I. Conifer water use across a Sierra Nevada ecotone. Am J Bot 88:911–918

Savage M (1994) Anthropogenic and natural disturbance and patterns of mortality in a mixed conifer forest stand in California. Can J For Res 24:1149–1159

Savage M (1997) The role of anthropogenic influences in a mixed-conifer forest mortality episode. J Veg Sci 8:95–104

Stephens SL, Skinner CN, Gill SJ (2003) Dendro-chronology based fire history of Jeffrey pine mixed-conifer forest in the Sierra San Pedro Martir, Mexico. Can J For Res 33:1090–1101

Taylor OC (1973) Oxidant air pollutant effects on a western coniferous forest ecosystem, Task C report, annual progress, 1972–1973. Study site selection and verification data on pollutants and species. EPA-600/3-78-052c, U.S. Environmental Protection Agency. NTIS No. PB 228 333/AS. Air Pollution Research Center, University of California, Riverside

Watson JG, Chow JC, Frasier CA et al (1999) Ambient air quality at Barton Flats and other California forests. In: Miller PR, McBride JR (eds) Oxidant air pollution in the montane forests of southern California: a case study of the San Bernardino Mountains, vol 134, Ecological studies. Springer, New York, pp 81–105

Westerling AL, Hidalgo HG, Cayan DR et al (2006) Warming and earlier spring increase western U.S. Forest Service wildfire activity. Science 313:940–943

White KL (1966) Structure and composition of foothill woodland in central coastal California. Ecology 47:229–237

Witty JH, Graham RC, Hubbert KR et al (2003) Contributions of water supply from the weathered bedrock zone to forest soil quality. Geoderma 114:389–400

Wood DL, Koerber TW, Scharpf RF et al (2003) Pests of native California conifers, vol 70, California natural history guides. University of California Press, Berkeley

Chapter 30
General Conclusions

François Lieutier and Timothy D. Paine

Knowledge and problems presented in chapters of the present volume clearly show that many similarities exist among the different Mediterranean forest systems regarding forest insect pests and diseases, and even ecosystem functioning. These similarities, however, correspond to two different situations. In some cases, the same species are present in different Mediterranean systems because they have been introduced and have found the same suitable conditions in separate locations for their establishment and invasion: same climate, same introduced host tree species, no competitors, and no natural enemies. A typical case is that of the *Eucalyptus* pests. In such situations, the system can be considered identical everywhere it has been introduced. One can also even suppose that this system may function by itself, with possibly very few interactions with the surrounding indigenous systems, especially when the introduced host tree and pest species largely differ from the indigenous ones. Thus, the scientific and practical approaches to addressing these situations can be relatively standardized. An interesting scientific subject in that context is precisely the relations between the functioning of the introduced system and that of the indigenous ones.

In other cases, the similarities among Mediterranean forest systems relate to species that are indigenous in their region, but have similar ecological counterparts in other Mediterranean systems, i.e., homologous guilds developing on homologous host trees. Such situations are very interesting because their comparative study can reveal general traits on the functioning of these guilds and, more generally, on the functioning of forest systems in the Mediterranean areas. Especially, as the basic

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components of ecosystem functioning are tritrophic interactions, a coordinated approach to research efforts on this aspect in homologous insect and disease guilds should be very fruitful. However, as a common characteristic of all Mediterranean forest systems is their heterogeneity, each of these systems inevitably has its own particularities. Above all, the five different Mediterranean regions have had very different human cultural and historical development so, consequently, the different type and extent of human impact may be significant. Comparative investigations on homologous guilds can, thus, also reveal the impact of these particularities on ecosystem functioning. Another scientifically and pragmatically interesting question in such homologous systems relates to the risks of invasion and damage resulting from introduction of insects and diseases from other Mediterranean systems: e.g., interspecific competition leading to elimination of one of the competitors or, alternatively, coexistence with possible changes in damage levels to the forests in both cases.

Because of their similarities and differences, the existence of various Mediterranean forest systems in different parts of the world, and even in different parts of a same region, represents an excellent opportunity for comparative approaches exploring generalizations and factors of variation in ecosystem functioning. Moreover, even if forest pests are presently the focus of similar approaches in the Mediterranean systems, the high species diversity of organisms living in these systems means that the basic biology of most species is still unknown. Comparative research on biodiversity, on identification of key species and their biology in forest Mediterranean systems is thus still heavily needed.

The Mediterranean forest systems should also be prioritized systems for the study of global change and prediction of its effects on forest guilds, with consequences on pest populations. For geographical and topographical reasons, the Mediterranean areas are indeed particularly exposed and susceptible to climate change. They have also been submitted to heavy human impacts for a long time, which are expected to greatly increase in the future, especially in forestry, as indirect consequences of climate change. Combined effect of climate and human action in the Mediterranean areas will certainly lead to dramatic change in the nature, level and extension of pest damage, as well as in the distribution of many species. These changes may result in considerable change in tritrophic interactions and, thus, in forest ecosystem structure and functioning.

The essential fields that deserve to be investigated with both scientific and applied objectives in the Mediterranean forest systems are highly diverse. However, all research fields should lean on two main general principles: (1) They all need to be thought in the context of global change; (2) The local peculiarities must be taken into account because of the heterogeneity and diversity of the Mediterranean systems. This will not be done without a real cooperation between different disciplines and between different countries and regions among the various Mediterranean areas. The present "MEDINSECT" 7-03-14 IUFRO group offers the structure for such cooperative research efforts.