

# Chapter 13

## The Multiple Causes of Forest Decline in Spain: Drought, Historical Logging, Competition and Biotic Stressors

**J. Julio Camarero, Juan Carlos Linares, Gabriel Sangüesa-Barreda, Raúl Sánchez-Salguero, Antonio Gazol, Rafael M. Navarro-Cerrillo, and José Antonio Carreira**

**Abstract** Climate warming is predicted to intensify drought stress in forests by amplifying the severity and frequency of droughts. This drying trend will potentially trigger forest dieback, characterized by tree growth decline and mortality. In drought-prone Spain, forest decline is mainly attributed to severe water shortage. This inciting factor causes a loss in tree vigor and interacts with predisposing or contributing factors that usually act at long time scales. Combined, these factors drive complex patterns of forest decline. Here, we illustrate four case studies on forest decline in Spain, evaluated using dendroecology. These declines were triggered by drought, interacting with other causal factors including past logging in Pyrenean silver fir, increased competition induced by land-use changes in Spanish

---

J.J. Camarero (✉) • G. Sangüesa-Barreda • A. Gazol  
Pyrenean Institute of Ecology (IPE-CSIC), Avenida Montañana 1005, Zaragoza, 50059 Spain  
e-mail: [jjcamarero@ipe.csic.es](mailto:jjcamarero@ipe.csic.es); [gsanguesa@ipe.csic.es](mailto:gsanguesa@ipe.csic.es); [agazolbu@gmail.com](mailto:agazolbu@gmail.com)

J.C. Linares  
Department of Physical, Chemical and Natural Systems, Universidad Pablo de Olavide, Ctra. Utrera km. 1, Seville 41013, Spain  
e-mail: [jclincal@upo.es](mailto:jclincal@upo.es)

R. Sánchez-Salguero  
Pyrenean Institute of Ecology (IPE-CSIC), Avenida Montañana 1005, Zaragoza, 50059 Spain  
Department of Physical, Chemical and Natural Systems, Universidad Pablo de Olavide, Ctra. Utrera km. 1, Seville 41013, Spain  
e-mail: [rsanchez@upo.es](mailto:rsanchez@upo.es)

R.M. Navarro-Cerrillo  
Department of Forest Engineering, ERSAF, University of Córdoba, Campus de Rabanales, Ctra. IV, km 396, Córdoba 14071, Spain  
e-mail: [rmnavarro@uco.es](mailto:rmnavarro@uco.es)

J.A. Carreira  
Centro de Estudios Avanzados de la Tierra (CEACTierra), Universidad de Jaén, 23071 Jaén, Spain  
e-mail: [jafuente@ujaen.es](mailto:jafuente@ujaen.es)

fir, variation in drought vulnerability of planted pine species, and mistletoe infection in Scots pine. These case studies demonstrate that multiple causes drive forest decline in drought-prone regions. Differentiating the causal factors and inferring their interactions was feasible through tree-ring analyses, which provide robust reconstructions of changes in tree vitality through time.

**Keywords** Drought • Forest dieback • Stress • Tree death • Tree growth

## 13.1 Introduction

Climatic change is among the major drivers of forest decline at present (Allen et al. 2015) and in the past (Foster et al. 2006). Forest decline or dieback is a phenomenon affecting trees worldwide, causing a premature loss of vitality, growth decline, canopy dieback, and rising mortality rates (Muller-Dombois 1992). In water-limited regions, climate warming may intensify drought stress and accelerating forest decline processes, preferentially affecting the most vulnerable individuals, populations and species (McDowell et al. 2008; Anderegg et al. 2016). Climate warming without increases in precipitation is accompanied by aridification and extreme drought events can lead to abrupt and rapid changes in forest dynamics including severe forest decline (Allen et al. 2015).

Drought-triggered forest decline can be also predisposed by other factors, which act synergistically by reducing tree vitality (*sensu* Manion 1991). Competition is a major contributor to tree mortality in temperate (Das et al. 2011; Amoroso and Larson 2010) and dry Mediterranean forests (Bravo-Oviedo et al. 2006). In regions with intensively managed forests, such as Europe and north-eastern America (Reams and Huso 1990), past thinning, harvesting, and reforestation shape the current forest structure and composition, often resulting in forests more susceptible to drought. For instance, reforestation with high initial densities or using genotypes with a low tolerance to drought can contribute to drought-induced decline (Sánchez-Salguero et al. 2012). In stands exploited in the past then abandoned, the establishment of conservation measures may lead to dense forests that are more prone to drought-induced decline and death (Franklin et al. 1987; Peet and Christensen 1987; Waring 1987). In addition to stand history, climate warming may increase the incidence of biotic stressors as mistletoes, insects and pathogenic fungi, making forests more prone to drought-associated decline (Ayres and Lombardero 2000).

Most Spanish forests are subjected to periodic drought stress, which makes them a good system to study forest decline (Martínez-Vilalta and Piñol 2002; Camarero et al. 2015a). The application of dendroecology to study forest decline corroborates observations that trees with pronounced leaf shedding or exhibiting crown dieback also exhibit low rates of growth, which often portend tree death (LeBlanc and Raynal 1990; Ogle et al. 2000; Bigler and Bugmann 2003; Dobbertin 2005;

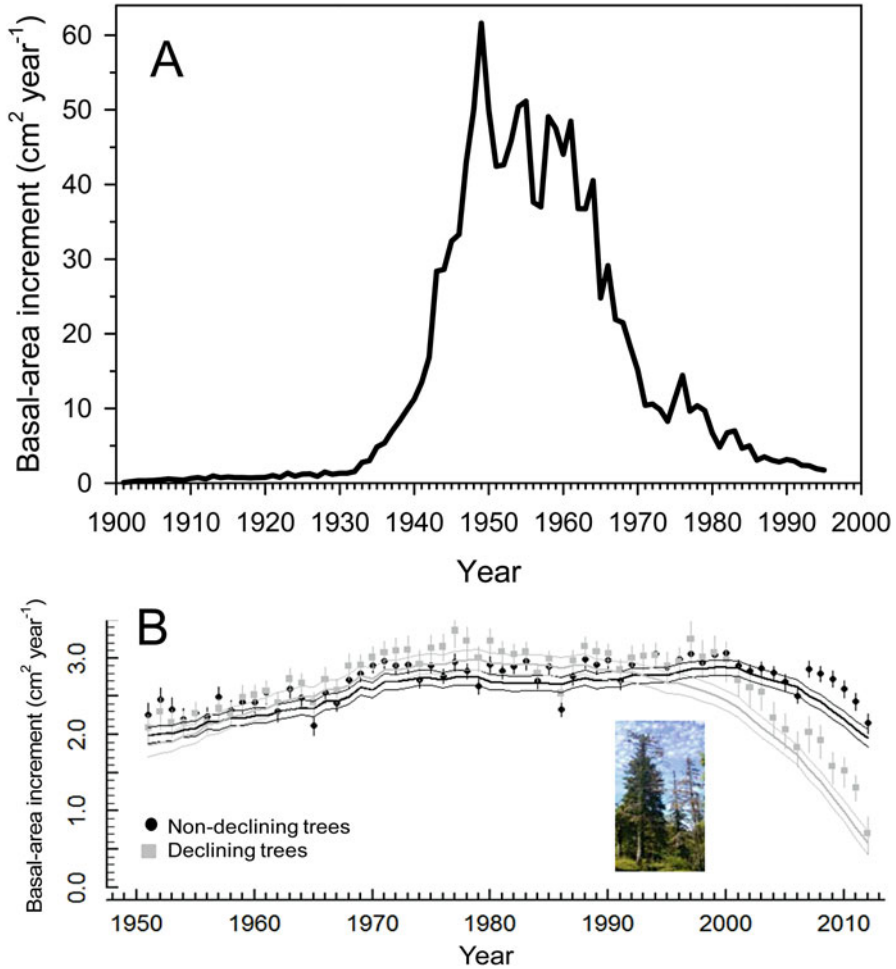
Amoroso and Larson 2010). Here, we illustrate four case studies on forest decline in Spain, evaluated using dendroecology. We show how drought stress triggers decline and interacts with predisposing or contributing factors (*sensu* Manion 1991) in four case studies: past logging in the case of Pyrenean silver fir (*Abies alba* Mill.), increased competition induced by land-use changes in the case of Spanish fir (*Abies pinsapo* Boiss.), variation in drought vulnerability of several planted pine species, and mistletoe infection in the case of natural Scots pine stands. We use these case studies to: (i) show the complex etiology of forest decline since tree dieback and death are attributed to drought interacting with other stressors; and (ii) to demonstrate how tree-ring analyses applied to this ecological issue pinpoints the timing and temporal patterns of forest decline.

### 13.2 Silver-fir Decline: Predisposed by Historical Logging and Triggered by Drought

Since the 1980s, silver fir decline has been documented in the central and western Spanish Pyrenees. Loss in tree vitality is characterized by needle yellowing and shedding, abnormal crown architecture, growth decline and elevated mortality, which has been mainly attributed to severe late-summer water deficit accentuated by warmer temperatures (Camarero et al. 2011). Interestingly, growth rates of silver fir exhibit a post-1980s decline only in the Spanish Pyrenees, whereas in mesic sites of the species distribution in central and eastern Europe and Italy, silver fir shows enhanced growth during the twentieth century (Büntgen et al. 2014; Gazol et al. 2015).

Many of the most affected Pyrenean stands are characterized by summer drought causing sub-optimal climatic conditions, low productivity, and low growth rates (Camarero et al. 2011). However, in these declining stands, many dying or recently dead trees showed growth releases in the 1950s during a period of intense logging in the area (Cabrera 2001) (Fig. 13.1a). The post-logging releases lead us to postulate that past logging predisposed the declining stands to drought-triggered dieback (Camarero et al. 2011). Stand thinning by high-grading the large-diameter trees would have favored the persistence of small-diameter and slow-growing trees, which may be the most vulnerable to drought stress. In heavily-thinned stands, opening of large gaps also alters forest microclimatic conditions, increasing water demand at tree level which negatively affects silver-fir vigor (Ausseau 2002). At some sites, thinning can favor the spread of root-rot fungi (Oliva and Colinas 2007), but their abundance is not higher in declining than non-declining forests (Sangüesa-Barreda et al. 2015).

This case study demonstrates the need to account for predisposing historical factors, which act as legacies and condition the responses of trees to drought. Growth responses to predisposing factors can be quantified and used to evaluate



**Fig. 13.1** Tree-ring signatures characterizing silver-fir (*Abies alba*) dieback in the Spanish Pyrenees. The upper plot (a) shows a typical growth curve of a dead silver fir which showed a growth release in the 1950s related to past thinning. The tree was sampled in a declining silver fir forest (Paco Ezpela, Huesca, northern Spain; 42° 45'N, 0° 52'W, 1230 m a.s.l.) where mortality reached 50% of trees after the 2012 severe drought. The lower plot (b) shows how growth (ln-transformed basal area increment) diverges between coexisting declining (inset image) and non-declining trees at this forest after the 1990s. Points show growth data of each vigor class and lines correspond to statistical models (General Additive Mixed Models) fitted to these data (lines show mean fitted values with standard errors) to highlight long-term growth trends. Figures modified from Camarero et al. (2011, 2015a)

tree-ring series from non-declining trees or stands to search for the early-warning signals of decline that portending tree death (Pedersen 1998; Bigler et al. 2004; Cailleret et al. 2016). In this case study, silver fir behaves as a long-term memory

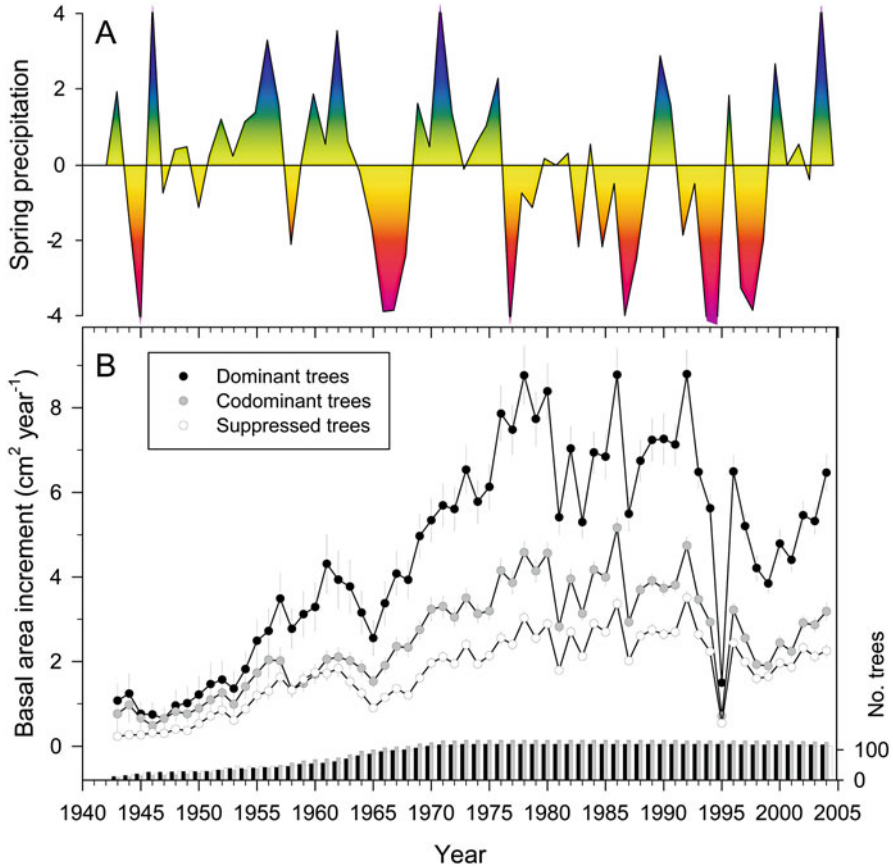
species (Fig. 13.1b) because its tree-ring growth patterns are useful predictors of tree death and can be used as early-warning signals of decline and impending mortality (Camarero et al. 2015a).

### 13.3 Spanish fir Decline: Predisposed by Intense Competition and Triggered by Drought

The recent decline of Spanish fir, a drought-sensitive conifer that is endemic to southern Spain and northern Morocco, shows how drought stress and increased stand density, promoted by changes in land use and stand development, can contribute to a loss of tree vigor and tree death (Linares et al. 2009). In dense stands with trees showing closed canopies, competition between trees drives self-thinning and density-dependent (e.g., crowding-dependent) mortality occurs (Oliver and Larson 1996). Trees with different diameters, basal areas and height classes compete differently for light, water and other resources (Peet and Christensen 1987; Orwig and Abrams 1997; Martin-Benito et al. 2008). In general, larger and taller trees are better competitors and more likely to survive.

Linares et al. (2009, 2010) showed the importance of competition in stand dynamics after land-use changes, as a contributing factor in the decline as a contributing factor in the decline of Spanish fir. The long-term changes in basal area increment of Spanish fir in relict stands were reconstructed from tree rings to investigate how density-dependent factors modulate the responses of radial growth to climatic stress (Linares et al. 2009). The likelihood of mortality of Spanish fir increased with decreasing elevation, indicating the influence of drought stress on mortality. Mortality was not greater in smaller tree size classes; rather, high mortality was linked to stands with closed overstories and homogeneous structures (Linares and Carreira 2009). Conversely, Spanish fir stands with lower mortality rates corresponded to more open and structurally heterogeneous stands (Linares et al. 2009). This example illustrates that both drought and stand structure have the potential to profoundly alter tree growth, vigor and mortality.

Several studies have shown that tree mortality rates are inversely related to radial-growth rates (Waring 1987; Wyckoff and Clark 2000; van Mantgem et al. 2003; van Mantgem and Stephenson 2007; Cailleret et al. 2016). Similarly, the dendroecological assessment of the growth trends in Spanish fir was useful to identify trees with higher probabilities of decline and death (Linares et al. 2009). In this study, the low mean growth rate of Spanish fir was mainly determined by high levels of competition (Fig. 13.2), whereas growth trends indicating decline preceding death were similar among dominant, codominant and suppressed trees and related to climatic variation. Trends of radial growth decline were strongly related to long-term warming trends, while inter-annual growth variability of trees was related to precipitation. These two climate-growth relations decreased in significance as



**Fig. 13.2** Spring (March to May) precipitation (a) expressed as standardized values) and basal-area increment (b) measured in dominant, co-dominant, and suppressed Spanish fir (*Abies pinsapo*) trees located near the lowermost elevation limit (36° 43'N, 4° 57'W, 1200 m a.s.l.) of the species' altitudinal range in southern Spain. Competition is estimated using a spatially-explicit competition index values (Linares et al. 2010). Bottom bars indicate the number of tree-rings series measured. Error bars represent the standard error. Figures modified from Linares et al. (2010)

competition (indicated by tree density) increased. To address potential confounding effects of changing phenology on climate-growth relationships, Linares et al. (2012) showed that climate warming during the second half of the twentieth century did not lead to extended growing seasons in the mid- to low-elevation Spanish fir populations where mortality was greatest. Specifically, non-linear responses of growth cessation to water availability offset the linear effects of increasing temperature on earlier budburst date. These results support the contention that observed growth decline and death of Spanish fir result from interactions between competition over long time scales and drought over short time scales (Linares et al. 2010).

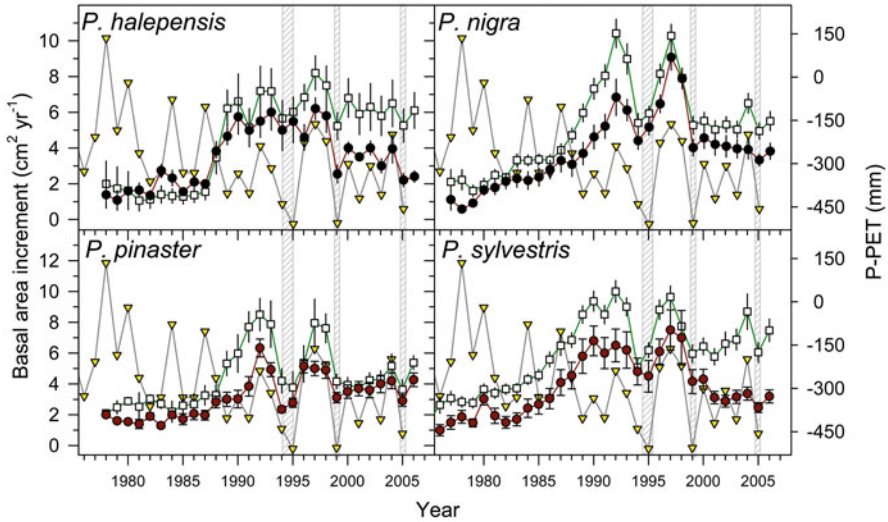
The response to only the most recent drought raises questions about cumulative predisposing stress factors interacting with climatic stress. Extreme climate events, such as successive and severe droughts, may cause abrupt growth declines and pulses of elevated tree mortality. These events are expected to more severely affect tree populations growing near their climatic tolerance limit. Very low annual precipitation was detected in 1994–1995, with similar low rainfall during 1945–1946, 1954–1955, 1965–1967, 1977 and 1987 (Fig. 13.2). However, only the 1994–1995 droughts caused decline in Spanish fir populations (Linares and Carreira 2009).

In summary, increased competition due to changes in land use predisposed Spanish fir to growth decline triggered by drought stress (Linares et al. 2010). Furthermore, various stressors lead to increases in severity of drought impacts on the forest, without corresponding increases in drought intensity. For example, if tree-to-tree competition reduced growth in a significant proportion of a population of susceptible trees, any drought could severely damage or kill more trees than it would in a more heterogeneous stand (Suarez et al. 2004; Linares et al. 2010). Thus, stressors may interact with competition predisposing trees to being killed by drought, as trees subjected to high competition are more likely surpassing their physiological thresholds of drought tolerance (McDowell et al. 2008, 2011).

### 13.4 Species-Specific Decline in Pine Plantations Triggered by Drought

In many countries in the Mediterranean Basin, intensive land uses such as logging and overgrazing by rural populations caused deforestation that motivated governments to support reforestation. In Spain, extensive plantations of Scots pine (*Pinus sylvestris* L.), Aleppo pine (*Pinus halepensis* Mill.), black pine (*Pinus nigra* Arn.) and maritime pine (*Pinus pinaster* Ait.) were established during the 1950s (FAO 2006). In the semi-arid southeastern Spain, many pine plantations were planted beyond the species natural climatic limits. During cool and wet climate of the 1970s, growth rates of planted pines were high but they were not sustained when climate became warmer and droughts occurred in 1994–1995, 1999, and 2005 (Sánchez-Salguero et al. 2012). During the warm and dry climate of the 1990s and 2000s several of the planted pine stands showed pronounced needle shedding or defoliation, growth decline and extensive mortality (Navarro-Cerrillo et al. 2007).

The four planted pine species differ in their vulnerability to drought, indicated by their natural distribution, ecophysiology and functional traits, which affected their success in semi-arid, southeast Spain. Scots pine showed the most intense growth decline and highest mortality rates (Fig. 13.3) as it is naturally distributed in Eurosiberia and is most vulnerable to drought-induced xylem embolism (Martínez-Vilalta and Piñol 2002). Drought-tolerant Aleppo pine, naturally distributed in the Mediterranean, was least affected (Camarero et al. 2015a). The other two Mediterranean species, black pine and maritime pine, occupied intermediate positions



**Fig. 13.3** Recent growth trends of basal area increment of four pine species planted at south-eastern Spain ( $37^{\circ} 22' N$ ,  $02^{\circ} 50' W$ ) according to their recent crown defoliation (*empty squares*, defoliation  $<50\%$ ; *filled circles*, defoliation  $\geq 50\%$ ). Years characterized by droughts (1994–1995, 1999 and 2005) correspond to growth decline, particularly in the most defoliated trees and the species less tolerant to drought as Scots pine (*Pinus sylvestris*). The right y-axis shows the annual water balance (*lines with triangles*,  $P - PET$ , difference between precipitation and potential evapotranspiration; note the reverse scale). The *vertical error bars* show standard errors. Figures modified from Sánchez-Salguero et al. (2012)

within this vulnerability ranking and did not present such marked growth loss. However, the decline of trees due to warmer temperatures and droughts causing water shortage during the growing season was not homogeneous within or among stands. Some individuals showed more defoliation and growth loss than conspecifics at the same site and apparently subjected to similar climatic, topographic, and edaphic conditions (Sánchez-Salguero et al. 2012).

Dendroecology allowed investigation of the decline processes of different pine species and tree vigor classes in response to successive droughts. A divergence in radial growth of trees with defoliation levels higher or lower than the 50% crown transparency was most evident in Scots pine. In contrast, growth differences were lacking between maritime pine with high and low defoliation levels (Fig. 13.3). This difference suggests that maritime pine can be considered a drought-tolerant species, which is consistent with the observed low growth sensitivity of natural maritime pine forests in response to temporal variability in drought (Camarero et al. 2015b).

Local site conditions may have predisposed some planted trees to drought more than others. Topographic variation would explain why most defoliated trees were growing on steeper sites with shallow soils, where soil water availability is lowest (Navarro-Cerrillo et al. 2007). Such predisposing factors may cause persistent



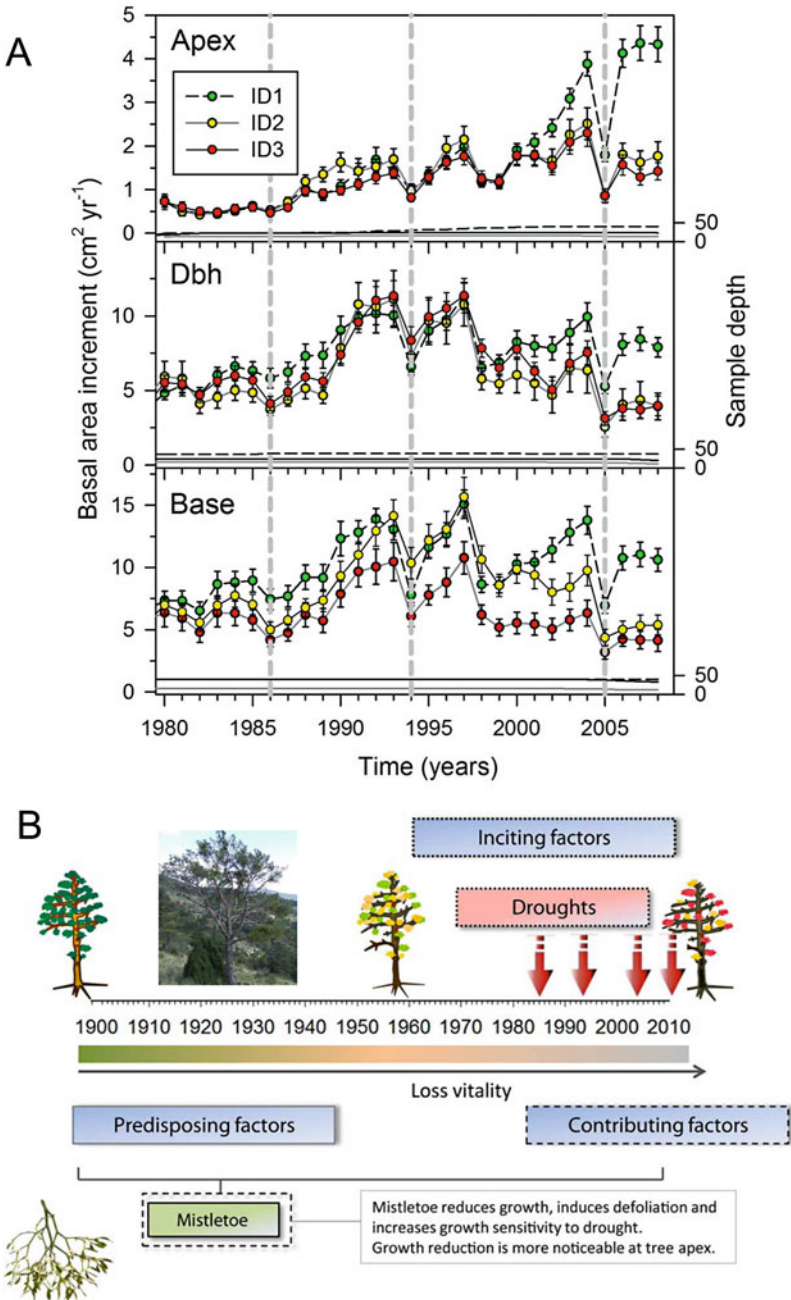
differences in vigor among trees of the same species and explain the positive relationships between wet site conditions, tree size and growth rates reported by Sánchez-Salguero et al. (2012). These differences in vigor are particularly relevant to forecast the probability of recovery of defoliated trees, especially for species less resistant to drought-induced xylem embolism such as Scots pine (Martínez-Vilalta and Piñol 2002). The decline of Scots pine plantations described in south-eastern Spain is characterized by a rapid growth reduction and widespread defoliation making the future existence of these plantations unlikely under the warmer and drier conditions predicted for most semi-arid regions of the Mediterranean Basin (Giorgi and Lionello 2008).

### 13.5 Scots Pine Decline driven by Interactions Between Mistletoe Infestation and Drought

An increasing number of forest declines involving several causal factors including drought and biotic stressors such as mistletoes, insects, and root-rot fungi are being reported worldwide (Ayres and Lombardero 2000; Carnicer et al. 2011). This research contrasts recent reviews on forest decline that conclude there is a research gap on the roles of biotic stressors in forest decline (Allen et al. 2010, 2015). However, studies on interactions between drought and biotic stressors as drivers of forest decline are notably scarce. These types of interactions may be complex and difficult to unravel because the drivers influence tree growth and vigor at different spatial and temporal scales and biotic stressors affect trees in different ways. For example, insect outbreaks cause defoliation, root-rot fungi affect roots, and mistletoes alter crown architecture and branch growth.

Hemiparasitic plants, such as mistletoes, obtain water and nutrients from host trees. Consequently, mistletoe infection may make host trees more sensitive to the negative effects of drought by enhancing water loss and reducing carbon gain of infected branches (Zweifel et al. 2012). Drought and mistletoe infection have been mainly studied separately; how drought and mistletoe interact and induce forest decline is not fully understood (but see Sangüesa-Barreda et al. 2013). Tree-rings allow reconstruction of the growth of infected trees to infer when mistletoe infection started and its effect on growth, and how it predisposes trees to drought-induced decline.

European pine mistletoe (*Viscum album* L. ssp. *austriacum*) is limited by low temperatures and rising temperatures may increase its abundance and promote an upslope or altitudinal expansion of its range (Dobbertin et al. 2005). Increased incidence and spread could accelerate forest decline in the most infected pine stands at dry locations (Dobbertin and Rigling 2006). Similar impacts have been described for other mistletoe affecting conifer species elsewhere (Alfaro et al. 1985; Vallauri 1998; Noetzli et al. 2004; Tsopelas et al. 2004).



**Fig. 13.4** Drought and mistletoe infestation contribute to growth decline in Scots pine. Growth patterns of mistletoe-infested trees (a) and scheme showing the Scots pine dieback process of

Dendroecology was applied to determine how mistletoe infection and drought stress modified the long-term growth patterns in Scots pine by exploring changes in growth at different heights, since mistletoe is mainly present in upper exposed tree crowns (Sangüesa-Barreda et al. 2012). Long-term changes in radial growth were assessed at the tree apex, diameter at breast height (dbh), and at the tree base. Basal area increment was used to quantify and compare growth trends of trees with different degrees of mistletoe infestation: trees without mistletoe mats (class ID1), moderately infected trees with mistletoe present in one or two thirds of the crown (class ID2), and severely infected trees with mistletoe present throughout the whole crown (class ID3). As well, drought sensitivity and drought recovery were calculated as the relative changes in growth for the three most severe droughts affecting the study area over the last three decades. In 1986, 1994–1995 and 2005 growing-season precipitation was  $\leq 48\%$  of the mean for the 1950–2015 period.

Mistletoe infection negatively affected growth from the apex to the stem base (Fig. 13.4a), but the effect was more noticeable near the tree apex where most mistletoes occur and induce more needle shedding than at other sampled heights. Mistletoe infection of Scots pine caused an average loss of 64% in basal area increment at the tree apex, whereas the loss of basal area increment was c. 51% at the other two heights. Notably, mistletoe most commonly affected the tallest trees with biggest crowns and diameters, which are most exposed to mistletoe seed deposition because birds prefer to perch in the top of tall trees (Sangüesa-Barreda et al. 2012, 2013). These canopy-dominant trees also had the highest growth rates, supporting the hypothesis that large and fast-growing trees are more prone to mistletoe infection and growth decline.

The basal area increment of severely and moderately infected trees diverged from that of non-infected trees since 2001 and the growth loss of infected trees was magnified by drought in 2005. These results indicated a strong interaction between mistletoe infection and drought stress that lead to a short-term reduction of tree growth, and preceded the death of many of the most severely infected trees. Mortality rates were 7–10% in the most affected stands (Sangüesa-Barreda et al. 2012). Interestingly, the growth divergence between infected and non-infected trees was relatively recent (c.10 years). Further research will test if the timing of divergence is different at wetter sites, but preliminary data suggest that divergence was much longer (c. 30 years) as drought stress diminishes. Tree-rings provide information on radial growth and wood formation and represent a proxy of water-use

←  
**Fig. 13.4** (continued) infested trees in drought-prone sites following the Manion (1991) model. **(b)** Radial-growth data was quantified at the tree apex, at 1.3 m where the diameter at breast height (dbh) is measured, and at the base of trees with different mistletoe infestation degree **(a)** and responses to drought (*dashed vertical lines*). In the *upper plot* the *right y axis* shows the sampled depth (number of measured radii) and error bars are standard errors. We classified the infested-trees in three classes: ID1, trees without mistletoe; ID2, moderately infested trees; and ID3, severely infested trees. In the *lower plot (b)* the image shows a tree heavily infested by mistletoe (class ID3). Figures modified from Sangüesa-Barreda et al. (2012)

efficiency and long-term changes in tree functioning. The discrimination between the carbon of atmospheric CO<sub>2</sub> and the carbon fixed by trees as woody tissues can be quantified by analyzing in <sup>13</sup>C/<sup>12</sup>C isotope ratios in tree-ring wood or cellulose (McCarroll and Loader 2004; Saurer et al. 2004). This approach was followed to assess how the combined effect of mistletoe infection and drought affected radial growth and water-use efficiency in Scots pine. The water-use efficiency of the most severely infected trees decreased during the last 5 years prior to sampling, although their radial growth rates were low for more than 10 years (Sangüesa-Barreda et al. 2013). Growth of severely infected trees was more sensitive to drought stress than non-infected trees. Although infected and non-infected trees displayed similar increasing trends of water-use efficiency, the synergistic effect of drought stress and mistletoe in severely infested trees caused a marked growth loss and reversed any potential increase of water-use efficiency due to the rise in atmospheric CO<sub>2</sub> concentrations. Consequently, rising atmospheric CO<sub>2</sub> concentrations could not compensate for the negative impacts of drought and mistletoe on tree growth and water-use efficiency in Scots pine forest under xeric conditions. Finally, these findings suggest mistletoe infection requires more time to cause severe growth loss at mesic than at dry sites, i.e., the growth divergence between infected and non-infected trees should last longer and be less harmful to trees if drought stress is alleviated.

This is not the first study showing that potential fertilization effect of increasing atmospheric CO<sub>2</sub> concentrations do not override the negative effects of stress factors, in this case drought and mistletoe infection on growth and water-use efficiency of affected trees. In declining silver fir trees growth decreased and water-use efficiency stopped rising as a consequence of severe droughts in the 1980s and 1990s, despite rapidly increasing atmospheric CO<sub>2</sub> concentration during the late twentieth century (Linares and Camarero 2012). Both the mistletoe-pine and the silver fir forest-decline examples show that drought and other stress factors override the increased availability of atmospheric carbon, thus causing a persistent reduction in growth rates and often leading to tree death. If warmer and drier conditions persist, Scots pine and silver fir stands currently showing severe forest decline will likely experience changes in stand structure and composition of dominant trees.

### 13.6 Summary and Further Remarks

Several recent studies have documented forest decline and increased rates of tree mortality worldwide, often associated with drought in recent decades (Allen et al. 2010, 2015; van Mantgem et al. 2009). There is concern that climate warming will exacerbate drought stress by rising evapotranspiration rates, causing more widespread and intense forest decline (Williams et al. 2013). In addition, some authors suggest that warmer conditions could favour the spread and incidence of biotic stressors (e.g., mistletoe, herbivore insects and invasive pathogens) making them more aggressive to trees (Ayres and Lombardero 2000). Dendroecology

provides a long-term perspective to ascertain if and how forest decline is connected to recent climate warming and drying trends, in particular in arid areas of the northern hemisphere (Dai 2013).

Here, four case studies of forest decline in Spain illustrated various growth patterns and responses of declining trees to different combinations of stressors. In all four cases, drought stress was an inciting factor (*sensu* Manion 1991), which is common in declining Mediterranean (Sarris et al. 2007) and other drought-prone forests (Suarez et al. 2004; Williams et al. 2013). Severe drought-triggered abrupt growth reductions were observed in mesic Pyrenean silver-fir forests, where water deficit was amplified by warmer summer temperatures and increased evapotranspiration rates (Vicente-Serrano et al. 2015). Evidently, rare but severe droughts could be relevant disturbances shaping the dynamics of humid temperate forests, particularly if climate continues warming (Pederson et al. 2014). The case studies also demonstrate that factors other than drought cause forest decline, such as previous logging (silver fir), competition (Spanish fir), species-specific tolerance to drought (pine plantations), and mistletoe infestation (Scots pine). Such predisposing or contributing factors (*sensu* Manion 1991) often act at longer time scales than punctuated droughts, and their attribution is complicated because forest decline and tree death can occur years or decades after those factors started affecting trees. In this sense, a major application of dendroecology is to forecast tree vigor or predict the probability of tree death based on measured tree-ring variables (Cailleret et al. 2016), including width, anatomy (Pellizzari et al. 2016), or isotopes (Levanič et al. 2011). In addition to statistical characteristics of the tree-ring series, forecasts of vigor may be enhanced by data on climatic stress (e.g., drought severity), (Camarero et al. 2015a), and variables reflecting long-term predisposing and contributing factors (e.g., management and use, competition, some biotic stressors). Including the long-term stressors would require novel approaches and tools to consider legacy effects and decipher how the ecological memory is imprinted on tree-ring records (Ogle et al. 2015).

The use of dendroecology to pinpoint the start of drought-triggered growth decline has several important outcomes and applications. First, identifying the timing of growth decline is helpful to attribute stressors (e.g., drought or logging) and to quantify tree recovery from their impact stressors. Second, if the tree-ring variables exceed a critical threshold, they can be used as early-warning indicators of portending tree death (Camarero et al. 2015a). Consequently, growth trends or growth responses to climate, including post-drought growth resilience, could be used as valuable traits to predict the probability of drought-induced damage in forests (Anderegg et al. 2015; Gazol et al. 2016). Third, since radial growth is considered a long-term proxy of tree vigor (Dobbertin 2005), future directions on forest-dieback research could bridge post-drought changes in radial growth with primary growth. Primary growth (e.g., shoot and root elongation, bud and needle production, and reproduction) is a major component of tree performance and determines canopy architecture (Jalkanen 1995; Vennetier et al. 2013). Fourth, dendroecological studies can address forest decline from a modern pathological perspective by quantifying critical thresholds of disease and tree death required to

maintain dynamic and resilient stands able to withstand climate change and new threats from biotic stressors (Manion 2003).

Finally, tree-ring data can be used to parameterize empirical models of tree growth to project forest responses to CO<sub>2</sub>-concentration and climate change scenarios and produce probabilistic predictions of dieback events and maps of forest vulnerability (Charney et al. 2016). These outcomes would contribute to science-based adaptive management strategies under future climate and management scenarios.

**Acknowledgments** We thank several Spanish (CGL2015-69186-C2, FUNDIVER; CGL2013-48843-C2-1-R, CoMo-ReAdapt) and European (COST Action STReESS—Studying Tree Responses to extreme Events: a Synthesis, FP1106) projects for funding and promoting the development of this research. A. Gazol is supported by a Postdoctoral grant (MINECO-FPDI 2013-16600, FEDER funds). We sincerely thank L. Daniels for her insightful comments on a previous draft of this chapter.

## References

- Alfaro RI, Bloomberg WJ, Smith RB, Thomson AJ (1985) Epidemiology of dwarf mistletoe in western hemlock stands in south coastal British Columbia. *Can J For Res* 15:909–913
- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N 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
- Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere* 6:129
- Amoroso MM, Larson BC (2010) Stand development patterns as a consequence of the mortality in *Austrocedrus chilensis* forests. *For Ecol Manag* 259:1981–1992
- Anderegg WRL, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw JD, Shevliakova E, Williams AP, Wolf A, Ziaco E, Pacala S (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349:528–532
- Anderegg WRL, Klein T, Bartlett M, Sack L, Pellegrini AFA, Choat B, Jansen S (2016) Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *PNAS* 113:5024–5029
- Aussenac G (2002) Ecology and ecophysiology of circum-Mediterranean firs in the context of climate change. *Ann For Sci* 59:823–832
- Ayres MP, Lombardero MJ (2000) Assessing the consequences of climate change for forest herbivore and pathogens. *Sci Total Environ* 262:263–286
- Bigler CJ, Bugmann H (2003) Growth-dependent tree mortality models based on tree rings. *Can J For Res* 33:210–221
- Bigler CJ, Gričar J, Bugmann H, Čufar K (2004) Growth patterns as indicators of impending tree death in silver fir. *For Ecol Manag* 199:183–190
- Bravo-Oviedo A, Sterba H, del Rio M, Bravo F (2006) Competition-induced mortality for Mediterranean *Pinus pinaster* Ait. and *P. sylvestris* L. *For Ecol Manag* 222:88–98
- Büntgen U, Tegel W, Kaplan JO, Schaub M, Hagedorn F, Bürgi M, Brázdil R, Helle G, Carrer M, Heussner K-U, Hofmann J, Kontić R, Kyncl T, Kyncl J, Camarero JJ, Tinner W, Esper J, Liebhold A (2014) Placing unprecedented recent fir growth in a European-wide and Holocene-long context. *Front Ecol Environ* 12:100–106
- Cabrera M (2001) Evolución de abetares del Pirineo aragonés. *Cuad Soc Esp Ciencias Forestales* 11:43–52
- Cailleret M, Bigler C, Bugmann H, Camarero JJ, Čufar K, Davi H, Mészáros I, Minunno F, Peltoniemi M, Robert EMR, Suarez ML, Tognetti R, Martínez-Vilalta J (2016) Towards a

- common methodology for developing logistic tree mortality models based on ring-width data. *Ecol Appl* 26:1827–1841
- Camarero JJ, Bigler C, Linares JC, Gil-Pelegrín E (2011) Synergistic effects of past historical logging and drought on the decline of Pyrenean silver fir forests. *For Ecol Manag* 262:759–769
- Camarero JJ, Gazol A, Sangüesa-Barreda G, Oliva J, Vicente-Serrano SM (2015a) To die or not to die: early-warning signals of dieback in response to a severe drought. *J Ecol* 103:44–57
- Camarero JJ, Gazol A, Tardif JC, Conciatori F (2015b) Attributing forest responses to global-change drivers: limited evidence of a CO<sub>2</sub>-fertilization effect in Iberian pine growth. *J Biogeogr* 42:2220–2233
- Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G, Peñuelas J (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *PNAS* 108:1474–1478
- Charney ND, Babst F, Poulter B, Record S, Trouet VM, Frank D, Enquist BJ, Evans MEK (2016) Observed forest sensitivity to climate implies large changes in 21st century North American forest growth. *Ecol Lett* 19:1119–1128
- Dai A (2013) Increasing drought under global warming in observations and models. *Nat Clim Chang* 3:52–58
- Das A, Battles J, Stephenson NL, van Mantgem PJ (2011) The contribution of competition to tree mortality in old-growth coniferous forests. *For Ecol Manag* 261:1203–1213
- Dobbertin M (2005) Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *Eur J For Res* 124:319–333
- Dobbertin M, Hilker N, Rebetez M, Zimmermann NE, Wohlgemuth T, Rigling A (2005) The upward shift in altitude of pine mistletoe (*Viscum album* ssp. *austriacum*) in Switzerland—the result of climate warming? *Int J Biometeorol* 50:40–47
- Dobbertin M, Rigling A (2006) Pine mistletoe (*Viscum album* ssp. *austriacum*) contributes to Scots pine (*Pinus sylvestris*) mortality in the Rhone valley of Switzerland. *For Pathol* 36:309–322
- FAO (2006) Global planted forests thematic study: results and analysis, Food and Agriculture Organization of the United Nations. In: Del Lungo A, Ball J, Carle J (eds) *Planted forests and trees*. Working Paper 38, Rome, Italy
- Foster DR, Oswald WW, Faison EK, Doughty ED, Hansen BCS (2006) A climatic driver for abrupt mid-holocene vegetation dynamics and the hemlock decline in New England. *Ecology* 87:2959–2966
- Franklin JF, Shugart HH, Harmon ME (1987) Tree death as an ecological process. *Bioscience* 37:550–556
- Gazol A, Camarero JJ, Gutiérrez E, Popa I, Andreu-Hayles L, Motta R, Nola P, Ribas M, Sangüesa-Barreda G, Urbinati C, Carrer M (2015) Distinct effects of climate warming on populations of silver fir (*Abies alba*) across Europe. *J Biogeogr* 42:1150–1162
- Gazol A, Camarero JJ, Anderegg WRL, Vicente-Serrano SM (2016) Impacts of droughts on the growth resilience of Northern Hemisphere forests. *Glob Ecol Biogeogr* 26(2):166–176.
- Giorgi F, Lionello P (2008) Climate change projections for the Mediterranean region. *Glob Planet Chang* 63:90–104
- Jalkanen R (1995) Needle Trace Method (NTM) for retrospective needle retention studies on Scots pine (*Pinus sylvestris* L.). *Acta Universitatis Ouluensis, Oulu*, p 84
- LeBlanc DC, Raynal DJ (1990) Red spruce decline on Whiteface Mountain, New York. II. Relationships between apical and radial growth decline. *Can J For Res* 20:1415–1421
- Levanič T, Cater M, McDowell NG (2011) Associations between growth, wood anatomy, carbon isotope discrimination and mortality in a *Quercus robur* forest. *Tree Physiol* 31:298–308
- Linares JC, Camarero JJ, Carreira JA (2009) Interacting effects of climate and forest-cover changes 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

- Linares JC, Camarero JJ (2012) From pattern to process: linking intrinsic water-use efficiency to drought-induced forest decline. *Glob Chang Biol* 18:1000–1015
- Linares JC, Carreira JA (2009) Temperate-like stand dynamics in relict Mediterranean-fir (*Abies pinsapo*, Boiss.) forests from Southern Spain. *Ann For Sci* 66:610–619
- Linares JC, Covelo F, Carreira JA, Merino JA (2012) Phenological and water-use patterns underlying maximum growing season length at the highest elevations: implications under climate change. *Tree Physiol* 32:161–170
- Manion PD (1991) *Tree disease concepts*. Prentice Hall, Englewood Cliffs
- Manion PD (2003) Evolution of concepts in forest pathology. *Phytopathology* 93:1052–1055
- Martin-Benito D, Cherubini P, del Río M, Cañellas I (2008) Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes. *Trees Struct Funct* 22:363–373
- Martínez-Vilalta J, Piñol J (2002) Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *For Ecol Manag* 161:247–256
- McCarroll D, Loader NJ (2004) Stable isotopes in tree rings. *Quat Sci Rev* 23:771–801
- McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, Kolb T, Plaut J, Sperry J, West A, Williams DG, Yepez EA (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 178:719–739
- McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M (2011) The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol Evol* 26:523–532
- Muller-Dombois D (1992) A natural dieback theory, cohort senescence as an alternative to the decline disease theory. In: Manion PD, Lachance D (eds) *Forest decline concepts*. The American Phytopathological Society, St. Paul, pp 26–37
- Navarro-Cerrillo RM, Varo MA, Lanjeri S, Hernández Clemente R (2007) Cartografía de defoliación en los pinares de pino silvestre (*Pinus sylvestris* L.) y pino salgareño (*Pinus nigra* Arn.) en la Sierra de los Filabres. *Ecosistemas* 16:163–171
- Noetzli KP, Müller B, Sieber TN (2004) Impact of population dynamics of white mistletoe (*Viscum album* ssp. *abietis*) on European silver fir (*Abies alba*). *Ann For Sci* 60:773–779
- Ogle K, Whitham TC, Cobb NS (2000) Tree-ring variation in pinyon predicts likelihood of death following severe drought. *Ecology* 81:3237–3243
- Ogle K, Barber JJ, Barron-Gafford GA, Bentley LP, Young JM, Huxman TE, Loik ME, Tissue DT (2015) Quantifying ecological memory in plant and ecosystem processes. *Ecol Lett* 18:221–235
- Oliva J, Colinas C (2007) Decline of silver fir (*Abies alba* Mill.) stands in the Spanish Pyrenees: role of management, historic dynamics and pathogens. *For Ecol Manag* 252:84–97
- Oliver CD, Larson BC (1996) *Forest stand dynamics*. Wiley, New York
- Orwig DA, Abrams MD (1997) Variation in radial growth responses to drought among species, site, and canopy strata. *Trees Struct Funct* 11:474–484
- Pedersen BS (1998) Modeling tree mortality in response to short and long-term environmental stresses. *Ecol Model* 105:347–351
- Pederson N, Dyer JM, McEwan RW, Hessl AE, Mock CJ, Orwig DA, Rieder HE, Cook BI (2014) The legacy of episodic climatic events in shaping temperate, broadleaf forests. *Ecol Monogr* 84:599–620
- Peet RK, Christensen NL (1987) Competition and tree death. *Bioscience* 37:586–594
- Pellizzari E, Camarero JJ, Gazol A, Sangüesa-Barreda G, Carrer M (2016) Wood anatomy and carbon-isotope discrimination support long-term hydraulic deterioration as a major cause of drought-induced dieback. *Glob Chang Biol* 22:2125–2137
- Reams GA, Huso MMP (1990) Stand history: an alternative explanation of red spruce radial growth reduction. *Can J For Res* 20:250–253
- Sánchez-Salguero R, Navarro-Cerrillo RM, Camarero JJ, Fernández-Cancio A (2012) Selective drought-induced decline of pine species in southeastern Spain. *Clim Chang* 113:767–785
- Sánchez-Salguero R, Camarero JJ, Gutiérrez E, González Rouco F, Gazol A, Sangüesa-Barreda G, Andreu-Hayles L, Linares JC, Seftigen K (2017) Assessing forest vulnerability to climate warming using a process-based model of tree growth: bad prospects for rear-edges. *Glob Chang Biol* 23:2705–2719. doi:[10.1111/gcb.13541](https://doi.org/10.1111/gcb.13541)



- Sangüesa-Barreda G, Linares JC, Camarero JJ (2012) Mistletoe effects on Scots pine decline following drought events: insights from within-tree spatial patterns, growth and carbohydrates. *Tree Physiol* 32:585–598
- Sangüesa-Barreda G, Linares JC, Camarero J (2013) Drought and mistletoe reduce growth and water-use efficiency of Scots pine. *For Ecol Manag* 296:64–73
- Sangüesa-Barreda G, Camarero JJ, Oliva J, Montes F, Gazol A (2015) Past logging, drought and pathogens interact and contribute to forest dieback. *Agric For Meteorol* 208:85–94
- Sarris D, Christodoulakis D, Körner C (2007) Recent decline in precipitation and tree growth in the eastern Mediterranean. *Glob Chang Biol* 13:1187–1200
- Saurer M, Siegwolf R, Schweingruber F (2004) Carbon isotope discrimination indicates improving water-use efficiency of trees in northern Eurasia over the last 100 years. *Glob Chang Biol* 10:2109–2120
- Suarez ML, Ghermandi L, Kitzberger T (2004) Factors predisposing episodic drought-induced tree mortality in *Nothofagus*—site, climatic sensitivity and growth trends. *J Ecol* 92:954–966
- Tsopelas P, Angelopoulos A, Economou A, Soulioti N (2004) Mistletoe (*Viscum album*) in the fir forest of Mount Parnis, Greece. *For Ecol Manag* 202:59–65
- Vallauri D (1998) Dynamique parasitaire de *Viscum album* L. sur pin noir dans le bassin du Saïgon (Préalpes françaises du sud). *Ann For Sci* 55:823–835
- van Mantgem PJ, Stephenson NL, Mutch LS, Johnson VG, Esperanza AM, Parsons DJ (2003) Growth rate predicts mortality of *Abies concolor* in both burned and unburned stands. *Can J For Res* 33:1029–1038
- van Mantgem PJ, Stephenson NL (2007) Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecol Lett* 10:909–916
- van Mantgem PJ, Stephenson NL, Byrne JC et al (2009) Widespread increase of tree mortality rates in the western United States. *Science* 323:521–524
- Vennetier M, Thabeet A, Didier C, Girard F, Cailleret M, Taugourdeau O, Ouarmim S, Sabatier S-A, Caraglio Y, Sabatier S-A, Cailleret M, Ouarmim S, Thabeet A (2013) Climate change impact on tree architectural development and leaf area. In: Singh BR (ed) Climate change—realities, impacts over ice cap, sea level and risks. <http://www.intechopen.com/books/export/citation/BibTex/climate-change-realities-impacts-over-ice-cap-sea-level-and-risks/climate-change-impact-on-tree-architectural-development-and-leaf-area>. Accessed 14 Nov 2016
- Vicente-Serrano SM, Camarero JJ, Zabalza J, Sangüesa-Barreda G, López-Moreno JI, Tague CL (2015) Evapotranspiration deficit controls net primary production and growth of silver fir: implications for Circum-Mediterranean forests under forecasted warmer and drier conditions. *Agric For Meteorol* 206:45–54
- Waring RH (1987) Characteristics of trees predisposed to die. *Bioscience* 37:569–574
- Williams AP, Allen CD, Macalady AK, Griffin D et al (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. *Nat Clim Chang* 3:8–13
- Wyckoff PH, Clark JS (2000) Predicting tree mortality from diameter growth: a comparison of maximum likelihood and Bayesian approaches. *Can J For Res* 30:156–167
- Zweifel R, Bangerter S, Rigling A, Sterck FJ (2012) Pine and mistletoes: how to live with a leak in the water flow and storage system? *J Exp Bot* 63:2565–2578