Pest Management in Tropical Forestry

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Introduction and Scope

The term "Pest" is used in the heading for this chapter in a broad sense to encompass all the living and nonliving agencies which damage living plants. In the text, however, it is mostly used in a narrower sense to include only various animals; while the terms "Diseases" and "Disorders" are used for damage caused by various groups of living plants (pathogens) and various nonliving agencies, respectively. In natural ecosystems, plants have evolved gradually over many years and have therefore become adapted to the environment and all the other components of

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their own ecosystem. Damage from pests and diseases does occur in natural ecosystems, but it is often greatly exacerbated in the unnatural conditions of managed and plantation forests. Natural ecosystems have also become changed by the international movement of plants, and inadvertently their pests and diseases, and by man-made changes to the environment.

The term "Tropics" is used to encompass all the geographical regions between the Tropics of Cancer and Capricorn at 23° 26' 16" (23.4378°) N and 23° 26' 16" (23.4378) S, which encompass a wide range of different climatic zones, varying from deserts to continually wet sites; hot sites to cold alpine sites; and maritime to inland sites. In general, tropical regions experience small seasonal changes in day length, solar radiation, air temperature and soil temperature, with diurnal rather than seasonal extremes. However, most regions experience very considerable seasonal changes in rainfall, which in total can range from 0 to 10,000 mm/an. Pests and diseases of trees have been reported from the tropics for many years; however, it was not until 1968 that F.G. Browne produced his basic text (Browne [1968\)](#page-40-0) in response to a resolution of the 8th British Commonwealth Forestry Conference (Gibson [1975\)](#page-41-0). Since then, many texts on pests and diseases limited to particular tropical regions, particular host families and genera or particular families of pests and diseases have appeared (Passos de Carvalho [1971;](#page-43-0) Gibson [1975,](#page-41-0) [1979](#page-41-0); Bakshi [1976](#page-39-0); Krugner [1980a,](#page-42-0) [b](#page-42-0); Evans [1984;](#page-41-0) Singh and Singh [1986;](#page-44-0) Bigger [1988;](#page-40-0) Su See [1999](#page-44-0); Old et al. [2000;](#page-42-0) Keane et al. [2001;](#page-42-0) Wingfield [2003;](#page-44-0) Richardson et al. [2007;](#page-43-0) Wingfield et al. [2008a](#page-44-0)).

In this chapter, diseases, pests, and disorders of trees are considered separately for convenience; however, several may affect the same trees at any one time under field conditions. It should also be emphasized that they form only a small part of the extremely complex ecosystems which occur in the various regions of the tropics. Thus all senescing, moribund, damaged, stressed, or even healthy plant tissues are colonized by a multitude of organisms which may be damaging, or may exist as endophytes, living inside the tissues until it becomes stressed from other causes.

Diseases

Disease can be defined as "a continuing harmful deviation from the normal functioning of a plant which is caused by organic disease – inducing agents and which is usually of sufficient magnitude to give rise to visible symptoms or effects" (Brooks [1953\)](#page-40-0). Biotic agents of disease are known as pathogens and the plants on which these organisms grow and obtain their nutrients as hosts. Given suitable environmental conditions, a disease will spread from affected plant tissues to other parts of the same plant, and to other plants in the vicinity. Reproductive structures of particular organisms, or other signs of infection, will also appear in time on, or inside, affected tissues.

Specific diseases are invariably caused by a combination of factors, particularly the interactions between the host and its environment, which may affect the growth and development of both the host and the pathogen, and with the pathogen itself. Broadly, the incidence and severity of a particular disease are influenced by the interactions between:

- (i) Host susceptibility
- (ii) Pathogen virulence
- (iii) Environmental factors

Environmental factors include temperature, rainfall, humidity, light, soil, and the multitude of other organisms associated with the host or in the surrounding air and soil (Agrios [2005\)](#page-39-0). These interactions are summarized in the "disease triangle" (Fig. 1).

The association of an organism with a host as the cause of a disease is not always readily apparent. Plant pathologists, therefore, must follow a series of rigorous experimental procedures first postulated by the nineteenth century medical bacteriologist Koch ([1882\)](#page-42-0) to prove conclusively that a causal relationship exists between the host plant and the pathogen. Failure to follow these procedures continues sometimes to lead to numerous erroneous reports of disease in plant pathology literature from the tropics and elsewhere.

Symptoms and Signs of Disease

Symptoms are the visible manifestations of the disease syndrome which appear in a sequence after infection has taken place; signs of disease are visible evidence of the pathogen itself, such as fungal fruitbodies, fungal hyphae, bacterial ooze, or virus particles which are present in at least some of the affected tissues. Every disease produces symptoms and signs, usually in a particular sequence, after an initial time lag or incubation period that follows infection. These symptoms may, or may not, be characteristic for particular diseases; diagnosis, therefore, requires great care and experience.

Disease symptoms can be either systemic, in which the entire plant sometimes is affected, although the pathogen may be restricted within the plant, or localized

Table 1 Symptoms of plant disease

where the disease is restricted to particular parts of the plant, sometimes to a single necrotic lesion. Various classifications are used for disease symptoms, based on either the nature of the physiological changes induced in the host, or the tissue affected (Table 1). These symptoms are not solely caused by pathogens; many can also be induced by certain pests and abiotic agents.

Agents of Disease

In general terms *fungi* (singular $=$ *fungus*) are the organisms most commonly associated with plant diseases. Many important plant diseases are also caused by bacteria (and phytoplasma) and viruses. Nematodes also cause a number of important plant diseases; although these organisms are animals they are studied by specialist Nematologists, who are generally considered under plant pathologists. Further plant-infecting organisms include parasitic plants (mistletoes, dodders, sandalwoods) and rarely certain algae may cause diseases on other plants.

Fungi and Fungus-like Organisms

Fungi form a separate Kingdom to plants, animals and prokaryotes, the Mycota. All fungi have heterotrophic life strategies, requiring organic materials to gain nutrition. Structurally, most fungi comprise minute thread-like filaments (hyphae) which aggregate into a network (mycelium) on which various reproductive structures may form (Petersen [2013\)](#page-43-0). Hyphae are usually dichotomously branched and divided into linear rows of cells by septa, forming cross-walls. Differentiation into particular tissue types varies considerably within this Kingdom. These tissue types have differing functions. Globose aggregates of hyphae, or sclerotia, permit perennation in a dormant state; rhizomorphs, formed by hyphae aggregating linearly into chords, enable spread through an unsuitable substrate and conduct nutrients over

long distances; stromata form secure bases on which to produce reproductive structures; and more or less complex reproductive structures of varied shape and size facilitate the production and dissemination of reproductive propagules.

Reproduction in most fungi is via the production of unicellular or multicellular sexual or asexual spores. Many fungi, particularly in the Ascomycota (see below) produce at least one type of asexual spore on suitable substrates under favorable conditions. Asexual spores are often produced in vast numbers, enabling these fungi to multiply rapidly and exploit a suitable substrate under favorable environmental conditions. Sexual spores are also produced in huge numbers by many fungi and often are sufficiently resilient to enable survival through periods where conditions are unfavorable for growth.

Traditionally, the fungi were classified and named according to characters of their sexual reproductive structures (teleomorphs) where these were known, or based on their asexual reproductive structures (anamorphs) and vegetative characters where sexual structures were not known. It is somewhat confusing that many fungi have at least two Latin names in use, one for the teleomorph and one for each anamorph. The name of the teleomorph must always take precedence over that of an anamorph. There is a current drive to give all fungi (and other organisms) only a single name, which would remove this confusion.

With the advent of molecular biological analyses, however, much of the confusion concerning the taxonomic placement of fungi can, in time, be resolved. The DNA of an organism is definitive and, using multigene sequences (e.g., Multilocus sequence typing, MLST), highly definitive interpretations of the relationships between individual organisms can be elucidated. The application of molecular biology techniques, therefore, has led to some adjustments to previous understanding of fungal taxonomy, although, in general, much of the taxonomic work based on morphological structures has proved to be highly accurate.

Classifications and systems for taxonomic assignments of the true fungi can be found in appropriate text books (e.g., Kirk et al. [2008\)](#page-42-0). Fungi and fungus-like organisms are responsible for a great variety of different diseases of plants; plant pathologists divide these into groups damaging various parts of the plant at different growth stages, although many pathogens affect several organs of a plant. Further confusion may arise when these diseases are given different common names, despite being caused by the same pathogen species.

A further Kingdom of organisms which includes numerous plant pathogens, many of which are highly damaging, is the Chromista. In terms of ecology, these organisms behave very similarly to the true fungi, but are completely distinct phylogenetically. In this Kingdom, the class Oomycetes includes pathogen species in the genera Pythium, Phytophthora, Phytopythium and Peronospora, several species of which cause some of the most damaging diseases of trees (Hayden et al. [2013](#page-41-0)).

Diseases Affecting Seeds

Various pathogens can invade seeds, during development of the fruit (or cones), at seed harvest and storage, or between sowing and germination. Seeds or fruits with fleshy external tissues are particularly at risk. The fungi may originate from infected flowers or fruits, extraneous organic matter in the seed batch, or from airborne and soilborne propagules. A particular risk noted currently is that of *Fusarium* circinatum (Gibberella circinata), which can be transmitted via seed transport. Although considered likely to be native in the highlands of Central America, it has spread to many other parts of the world, including North America, South America, South Africa, Japan, and Spain, where it is causing problems both with damping-off in nurseries and in pine plantations and forests in the field (Wingfield et al. [2008b\)](#page-44-0).

Diseases of Seedlings and Young Plants

Damping-Off Disease. Damping-off (Fig. [2\)](#page-6-0) refers to the death of seedlings prior to the development of lignified tissues. It can manifest as pre- or postemergent damping-off, depending on whether the root and/or shoot are killed before or after the plumule has emerged above soil level. The impact is variable, depending mainly on quality of the seed batch and nursery management (Lilja and Poteri [2013\)](#page-42-0). All tree seedlings are susceptible to some extent, although damage in *Eucalyptus* spp. and species in the Pinaceae are frequently reported. A variety of both true fungi and Oomycota can cause damping-off; under drier conditions, species in the (anamorphic) genera Fusarium, Cylindrocladium, Macrophomina and Rhizoctonia spp. may be involved, whereas in wetter nursery conditions, Pythium and Phytophthora spp. are usually responsible. All of these species grow rapidly, completing their life cycles of infection and sporulation within a few days and producing persistent propagules which can survive adverse soil conditions.

Symptoms of damping-off include a wet, soft rot of the emerging root and/or radicle, resulting in pre-emergent damping-off, or seedling emergence occurs, but the hypocotyl or stem base at soil level is infected and the seedling collapses on to the soil surface. In some broad-leaved trees, the infection may first affect the cotyledons, before rapidly spreading to the hypocotyl. Typical damping-off, however, is seen as rapidly expanding, roughly circular patches in which the most recently killed plants are located at the periphery.

Incidence is favored by wet, alkaline, highly organic soils, excessive seed density, and humid environments. Young transplants are also predisposed to infection by damage during pricking-out operations or when planted too deeply (Bloomberg [1985\)](#page-40-0).

Seedling Root and Collar Rots. Older, fully emerged seedlings with welldeveloped xylem and suberization of the cortex can also be attacked and damaged by the same soilborne fungi and oomycetes responsible for damping-off. As with damping-off itself, the problem frequently arises under poor management conditions, particularly waterlogging or a lack of water which causes stress to the plants.

Symptoms include decay of root cortex tissues, sometimes mainly at the root collar, leaving the internal vascular stele tissues, particularly the xylem, more or less intact. Aerial parts of affected plants are stunted, with yellow, wilted foliage. When the plants die, they usually become colonized by saprophytic fungi. Pathogenic sclerotia-forming fungi, such as Cylindrocladium spp., M. phaseolina and

Fig. 2 Damping off disease (a) pre-emergence damping-off in a bed of conifer seedlings. The large gap is where germinating seedlings were killed prior to the plumule emergence. (b) Multiple losses due to damping-off during raising *Acacia* seedlings in cells (Image **b** courtesy of Su See Lee)

various Rhizoctonia spp., may form microsclerotia in affected tissues, providing long-lived inoculum in the soil following disintegration of the tissues.

Non-Specific Seedling Blights. Many opportunistic fungi with rapid reproductive cycles can infect foliage and young, green shoots of forestry plants in the nursery. These diseases may be lethal to young plants, but usually do not kill older seedlings. Severe blight may lead to death of the apical shoot, however, resulting in stunting and multiple leaders on young plants, which are then considered to be of low quality.

Seedlings of most trees are susceptible to these problems, but seedling age, environmental conditions and the inoculum potential contribute greatly to disease incidence. High humidity, due to the high densities of young plants in the nursery, along with overwatering increase disease severity. Many fungi causing seedling blights, such as *Sclerotinia fuckeliana (Botrytis cinerea)* the cause of gray mold, Fusarium spp. and Cylindrocladium spp., have a broad host range. Others are more or less host specific, i.e., Colletotrichum acutatum f.sp. pinea the cause of terminal crook disease of pines (Dingley and Gilmour [1972](#page-40-0)) and Sphaeropsis sapinea (diplodia shoot blight) also on Pinus spp. and other conifers (de Wet et al. [2003;](#page-40-0) Fig. [3](#page-8-0)). These fungi are very widely distributed.

Symptoms of blight include the formation of water-soaked or resinous lesions on the foliage at the shoot tips of plants. The lesions become necrotic with time and the infection spreads into the green stem tissues causing cankers which gradually increase in size and may eventually girdle the shoot, causing dieback. Spread down the stem is not usually very extensive in older seedlings. Anamorphic reproduction of the causal fungi in or on each lesion produces huge numbers of conidiospores which are splash dispersed to neighboring plants. These new infections result in expanding foci of disease. Production of conidia, dispersal of conidia, and infection of the host plant are highly dependent on high humidity and the occurrence of rain or water splash. Incidence of disease is therefore highly correlated with rainfall and high humidity.

Host-Specific Foliage Diseases. The leaves of young trees, including nursery plants, are frequently attacked by highly host-specific fungi which have long and, in some cases, complex reproductive cycles. These diseases may be restricted in distribution, but can on occasion be very damaging on particular host species. Initial infections may be very scattered; however, during favorable conditions, spread to other foliage on the same individual plant or to foliage on neighboring plants may give rise to severe disease epidemics within the nursery phase or in the forest.

Microclimatic conditions favouring the production and dissemination of fungus spores and infection of the host have a marked effect on both disease incidence and severity. These conditions may vary for particular fungi, although high humidity, between 90 % and 95 % rh, is a general requirement. Optimum temperatures for infection and disease development may differ, however. The highly damaging pine needle blights caused by Dothistroma septosporum and D. pini (Dothistroma needle blight; Figs. [3a, b](#page-8-0) and [5a](#page-10-0)), Cercospora pini-densiflorae (syn. Mycosphaerella gibsonii; brown needle disease; Fig. [3d\)](#page-8-0) and Mycosphaerella dearnessii (brown spot needle disease), all require 100 % rh for infection and are favored by high relative humidity throughout the pathogen life cycle. These needle pathogens, however, have different temperature optima; D. pini grows most rapidly at $15-20$ °C, whereas for C. pini-densiflorae, the optimum is $25-30$ °C (Ivory [1967](#page-41-0)). The two species, therefore, rarely occur together. On the other hand, leaf rusts (Uredinales) and powdery mildews (Erysiphales; Fig. [4\)](#page-9-0) are generally favored by drier conditions during the majority of their life cycles, although high humidity is required for spore germination and infection.

Fig. 3 Foliar diseases. (a) Browning of young needles on radiata pine due to infection by Dothistroma septosporum; (b) excessive loss of needle on pine due to infection by Dothistroma septosporum; (c) Sphaeropsis (Diplodia) dieback of radiata pine shoots; (d) Needle browning on pine due to infection by Cercospora pini-densiflorae (syn. Mycosphaerella gibsonii) (Figure 3c courtesy of H. Hashimoto, Bugwood.org)

Typically, needle blights form small, discrete lesions, initially visible as palegreen spots that turn yellow and then red-brown as the tissues die. Lesions may extend rapidly, but others remain small. Reproductive structures of the causal fungi emerge from necrotic lesions (Fig. [5](#page-10-0)). These can impart particular colors or characters to the lesions. For example, lesions of Dothistroma needle blight are often red-brown and delimited by dark red lines, leading to one of the common names used in the past, "red band needle blight." Toxins may also be produced by fungi in these lesions; *D. septosporum* and *D. pini* produce dothistromin, which has structural affinities to the aflatoxins produced by Aspergillus species and is known to be required for virulence of D. septosporum (Bradshaw [2004\)](#page-40-0).

Symptoms of rusts are usually characteristic with large black, orange, or yellowcolored spores produced in erumpent sori in green tissues (Fig. [4a, b\)](#page-9-0). Foliage and shoot tissues turn necrotic at a later stage of disease development. Symptoms of powdery mildews include the characteristic white powdery appearance on the foliage or young shoots, formed by the development of fungal hyphae and asexual

Fig. 4 Symptoms of obligate pathogens on angiosperm trees. (a) Melampsora populina causing rust on foliage of hybrid poplar; (b) close-up of uredosori and teliosori of Melampsora populina; (c) powdery mildew on Acacia spp.; (d) sexual structures (cleistothecia) in which asci and ascospores of powdery mildews are formed (Figure 4c courtesy of Su See Lee)

conidia over the tissue surface. The powdery mildews produce structures known as haustoria into the epidermal cells of the host plant, which function to abstract plant nutrients preferentially into the pathogen. Extensive growth of the mildew results in foliar and shoot necrosis. In recent years, a rust disease of the Myrtaceae, guava rust (Puccinia psidii) has spread widely through Eucalyptus growing areas and is also affecting many other plants in the family (Glen et al. [2007](#page-41-0))

Spores of most foliar pathogens are disseminated in the air, following rain splash or through active ejection of the spores from reproductive structures.

Rust fungi (Uredinales) have complex life cycles. Several distinct types of spores are produced, with at least two distinct host plants (restricted to related genera) being infected.

Although the incidence of foliage diseases often correlates with environmental conditions at critical points in the life cycles of the host and pathogen, high plant densities in tree nurseries also increase the likelihood of infection by many pathogens, particularly because humidity is high around the plants and the short distance between affected and healthy plants expedites rapid spore transmission.

Stem Diseases. Stems of trees are attacked by many fungi, some of which are reasonably host specific. Such diseases often have restricted geographical

Fig. 5 Needle lesions on pines caused by (a) Dothistroma septosporum; (b) Lophodermium sp

distributions, but can be very damaging to particular hosts, given suitable conditions for infection and disease development. Some diseases, such as eastern gall rust of pines (causal agent: Cronartium quercuum f.sp. fusiforme) in Central America, are particularly important on nursery plants and young trees as the main stem of the plant is severely damaged, resulting in stunting or death over a period of 2–3 years (see Fig. [12\)](#page-20-0). The pathogen enters pine needles during wet weather following airborne dispersal of basidiospores from infected leaves of alternate hosts in the genus Quercus. Mycelia grow through the needles and may eventually reach the stem tissues, where the host responds through the production of large, ovoid to globular-shaped galls. The aecidia formed on the galls within 12 months, release aecidiospores which reinfect nearby Quercus spp., thus completing the heteroecious life cycle (Powers and Kuhlman [1997\)](#page-43-0). Western gall rust of pines (causal agent: Endocronartium harknessii) maybe a greater threat to tropical pines as the fungus has a reduced (autoecious) life cycle: the aecidiospores are able to reinfect pines directly, without passage through an alternate host. Based on inoculation experiments, many widely planted tropical pines are known to be highly susceptible to E. harknessii infection, but to date, this disease has not spread into tropical regions.

Stems of nursery seedlings may also be attacked by fungi with short simple reproductive cycles which may be more or less host specific (i.e., Phyllachora balansae on Cedrela spp. in Central and S. America; Dothiorella mahagoni on Swietenia macrophylla in the West Indies).

Fungal Diseases of Trees in the Forest

Although some diseases which affect seedlings can also infect older trees, there are many further diseases that infect only older trees.

Diseases of Roots. Fine roots of trees are attacked by a range of soilborne fungi and fungus-like organisms, but in good plant growth conditions cause little damage to the tree overall because the damaged roots are continually replaced. Under conditions favorable to the pathogen, or unfavorable to the tree, however, particular pathogens can become severely damaging. A widespread example of this type of damage is the problem caused by the oomycete *Phytophthora cinnamomi*, which is probably native in Papua New Guinea, but has been spread around the globe by human activities. Severe dieback of Eucalyptus marginata, other Eucalyptus spp. ("Jarrah die- back") and many other plant genera in Western Australia, Queensland, and Victoria demonstrates the severe destructive potential of alien invasive pathogens in general (Shearer et al. [2004;](#page-44-0) Weste [2003](#page-44-0)). Introduction of P. cinnamomi into previously uncolonised areas has led to severe epidemics in native and exotic forests in conjunction with mechanical disturbance of forests and interference with natural drainage.

Spread of P. cinnamomi and other Phytophthora species is by means of infected soil, soil run-off, or on young plants from infected nurseries. Good hygiene and sanitation of forest machinery can give some control; in Western Australia, strict regulations mean that any human activities in known affected areas must include sanitation plans for machinery leaving the area. Other *Phytophthora* spp. can cause similar root rots of trees under circumstances favorable to the pathogen (i.e., waterlogging). Associated symptoms include yellowing, stunting of leaves and shoots (e.g., little leaf disease of pines).

Recent work has demonstrated that species in the newly defined Oomycota genus Phytopythium may be involved in dieback of mature trees in parts of the tropics. In plantations of Cedrela odorata in Trinidad, a severe dieback in exotic provenances of the host tree appeared to be due to root infection by Phytopythium cucurbitacearum and/or P. vexans (Woodward et al. in prep.; Fig. [6](#page-12-0)). This genus, formerly known as Pythium clade K, is widespread in the tropics and has a wide host range including both herbaceous and woody plants. The interesting point in Trinidad is that the indigenous provenances of C. odorata were not showing symptoms of dieback, where adjacent plantations of a Colombian provenance had serious dieback, suggesting local adaptation to a probably native pathogen.

Fine roots of trees are also attacked by soilborne true fungi such as the wide host range Macrophomina phaseolina (Botryosphaeriales; charcoal root rot or black root rot; e.g., Barnard [1994](#page-39-0)) and the Hyphomycete Cylindrocladium spp. (Nectriaceae; teleomorphs are in the genus Calonectria; Crous [2002\)](#page-40-0). Where these diseases have infested soils by the production of microsclerotia, very high losses of roots may be incurred. *M. phaseolina* is associated with very high soil temperatures during the growing season.

Root Decay Fungi: The larger, secondarily thickened roots of trees are attacked by a range of nonhost-specific fungal pathogens which produce specialized peroxidase enzymes enabling the decay of lignified tissues. Such fungi are abundant in

any forested situation, driving the mineralisation of woody tissues and, hence, playing a major role in nutrient cycling (Boddy and Watkinson [1995\)](#page-40-0). Examples in tropical forest ecosystems include mainly Hymenomycetes, such as Phellinus noxius [brown root disease (Fig. [7](#page-13-0))], Armillaria spp., [Armillaria root rot (Fig. [8](#page-14-0))], Rigidoporous microporus (white root rot), R. vinctus [poria root rot] and Ganoderma spp. (red root rot; Fig. [9](#page-15-0); Lundquist [1987](#page-42-0); Mohammed et al. [2014\)](#page-42-0). The ascomycete Rhizina undulata can infect secondarily thickened roots of many gymnosperm trees causing death through killing the vascular cambium; the common name of Rhizina root rot is anomalous, as the pathogen does not degrade root tissues per se, but gains its nutrients from the vascular cambium.

Some of these fungi, however, can invade living tissues, such as bark, root cortex, cambium, and sapwood, as well as being able to degrade the cellulose and lignin of the sapwood and heartwood. Some root decay fungi require wounds for entry, and are unable to invade living tissues to any degree. Invasion of large heaIthy roots requires a high inoculum potential which is provided by mycelium from infected woody substrates in the soil derived from the previous forest

Fig. 7 Fungal "sock" growing up the lower trunk of Delonix regia (Courtesy of Charles Hodges)

vegetation. Mycelium of some of these fungi can penetrate a short distance through soil (e.g., some Armillaria spp.), but most can only invade root tissues which come into direct contact with infected woody debris from the previously colonized tree root systems (i.e., P. noxius; most tropical Armillaria spp.; root-infecting Ganoderma spp.; Lee [2004](#page-42-0); Mohammed et al. [2014](#page-42-0)). These diseases are therefore nearly always centered on an infected inoculum source, such as an old stump, root debris or fallen stem from the previous woody vegetation. Subsequently, spread may occur between crop trees by root–root contacts giving rise to characteristic roughly circular expanding disease foci.

It is very likely that root decay fungi are widespread at low inoculum potentials in undisturbed indigenous tropical forests, existing in an ecological balance in the ecosystem as saprotrophs, but occasionally causing mortality to native trees that are stressed by other agents. Felling trees can cause heavy stress, upsetting the ecosystem balance and providing large volumes of woody substrate for colonization by these and other saprophytic decay fungi. Events such as windthrow and stem breakage have similar effects in natural forests (i.e., brown root disease in Vanuatu), but disease foci do not enlarge rapidly, presumably because the forests are normal, with mixed species and varied age classes present. Phellinus noxius sometimes occurs on broken branches in the canopy in these

Fig. 8 Symptoms of Armillaria infection in broad-leaved trees. (a) Typical fruiting bodies of Armillaria sp.; (b) clearing forming in stand of *Pinus* sp. following killing by *Armillaria*; (c) Typical mycelial sheath of Armillaria in the vascular cambium region of the lower trunk

forests, outside the subterranean environment, which is considered this pathogen's usual habitat.

Root diseases require soil conditions conducive to spread and large food bases to provide the resources needed to persist and penetrate the roots of host trees. The persistence of inoculum for these pathogens depends on the size and durability of the woody substrate which is colonized. Stumps of trees left from felling operations, or from copping, for example, are particularly suitable as persistent substrates disease sources. In plantations of palms or rubber, the stumps of the previous crop are frequently sources of inoculum for the subsequent crop (Arrifin et al. [2000](#page-39-0)).

Diseases of Green Shoots and Foliage. The foliage and young shoots (before extensive suberization) of trees are frequently attacked by a wide range of fungi, some of which are host specific. These pathogens may have simple life cycles that may repeat once or twice each year (e.g., Dothistroma needle blight of pines), or more complex life cycles extending over 2 or more years, sometimes involving an alternate host, as in many foliage and stem rusts. In general terms, these diseases are very common and widespread on trees, although the amount of foliage damage is usually too little to cause notable growth reductions on the tree as a whole. In some instances, however, severe disease has been reported on forest trees in tropical countries. This problem was usually considered to affect exotic tree species grown in regions particularly favorable for development of the pathogen involved. More recently, however, these problems have been increasing on indigenous trees, partly

Fig. 9 Fruiting bodies of Ganoderma (red root rot) forming at the base of a dead Acacia sp

due to the increasing effects of alien invasive pathogens (e.g., Santini et al. [2013](#page-43-0)) and also due to climate change.

One example of pathogens with a simple life style is Dothistroma needle blight (DNB) of pines caused by the ascomycetes Dothistroma septosporum (sexual state: Mycosphaerella pini) and D. pini (sexual state unknown) (Fig. 3). Although this disease was, arguably, first observed in western Russia in 1911 (Bulman et al. [2013](#page-40-0)), it was not until the mid-twentieth Century that the large monocultures of Pinus radiata established in the highlands of East and Central Africa, Chile, and New Zealand were severely damaged in large-scale epidemics of DNB. Under conditions highly conducive to infection and disease development, D. septosporum has a minimum life cycle of approximately 40 days, and can have several generations per year during the prolonged periods of high relative humidity encountered in highland areas of East and Central Africa, for example. Vast numbers of conidia are produced by D. septosporum, enabling rapid multiplication of the pathogen and the onset of an epidemic in a short period of time. Spread of the conidia in mist droplets after splash dispersal from the acervuli also promoted rapid spread from plantation to plantation, and between regions over a few years. The near simultaneous appearance of DNB in cool parts of East Africa, Central Africa, Chile, and New Zealand probably arose due to diseased needles present in seed lots that were moved intercontinentally (Bulman et al. [2013\)](#page-40-0).

Pinus radiata and several other Pinus spp. susceptible to DNB can become more resistant with increasing age. Thus, young trees which are not killed within a few years gradually become less damaged. The time required for this change in susceptibility to occur depends on the extent of damage to the young tree, the susceptibility to DNB of the individual tree, and the disease risk at that particular site (Bulman et al. [2013](#page-40-0)). More recently, however, DNB has caused more severe disease on older trees, suggesting that changing climatic conditions may have reduced the abilities of trees to resist infection. Genetically controlled resistance to DNB occurs in several Pinus spp. (e.g., Ivory and Paterson [1970](#page-41-0); Bulman et al. [2013\)](#page-40-0), and between-provenance variations are now being considered for replacement plantations in some regions.

DNB is managed in *P. radiata* plantations of New Zealand by regular high pruning to reduce humidity under the canopy and by the application of copperbased fungicides (Bulman et al. [2013](#page-40-0)). This latter technique, first utilized in East Africa by Gibson and coworkers (Gibson [1974\)](#page-41-0), is a rare example of the use of fungicides in forestry being economically viable.

Other Mycosphaerella spp. causing severe needle blights of several Pinus spp. utilized in tropical plantations include Cercospora pini-densiflorae, the cause of brown needle disease of Pinus caribaea, P. merkusii, and P. roxburghii in Africa, Asia, and Central America (Fig. [2d;](#page-6-0) Bednářová et al. [2013\)](#page-40-0). Infection by this pathogen occurs at temperatures above 20 $^{\circ}$ C, resulting in a climatic separation from needle blights caused by *D. septosporum* and *D. pini*, which require lower temperatures to complete their life cycles. M. dearnessii causes brown spot needle blight in the Southern USA, and has spread further in N America, into Central America, South America, Colombia, and more recently into Europe and South China (Bednářová et al. [2013](#page-40-0)).

There are numerous leaf spot diseases and blights that affect young shoots and foliage of tropical trees. Diplodia shoot blight is a common disease affecting pines in both temperate and tropical regions (Capretti et al. [2013;](#page-40-0) Fig. [2c\)](#page-6-0). Eucalyptus spp. can be affected by a range of Mycosphaerella spp., particularly when in plantations (Crous [1998](#page-40-0); Crous et al. [2007;](#page-40-0) Fig. [10](#page-17-0)); Cylindrocladium shoot blight is also prevalent on eucalypts under conditions conducive to infection and disease development (Roux et al. [2005;](#page-43-0) Fig. [11](#page-18-0)). In many cases, there is insufficient damage to foliage for these diseases to cause lasting effects on the host, although when combined with the impacts of other pests and diseases, losses can increase greatly.

Rust pathogens also attack green foliage of both gymnosperms and angiosperms. When alternate hosts are also present in abundance, these pathogens may become highly damaging, as the inoculum required to infect the tree is produced on the alternate hosts. Moreover, the short, repeating life cycle of macrocyclic rust species may be produced on the alternate host plants, meaning that populations of the pathogen may build up rapidly. This situation occurs with leaf rust of teak in S.E. Asia and elsewhere in the tropics caused by Olivea tectonae and with the many Acacia rusts (Punithalingam and Jones [1971;](#page-43-0) Mulder and Gibson [1973;](#page-42-0) Daly et al. [2006](#page-40-0)). Microcyclic needle- and shoot-infecting rusts of pines are also known in temperate climates (i.e., *Endocronartium harknessii*) but to date have not been

Fig. 10 Mycosphaerella leaf spot on Eucalyptus nitens foliage

recorded in tropical countries. Macrocyclic leaf rusts are quite common on pines in natural forests and adjacent planted areas, but their effects are usually insignificant. A leaf rust (Aecidium fragiforme) is common on Agathis macrophylla in S.E. Asia (Punithalingam and Jones [1971\)](#page-43-0).

Foliage of angiosperms is frequently affected by powdery mildews, especially under warm humid conditions. These problems all have similar symptoms characterized by leaf necrosis preceded by a white powdery external growth of sporulating mycelia on all green surfaces; during aging of the mycelium, small brown dots appear, turning black on maturity. These structures are the cleistothecia, containing asci and ascospores, and are capable of withstanding environmental conditions unsuitable for host or pathogen growth. Powdery mildews are commonly seen on young plants of Eucalyptus spp., Acacia spp. (Fig. [3c, d\)](#page-8-0), Tectona grandis and many other trees, and may occasionally cause severe disease on mature trees (Limkaisang et al. [2006\)](#page-42-0).

Diseases of Flowers and Cones. Certain diseases attacking young shoots and foliage, such as powdery mildews and some needle diseases may also attack flowering parts of trees and can then be dispersed on seeds and fruits (including cones). In addition to these damaging agents, however, some diseases occur only on the flowers or cones. On graminaceous plants, smut diseases are common worldwide, but are rare on trees. One example is the smut of *Triplochiton scleroxylon* in West Africa caused by *Mycosyrinx nonveilleri* (Ofong [1978\)](#page-42-0); as with smut infections in other host plants, the flowers and fruits of the host become distorted and partially replaced by spores of the fungus. Although these infections may have little effect on the growth of the tree, the production of seed can be serious affected. Moreover, in trees, smut infections are systemic and persist from year to year. Cronartium conigenum attacks cones of pines, resulting in the replacement of seed by bright orange-colored aecidiospores of the fungus. This problem is quite common on Pinus oocarpa in Central America, where seed losses can be serious (Gibson [1979\)](#page-41-0).

Diseases of Woody Stems. Woody tissues of trees, present in large amounts in the main stems and branches, are attacked by fungal pathogens which cause

Fig. 11 Cylindrocladium shoot blights on (a) seedlings of Eucalyptus grandis and (b) Pinus palustris (Images courtesy of Edward L. Barnard, Florida Department of Agriculture and Consumer Services, Bugwood.org)

symptoms such as sunken cankers, swollen galls, or, internally, decay of the sapwood or heartwood. Many of these fungi require wounds for initial establishment. Decay fungi, moreover, can cause considerable loss of timber. Cankers and galls can also lead to breakage. "Pink disease", a canker caused by the fungus Erythricium salmonicolor, is present throughout the tropics, attacking a very wide range of hosts, including tree crops such as rubber and many forest trees. It is particularly well-known on *Eucalyptus* spp. in Southern India (Keane et al. [2001\)](#page-42-0), but has also caused major problems on many other tropical tree species (Roux and Coetzee [2005](#page-43-0)). Small necrotic lesions developing in young bark are associated with extensive superficial wefts of white mycelia over unaffected bark. In conditions of high humidity, this mycelium becomes more obvious and turns pink in color. Underlying phelloderm and secondary phloem tissues become necrotic, with pink pustules of sterile mycelia. The fruiting body of the pathogen, a thin, pink smooth resupinate basidiome forms on the under-surface of branches; in addition, orangered pustules of the conidial "necator" anamorph may form on upper surfaces of branches. The death of young branches spreads down the tree under suitable environmental conditions and into the main stem. Cankers can girdle the stem causing top-die back, stem breakage, or death of the whole tree. Infections are dormant in dry weather and diagnosis is very difficult at these times. Trials in

Vanuatu suggested that provenances of *Cordia alliodora* are all similarly susceptibility to "pink disease," and losses can be significant.

Other fungi also cause cankers on *Eucalyptus* spp., but most are infrequent. Very high mortality occurred in young plantations of E . grandis and E . saligna in Surinam following attack by *Diaporthe cubensis* (syn. *Endothia havanensis*; Boerboom and Maas [1970;](#page-40-0) Hodges [1980\)](#page-41-0), a pathogen present in many parts of the world where Eucalyptus spp. are grown, caused girdling cankers at the stem base in young trees, and at higher points on the stems leaving trees disfigured or dead (Conradie et al. [1990](#page-40-0)). Various Cytospora spp. also cause stem cankers on Eucalyptus, which can become very large after many years. Losses are variable and depend on the host species.

Cankers which can be highly damaging may occur on other tree species. Certain rust fungi that damage tree branches and stems may induce the formation of cankers on infected host tissues, eventually resulting in dieback of affected branches and top-dieback of trees if the infection girdles the main stem. Rust pathogens causing canker diseases on conifers are usually macrocycIic with complex Iife cycIes involving stages on alternate hosts. The galls and cankers, however, are perennial, gradually increasing in size over many years. Fusiform rust, for example, caused by Cronartium quercuum f.sp. fusiforme, is common on some pines in the USA (Powers and Kuhlman [1997;](#page-43-0) Fig. [12\)](#page-20-0), but to date has not spread into tropical pine plantations because of the absence of suitable alternate host species, in this case Quercus spp.

Several rust pathogens that affect tropical angiosperm trees are microcycIic and have repeating life cycles on the same host. Very few of these rusts, however, have been reported to cause significant damage on important tropical forest trees. Examples include stem rust of Cordia alliodora caused by Puccinia cordiae in Central and South America (e.g., Pardo Cardona [1998\)](#page-43-0), and the Caribbean and stem rust of Paraserianthes falcataria (syn. Adenanthera falcataria; Albizia falcataria; Falcataria moluccana), caused by Uromycladium tepprianum, in the Philippines (Old and Santos Cristovao [2003](#page-42-0)).

Tree stems are also frequently attacked internally by decay fungi. The decay process is natural, and is of great importance in forest ecosystems, as it releases nutrients sequestered in the woody tissues for cycling within the ecosystem. For timber production, however, excessive amounts of decay are detrimental to yield, and therefore have a negative impact on what humans may require from the forest. It has long been believed that decay fungi colonize stems and larger branches through wounds, although this assumption has been challenged more recently (Parfitt et al. [2010\)](#page-43-0). Regardless of the mode of entry, fungi commonly establish and cause serious decay in heavily lignified tissues of trees. The decay fungi themselves are almost all in the phylum Basidiomycota, class Hymenomycetes, although there are a few Ascomycota that can also cause decay in standing trees. Within the Hymenomycete decay fungi, two broad groups are recognized:

1. White rot fungi: these species are effective in degrading wood, being able to produce manganese-dependent lignin peroxidase enzymes, and also, in most

Fig. 12 Symptoms of Cronartium fusiforme on pine. (a) Fusiform gall covered in aecidia releasing aecidiospores on shoot of pine; (b) teliosori on the underside of a *Quercus* leaf (Figure 12a courtesy of Clemson University – USDA Cooperative Extension Slide Series, Bugwood.org; 12b courtesy of Robert L. Anderson, USDA Forest Service, Bugwood.org)

species, laccases. Other species may also produce lignin peroxidases. In effect, these peroxidases are "stress" enzymes, produced by the fungi in adverse growing environments, yet enabling the fungi to degrade the highly resistant lignified woody tissues. The degradation process results in a bleaching of the wood, hence the common name of "white rot." Examples in tropical trees include Stereum sanguinolentum in Pinus patula damaged by elephants (Fig. [13\)](#page-22-0) or water buffalo (Lundquist [1987](#page-42-0); Dublin [1995](#page-41-0))

2. Brown rot fungi: in contrast to white rot fungi, the brown rot species cannot degrade lignified material, but can access the cell wall carbohydrate polymers

(cellulose, xylans) in wood directly. The result of this type of decay is a crumbling wood structure, which is dark brown in color. There is some oxidation of the phenolic compounds left, hence the brown color of the products. An example affecting tropical trees is Pseudophaeolus baudonii.

Patterns of degradation also differ between fungi in these two main groups (Schwarze et al. [2000\)](#page-43-0). Broadly, however, most decay fungi should be considered highly specialized saprotrophs. The heartwood of trees is, in almost all species, dead, and cannot respond to the presence of the fungi. Heartwood in many trees contains high concentrations of antifungal compounds, although decay fungi are well adapted to detoxifying such compounds, due to production of peroxidases. The main active response that is seen in attacked trees, therefore, is at the boundary between the heartwood and sapwood, where considerable discoloration is often seen. Other responses that occur, depending on the host species, include the release of resins, kino or gums. In many cases decayed areas are compartmentalized by the host tissues (e.g., Shigo and Marx [1977](#page-44-0)), although the walls of the compartments may be breached by further growth of the fungi (Pearce [1996\)](#page-43-0).

Growth of the decay fungi into the sapwood is usually prevented by the high oxygen tension and water content, plus active responses of this tissue (Boddy and Rayner [1983;](#page-40-0) Pearce [1996](#page-43-0)). When a tree is stressed by factors such as drought or waterlogging, however, decay fungi may breach the reaction zone and enter the sapwood.

Certain fungi, mostly Ascomycota in the Ophiostomataceae, colonize sapwood and heartwood through wounds, living on easily assimilable soluble compounds in the wood, such as simple sugars and amino acids. These stain fungi can have serious economic consequences, as the green, gray, or blue staining in the tracheids is seen as a problem by end-users, despite the inability of such fungi to cause decay (Jacobs and Wingfield [2001\)](#page-41-0). The problem mainly arises in humid cIimates when felled trees are left too long before conversion into pulp or sawn timber.

Systemic Diseases. Wilt-causing fungi specifically colonize vascular tissues of affected plants, when the pathogens may be confined to the xylem until the plant dies. These pathogens produce toxins which spread rapidly in the vascular system resulting in loss of the ability to control water relations in the host and, as a consequence, wilting of the foliage of foliage and young shoots. Affected plants or parts of plants become stunted. Internally, the xylem companion cells respond by producing polyphenol oxidases, which cause dark streaking in the affected vessels. Further companion cell responses that occur, depending on the host tree, include the formation of tyloses and gums/gels, which plug the affected xylem. Specialized asexual bud cells of wilt-causing fungi are swept upwards in the xylem sap, lodging against perforation plates at the ends of vessels. These spores germinate, the germ tubes penetrate through the perforation plates, and further bud cells are released in the next vessel.

Wilt pathogens typically invade via the roots, as with Fusarium and Verticillium wilts, or are insectborne into stem tissues as with Dutch elm disease which occurs in temperate regions of Europe, N. America, Asia and New Zealand. Several wilt

Fig. 13 Elephant damage and subsequent decay. (a) African elephant asleep, leaning against a tree; (b) internal decay caused by Stereum sanguinolentum is evident in damaged trees; (c) fruiting bodies of Stereum sanguinolentum on fallen timber (Figure 13a courtesy of Joy Viola, Northeastern University, Bugwood.org)

diseases are well-known in tropical countries, such as sissoo wilt on Dalbergia sissoo in the Indian subcontinent (Al Adawi et al. [2013\)](#page-39-0), Sandragon wilt on Pterocarpus indicus in The Seychelles (Fig. [14](#page-24-0); Boa 2014, personal communication) and other more recently discovered Ceratocystis wilts in various regions of the world (Harrington [2013](#page-41-0)), including C. fimbriata in teak (Tectona grandis) plantations in Brazil (Firmino et al. [2012\)](#page-41-0).

Bacteria

Bacteria are prokaryotic, unicellular organisms, visible at high magnifications with the compound microscope, which are composed of a cell wall around apparently homogenous contents. Plant pathogenic bacteria are rod-like in shape, with aerobic or facultatively anaerobic metabolism, and often possess external flagellae (Waller et al. [2001](#page-44-0)). Bacteria cause diseases in all major groups of the plant kingdom, particularly among angiosperms, although most species are saprotrophic. The importance of bacteria lacking cell walls, termed phytoplasma, as pathogens of forest trees is being increasingly recognized (Griffiths [2013](#page-41-0)).

Bacterial infections of plants lead to similar symptoms to those occurring with fungal or fungus-like pathogens, including chlorosis, localized necrosis (leaf spots), general necrosis (shoot blights), rots, cankers, scabs, wilting, stunting, galls, fasciation, vascular wilts and gummy exudations. Symptoms often depend on the ability of the bacteria to produced toxins (chlorosis, necrosis and wilting) or enzymes (rotting). Certain bacteria are known to insert plasmids into host cells, which cause the host to produce conditions more conducive to bacterial reproduction, as in crown galI caused by Agrobacterium tumefasciens (Waller et al. [2001](#page-44-0)).

Bacteria cannot penetrate the outer protective tissues (cuticle; epidermis; phellem) of plants and must, therefore enter through wounds, natural openings, or through less-protected surfaces, such as the stigma (Manners [1982](#page-42-0)). Release of the bacteria from infected plants usually occurs as gummy exudations or sap flow, following which further dissemination is expedited by wind, rain, insects, nematodes, other animals, and human activities. Transmission also occurs during vegetative propagation, either on contaminated tools, or on the affected plants themselves and occasionally by seed.

Diagnosis is made by isolation of bacteria from affected plant parts using standard procedures, identification by laboratory tests and the induction of symptoms on host plants in inoculation tests (Waller et al. [2001](#page-44-0)). More recently, powerful molecular tests for diagnosis of bacterial infections in plants have been developed (e.g., Pirc et al. [2009](#page-43-0)).

In tropical countries bacterial leaf spots and shoot blights, caused by *Pseudo*monas spp. and Xanthomonas spp., have been reported on Azadirachta indica, Cassia spp., coffee, Cunninghamia lanceolata, Khaya spp., mango, Pinus radiata and Tectona grandis by various authors (Anonymous [1985;](#page-39-0) Gibson [1975;](#page-41-0) Langridge and Dye [1982](#page-42-0); Spaulding [1961\)](#page-44-0). These diseases are not generally very severe, but can result in die-back of affected shoots or even mortality of small plants (Langridge and Dye [1982\)](#page-42-0). Kairu et al. ([1984\)](#page-41-0) reported that application of the fungicide Captafol to control coffee berry disease produced large iatrogenic increases in incidence of bacterial blight caused by Pseudomonas syringae. Similarly, bacterial blight of P. radiata reported from New Zealand by Langridge and Dye [\(1982](#page-42-0)) may also be a similar iatrogenic effect of fungicides applied to control

Fig. 14 Wilt of Pterocarpus indicus in The Seychelles islands, caused by a form of Fusarium $oxysporum$. (a) Severe loss of foliage along with crown dieback. (b) Staining in the vascular system, indicative of a wilt disease; (c) Staining in the secondary phloem tissues near the base of the trunk (Courtesy of E. Boa)

terminal crook disease. Minor bacterial cankers and galls, caused by Agrobacterium tumefaciens, Corynebacterium spp., Pseudomonas savastanoi and Xanthomonas khayae, have also been reported on Eucalyptus spp., olive, and Pinus spp. (Gibson [1975,](#page-41-0) [1979](#page-41-0); Spaulding [1961;](#page-44-0) Coutinho et al. [2002](#page-40-0)).

Several serious bacterial wilts occur on trees, caused by species such as Ralstonia solanacearum and R. tectonae. Affected hosts include Cassia spp., Eucalyptus spp., Paraserianthes falcataria, Pinus spp. and Tectona grandis (Da Cruz and Dianese [1986;](#page-40-0) Gibson [1975](#page-41-0), [1979;](#page-41-0) Sharma and Sankaran [1987;](#page-44-0) Supriadi and Sitepu [2001\)](#page-44-0). There are also several known bacterial blights and diebacks now becoming more predominant on Eucalyptus species and hybrids (e.g., Coutinho et al. [2002;](#page-40-0) Arriel et al. [2014](#page-39-0)).

One group of bacteria, known as xylem-limited bacteria, can also cause major problems in trees. The type species in this group, Pseudomonas syzygii, causes

dieback of cloves in Indonesian plantations (Roberts et al. [1990\)](#page-43-0). A further species, Xylella fastidiosa, has recently been found causing dieback and mortality of cultivated olives in the Mediterranean region (Loconsole et al. [2014\)](#page-42-0).

Problems caused by Phytoplasma, cell-wall free prokaryotes, are becoming more widely recognized as problems in trees (Griffiths [2013\)](#page-41-0). As with viruses, Phytoplasma are mainly insect-transmitted. These organisms are often restricted to phloem tissues, and are sensitive to tetracycline or penicillin antibiotics. Several tree diseases are caused by Phytoplasmas, including spike disease of Santalum album, elm phloem necrosis, stubborn disease of citrus, lethal yellows of coconut, citrus greening and various witches' brooms, most notably of Paulownia and ash.

Control of bacterial diseases can best be achieved using resistant varieties; however, this can have severe limitations and thus use must be made of other control options such as (1) excIusion of the pathogen by quarantine and hygienic measures; (2) reduction of avoidable inoculum by crop sanitation, crop rotation, and treatment of planting materials; (3) protection of plants by the use of bactericidal chemicals; and (4) the use of modified cultural practices either to minimize transmission of the bacteria (i.e., suitable watering processes) or to reduce infection (i.e., pruning in dry weather).

Viruses Diseases

Viruses are highly specialized disease-causing agents, with little or no metabolic machinery, that are entirely dependent on a host for replication. They comprise nucleic acid, either RNA or DNA, encoding for replication, along with satellite nucleic acids encoding proteins that support replication (Agrios [2005](#page-39-0)). Outside the host organism, the nucleic acids are enclosed in a protein coat or "capsid." On entering a suitable host, the protein coat is lost and the DNA or RNA takes over the metabolism of the plant cell, so that the virus nucleic acids are replicated. Once the replication phase is complete, the virus capsid is added and the host cell dies. A further group of infectious particles similar to true viruses are the viroids, which exist as naked RNA, lacking a capsid (Agrios [2005\)](#page-39-0).

Virus diseases of trees are probably much more common than is obvious from the literature (Cooper [1993;](#page-40-0) Büttner et al. 2013). In trees, however, it is difficult, if not impossible to find individuals that have no virus infections, even when it is not obvious that the hosts are suffering in any way from such infections. The problems are recognized when the infected plants are displaying symptoms in the aerial tissues such as chlorosis (mosaics, mottling, yellowing, flecking), growth disturbances (galls, distortions on foliage and shoots, witches' brooms, stem pitting), necrosis (localized or systemic), wilting of the whole plant, and other physiological disturbances. Although problems caused by virus disease on roots are not visible, Hollings ([1983\)](#page-41-0) suggested that roots of Theobroma cacao infected by cocoa swollen shoot virus are also swollen and necrotic.

Virus particles are unable to penetrate intact plant cell walls and require suitable vectors and cell damage to enter the host; rarely, transmission can be via rootgrafting, or in seed and pollen (Cooper [1993](#page-40-0); Hollings [1983](#page-41-0)). The most common natural vectors of plant virus diseases are arthropods, particularly sap-sucking

insects and mites, although nematodes and fungi can also act as vectors. Human activities, such as those during vegetative propagation, pruning and cultivation are also important vectors in horticulture and forestry.

Diagnosis of suspected virus diseases is usually through the application of the serologically-based ELISA (enzyme-linked immunosorbent assay) test, along with confirmation either by cross-infection tests on a range of sensitive test plants. ELISA is based on antibodies raised against known viruses (Cambra et al. [2006\)](#page-40-0). Currently, molecular methods, particularly PCR- or quantitative PCR-based techniques are used for many virus infections in agricultural and horticultural plants (Büttner et al. 2013). Development of these methods for virus infections of forest trees, however, lags behind their application in agriculture and horticulture.

More than half of the known groups of plant viruses have been detected in trees and shrubs, the most frequent being "opportunist" viruses with wide host ranges which have spherical particles approximately 30 nm in diameter (Cooper [1993\)](#page-40-0). Although viral infections of woody plants are undoubtedly common, few have been reported on forest trees. It is highly likely, however, that trees can act as reservoirs for many viruses, which could then be transferred to nearby crop plants by suitable insect vectors.

Control of virus diseases is very difficult, particularly in perennial plants. Quarantine measures are in place to try and exclude the organism or its vectors from regions from where that virus is absent. Vectors may be controlled by chemical or other means. In agriculture and some horticultural crops, resistant or tolerant cultivars may be developed (Agrios [2005\)](#page-39-0). Further methods of control include elimination of the virus from hosts by meristem tip culture and/or thermotherapy or through antiviral chemotherapy. Hygienic propagation and cultivation procedures are essential in horticulture to minimize dissemination.

A number of possible viral infections have been reported on several tropical broad-leaved trees, including Acacia spp., Cassia spp., Paraserianthes falcataria, and Swietenia macrophylla (Gibson [1975](#page-41-0)), but conclusive proof through diagnosis is lacking to date. Knowledge regarding viral infections of conifers in the tropics remains fragmentary. Diseases known to be linked to viroid infection in trees are very rare, although cadang-cadang of the palm Cocos nucifera has received some attention (Maramorosch [1979](#page-42-0); Semancik et al. [1987\)](#page-44-0).

Nematodes

Pine wilt disease, caused by Bursaphelenchus xylophilus, is causing large losses to pines in several regions of the world, where the nematode has been introduced by human activity (Kamata and Takeuchi [2013](#page-41-0)). Native in North America where it is saprotrophic on native Pinaceae, $B. x$ ylophilus is vectored by long-horned beetles in the genus Monochamus, and has established in various regions, including temperate and subtropical areas in Asia and the west of the Iberian Peninsula. This disease causing organism poses a major threat to pines in many regions of the world where these conifers are grown.

A nematode *Bursaphelenchus coccophilus*, thought to be native in South America, is spreading in Central America and the Caribbean, attacking several palm species including coconut, African oil palm, and date palm. Symptoms include a red ring in the cross-section through a felled palm. It is likely that the nematode is vectored by Rhyncophorus spp. leading to concern that the pathogen will be spread rapidly in Europe by the red palm weevil, R. ferrugineus, that has recently been introduced there (Kamata and Takeuchi [2013\)](#page-41-0).

Parasitic Higher Plants and Algae

The most common algal species that infects plants is *Cephaleuros virescens*, which causes a disease commonly known as red rust on foliage of tropical woody plants. including tea, cocoa, rubber, and forest trees such as *Albizia* spp., *Cassia* spp., Khaya spp., Swietenia macrophylla, Tectona grandis, and Lophostemon confertus (Tristania conferta) (Gibson [1975](#page-41-0)). The disease is most common in hot, humid climates, affecting the foliage of heavily shaded, suppressed branches.

On trees, the most important angiosperm families that include genera partially or wholly parasitic on plants are the Loranthaceae (mistletoes), the Convolvulaceae (Dodders), and the Santalaceae (sandalwoods) (Waller et al. [2001](#page-44-0); Shaw and Mathiasen [2013](#page-44-0)).

Mistletoes are hemiparasitic, possessing chlorophyll enabling production of sugars, but requiring the host plant to provide water and minerals (Parker and Riches [1993\)](#page-43-0). A haustorium is produced into the stem or branch vascular tissue of the host plant. Two major groups of mistletoes are recognized, the dwarf mistletoes (Arceuthobium spp.) and the true or leafy mistletoes, which includes several different genera.

Dwarf mistletoes only affect coniferous trees, and are principally found in north temperate regions (Gibson [1979;](#page-41-0) Hawksworth and Wiens [1996](#page-41-0); Waller et al. [2001\)](#page-44-0), although some species occur in the native pine forests of Central America, where they cause considerable damage to individual trees or groups of trees. Arceuthobium spp. have greatly reduced foliage and an explosive seed dispersal mechanism.

True or leafy mistletoes affect many hardwoods and conifers throughout the world, with species of Amyema, Dendropemon, Dendrophthoe, Elytrante, Loranthus, Macrosolen, Phoradendron, Phthirusa, Psittacanthus, Struthanthus, and Tapinanthus commonly found in tropical regions (Watson [2001](#page-44-0)). The species have large green shoots and produce sticky seeds which are dispersed by animals, mainly birds. The part of the host which is colonized becomes swollen, often forming large galls and sometimes witches' brooms. Leafy mistletoes can cause significant damage to some trees, especially in even-aged stands, and were particularly noted on *Gmelina arborea* in Bangladesh (*Loranthus parasiticus*) by Ivory (unpublished) and on Tectona grandis (Waller et al. [2001\)](#page-44-0).

Recently, the parasitic plant *Tapinanthus globiferus* was reported at high infection rates in natural stands of Boswellia papyrifera managed for the production of frankincense in northern Ethiopia (Yirgu et al. [2014\)](#page-44-0).

Dodders (Cuscuta spp.) are trailing, leafless, yellow plants which form threadlike webs over the aerial parts of herbaceous and woody plants, including broadleaved and gymnosperm trees (Fig. [15a;](#page-28-0) Parker and Riches [1993\)](#page-43-0). Haustoria develop from the dodder stems into the host stems, enabling the abstraction by

Fig. 15 Parasitic plants. (a) Cuscuta sp. (dodder) growing throughout the crown of Cupressus sp.; (b) A quandong tree (Santalum acuminatum), growing on the root system of a nearby Eucalyptus sp., in Australia

the dodder of water and nutrients from the host vascular tissues. This process weakens the host; abundant growth of dodder may also lead to smothering of the host plant.

Sandalwoods are partial parasites on a wide range of woody plants, with a distribution ranging from India and Nepal, through Indonesia, Australia and into Polynesia. The plants are capable of effective photosynthesis, but are parasitic on other tree species from which they gain water and elements (Fig. 15b). Unlike the other species of parasitic plants described above, however, it is the parasite itself which is the valuable crop species. The best known species, *Santalum album* is used extensively for timber and the fragrant essential oils. Host species vary in their suitability for parasitism by particular *Santalum* spp., and are particularly needed by young sandalwood trees (Barrett and Fox [1995](#page-39-0)).

Epidemiology and Population Dynamics

Many bacteria and fungi are vectored by insects, usually through the pathogen being casually picked up from infective material and subsequently deposited on another suitable host (i.e., fire blight caused by Erwinia amylovora). More rarely, a more complex association with the vector and pathogen is involved, such as with olive knot caused by the bacterium *Pseudomonas savastanoi* and its vector *Dacus* oleae, Dutch elm disease caused by the fungus Ophiostoma novo-ulmi and vectors in the genus Scolytus spp., and with ambrosia beetles and pathogens (Kirisits [2013\)](#page-42-0).

Entry into the Host

Plant pathogens enter their hosts through a variety of means including (Agrios [2005\)](#page-39-0):

- 1. Natural openings, such as stomata, lenticels, hydathodes
- 2. Unprotected tissues lacking cutin or suberin, such as nectaries or stigmata
- 3. Natural wounds made by insects or other animals, by the plants being struck by hail or other materials in high winds or on the roots through abrasion against stones in the soil during movement in high winds; fresh leaf abscission scars can also provide wounds for entry of pathogen spores. Lightning may strike trees, blowing bark strips off, leaving elongated wounds that are colonized by decay fungi
- 4. Through wounds made by humans during management operations such as pruning or felling of adjacent trees
- 5. Through contamination of propagation materials and tools used in pruning or propagation.

Most pathogens, however, arrive at the host surface as propagules, usually a spore, which must germinate and subsequently enter the host. In the prepenetration phase, when the pathogen and host make contact, the resistant resting propagules must undergo one or more processes. Many spores, the main function of which is rapid multiplication of the pathogen exhibit, little dormancy, germinating immediately they land on a surface. Frequently, however, germination requires cues from various physical and chemical factors. Very high humidity or the presence of liquid water on the plant surface is required. Moreover, germination takes place within a particular range of temperature for each pathogen. Conidia of powdery mildews are exceptions to these rules, germinating at lower relative humidities, and sometimes inhibited by liquid water. Chemicals produced by either the host plant or within the spores themselves also affect germination. When spores of some species are present in high numbers, there may be mutual inhibition of germination by chemicals carried on the spore surface, regulating the spore densities for germination. Many exogenous chemicals from the aerial or subterranean parts of plants also affect germination. Spores often do not germinate in pure water but require carbohydrate or nitrogenous growth factors exuded from plant tissues, particularly roots. This is not usually a specific host fungus response but occurs in the presence of many nonhost plants also. Thirdly, the germ tubes or motile spores produced at germination must make direct contact with the host. This usually takes place by the growth of the germ tube, or the movement of motile zoospores, along diffusion gradients of chemicals (chemotropism) or electrical gradients (electrotropism). Germ tube growth of many fungi also responds to the topography of the plant surface (thigmotropism).

Following germination, the pathogen, through growth, releases chemicals which may be detected by the plant, and, via a series of signaling actions, the plant detects that a problem is present (e.g., Wasternack [2007;](#page-44-0) see section "Host Resistance to Infection"). The second phase is penetration of the host surface by the pathogen, which does not necessarily involve penetration of individual host cells: some pathogens, such as rusts and powdery mildews, grow intercellularly, producing specialized structures into host cells, invaginating the host plasmalemma, called haustoria (singular "haustorium"). A biochemical interface between the host and pathogen plasmalemmas enables the pathogen preferentially to take up nutrients form the host.

Spores or germ tubes of pathogens such as Nectria galligena and Pseudomonas mors-prunorum may enter stem tissues of trees through leaf scars, before developing to form cankers. Certain trees, such as many eucalypts and Cordia alliodora self-prune (Greaves and McCarter [1990\)](#page-41-0); pathogens that have colonized these branches may grow into the living stem, or through the heartwood, causing decay.

At points of emergence of lateral roots, poorly protected tissues occur giving certain pathogens direct access to the cortex and secondary phloem tissues of the parent root. Apart from being intimately associated with the infection processes for viruses and a few specialized bacteria and fungi, insects, mites and nematodes cause wounds in aerial tissues and in roots which permit entry by other nonspecialized pathogens. These pathogenic organisms may or may not be associated with particular insects and are not usually transmitted by the insect.

In the tropics, hail damage can sometimes be severe, damaging not only leaves, but also causing pitting on stem tissues. This problem results in sudden, massive and synchronous disease outbreaks, sometimes caused by opportunistic pathogens, such as *Sphaeropsis sapinea* on *Pinus radiata*, which can be lethal even to very large trees (Capretti et al. [2013\)](#page-40-0). Some of these pathogens are probably endophytic, existing inside the plant until another stressing agent (in this case hail damage) prevents containment of the pathogen by the host. Strong winds can cause branches to break and snap or twist woody stems of various sizes, exposing sapwood and heartwood of host trees to infection. Even gentle winds can cause cracking in branches, frequently at points where branching occurs: the wound between the branches is then weakened by the entry and action of decay fungi.

Colonization of the host is completed by the pathogen producing propagules for further dissemination, although in the case of some fungi, rapidly spreading asexual spores may be produced soon after initial penetration of the host.

Host Resistance to Infection

Spores of fungi and bacteria are widespread in the air, in and on the soil and in water. Impacting on plant surfaces must be very frequent. These contacts, however, rarely result in infection and disease; in the vast majority of cases no colonization occurs. Hence, plants are resistant to most pathogens.

This form of resistance is known as nonhost resistance. There are, however, other forms of resistance, represented by varying susceptibility of individual plants to a given pathogen that can attack that plant. In agriculture and horticulture, this

form of resistance has been exploited in selection and breeding programs for over 100 years in attempts to reduce the impacts of diseases such as black stem rust of wheat, or Fusarium and Verticillium wilts of tomato.

Resistance to host-specific pathogens is genetic and can be detected by analysis of progeny arising from cross-breeding between resistant and susceptible plants. The genetic control of resistance can be through the action of a single gene (monogenic), several genes (oligogenic) or by many genes (polygenic), and the extent of resistance conferred by these different mechanisms of control varies a great deal. Monogenic resistance, for example, can give almost total resistance to the pathogen, but eventually selects for individuals in the population of the pathogenic organism that can overcome the resistance gene. Eventually, therefore, the resistance breaks down completely and the crop may be lost; breakdown can take less than 5 years or in some instances much longer. Clearly, this type of resistance is not valuable in forest trees, where generation times are highly extended relative to annual crop plants. Oligogenic resistance can be similar, although tends to be more robust than monogenic resistance. In contrast, polygenic resistance results from the combined actions of many genes and is far more durable than either mono- or oligogenic resistance (Cheng et al. [1998](#page-40-0); Hamelin [2013\)](#page-41-0). Resistance of this type may be less complete than mono- or polygenic resistance, but for long-lived plants, it is undoubtedly more appropriate to accept some losses during the plant's lifecycle.

Resistance against given pathogens can also vary with age of the plant. Resistance of many pines against Dothistroma needle blight, for example, increases with maturity of the trees (see Fraser et al. [2015](#page-41-0)). As described earlier, many diseases attack young plants, but are almost unknown on older plants, and vice versa.

Hypersensitivity is a rapid, extreme form of resistance to pathogens, often controlled at the single gene level (Jones and Dangl [2006\)](#page-41-0). When the plant detects the presence of a pathogen through signaling, a hypersensitive plant responds very quickly, killing a small number of cells immediately adjacent to the pathogen. Obligate pathogens such as rust fungi cannot utilize dead cells and the attack is prevented. Other pathogens that can grow on dead and dying host cells may not be affected by hypersensitivity.

Plants also synthesize many secondary metabolites, some of which have antimicrobial action. Some are produced in healthy tissues, whereas others are produced in response to biotic or abiotic stresses. If these antimicrobial compounds accumulate rapidly enough around a point of pathogen attack, the pathogen may be inhibited and infection does not occur, or proceeds only slowly (Strange [2003](#page-44-0)). It is now understood that this process is controlled by a complex signaling cascade between the host and pathogen, the outcome of which varies depending on both the resistance of the host and the relative virulence of the pathogen (e.g., Wasternack [2007\)](#page-44-0).

Resistance mechanisms are similar in trees and herbaceous plants. Any differences arise due to the secondary tissues that are abundant in trees. Bark tissues and sapwood are typical of the tissues in trees that are capable of responding actively to attack; heartwood, as mentioned above, is dead. In sapwood, responses include the production of toxic compounds (as described in more general terms above), but also

include the formation of gums and gels and/or tyloses into the xylem or tracheids. Tangential ray parenchyma tissues in both the bark and sapwood can also respond actively to attack (Pearce [1996](#page-43-0)). Bark tissues, including the phelloderm and the secondary (redundant) phloem are also living and can respond to infections (Pearce [1996\)](#page-43-0).

Loss Assessment, Disease Forecasting and Risk Prediction

As we know that disease outbreaks in plants are to a great extent controlled by the environment, models have been constructed to predict the occurrence of disease, and the potential extent of damage. These models are best developed for agricultural crop plants, such as potatoes, or cereals, and are usually focused on specific host-pathogen combinations. Apple scab is modeled in many countries, allowing early warning to growers of the likelihood of disease development, when they should, therefore, use preventative measures against infection and disease development. For details on the development of crop disease forecasting methods, see Madden et al. ([2007\)](#page-42-0), which includes information on how to gather data to estimate crop losses.

Examples of models for predicting diseases of forest tree diseases are rare, however. The main economically important product from forests, of course, is timber, although other, nontangible forest products are becoming more recognized for their multiple values. Disease models for forests, however, remain largely focused on losses in timber. There are several models published for diseases of forest trees, such as Dothistroma needle blight (Möykkynen et al. [2015\)](#page-42-0), and for various diseases affecting temperate forests, including Heterobasidion root and butt rot (Pukkala et al. [2005\)](#page-43-0), Fusarium pitch canker (Möykkynen et al. [2014](#page-42-0)), and White pine blister rust (Kearns et al. [2014\)](#page-42-0).

Disease Management

Choices of disease management methods are rather restricted in the forest. In contrast, a wide range of management options are available to control diseases in the nursery environment.

In order to maximize the impact of any management methods on the pathogen, detail of the disease life cycle is required. Correct diagnosis of the problem is a very important step. The greatest effect will be achieved when control is targeted at the weakest point in the pathogen life cycle, such as the time soon after spore germination, or by applying the controls to the specific infection court for a given pathogen. Gathering data on the etiology of the disease takes time and effort and, therefore, costs money. But it can reap great rewards, in terms of reduced losses. A problem in tropical trees is that most of the data required are not available as yet, although work in South Africa is making great inroads into these deficiencies.

A problem that appears to be increasing currently, is the ingress of damaging alien invasive species in all continents of the world where trees are grown. Measures such as legislation and plant quarantine, seed disinfection, prohibition of imports, and

good hygiene in plant nurseries and plantations, can help to reduce damage from these pests, but once established, there is usually little that can be done.

Disease Avoidance

Diseases can be avoided by either the elimination of the pathogen following eradication of an introduced pathogen or exclusion of an alien pathogen, or by the replacement of susceptible species with nonhost species, or provenances of the same species with greater levels of resistance. In addition some diseases which cannot spread over long distances can be avoided by only planting uninfected sites.

Plant Quarantine. Most countries or trading areas have regulations on the import and export of plant materials that aim to reduce the probability of also transporting potentially invasive pests and pathogens along with the goods. The over-arching systems for these regulations are decided at an international level through the World Trade Organization, along with eight Regional Plant Protection Organizations (RPPO; e.g., EPPO, NAPPO), and National Plant Protection Organizations (NPPO). When invasive pests and pathogens are newly discovered, the aim is to have an upward flow of information from NPPO to RPPO. There are many flaws in the system, however. For example, if NPPOs do not report the discovery of a "new" problematic invasive species promptly, the further spread may occur, reducing the chances of preventing establishment. Moreover, the system does not prepare adequately for formerly unknown problems, species that were not recognized in their native environments where they co-evolved with their host and may cause little or no notable damage. Until very recently, WTO insisted that restrictions can only be used when "scientifically justifiable," to provide reasonable protection without unduly interfering with trade: this system, however, has been widely criticized, as steps could only be taken against known organisms, fully described and named. There are now steps to tighten the regulations to cover the potential for unknown pests and pathogens.

Currently, phytosanitary officers devise and monitor the regulations, and also are responsible for inspection of consignments of plant materials. Plant health certificates are issued by phytosanitary officers in the exporting countries and checked for detail and accuracy at ports of import. Some trading nations have very strict isolation facilities in which plants are maintained in strict quarantine immediately on arrival in the importing country. The time in quarantine varies depending on the plants and the potential problems they may be carrying.

Elimination of the Pathogen. In some instances, it may be feasible to eradicate a newly introduced pathogen which has yet to establish fully in a given area. Methods include the destruction and disinfection of suitable host plants within the infected area and in an appropriately-sized "cordon sanitaire" around the area. The procedure must be accompanied by regular surveys outside the area. Such efforts, however, have rarely proved effective in the medium term, except where initial detection of the problem occurred very soon after invasion, and the prescribed actions were both prompt and thorough. In the nursery, soilborne pathogens could be eliminated using sterilization procedures such as steam of chemical injections, but the whole nursery site would require treatment to provide even a moderate

degree of success. Many pathogens would recolonize sterilized soils very rapidly from adjacent soils, with potentially devastating effects on future seedling crops and transplants subsequently grown in those beds.

Replacement of Susceptible Species. When a disease outbreak occurs and the whole stand is threatened, then a logical approach is to fell the area and replace the affected species with an alternative tree that is not susceptible to the pathogen. The replacement species may not provide products (usually timber) of the same quality as the original tree planted on the site, and will, therefore, have a "cost."

Site Selection. This approach may be used to avoid infection when particular pathogens, which cannot spread readily from infected sites, are absent for some reason. This is well-known in parts of Africa where infection of highly susceptible trees, such as Pinus elliottii, can be avoided by planting only on old grassland sites where inoculum of Armillaria root disease does not exist due to the absence of large pieces of woody plant debris on which the fungus can persist.

Hygiene and Cultural Controls

Hygiene should be practiced at the local level in order to prevent or delay the introduction of a pathogen into a tree nursery or from there into the forest. Nurseries can be sited away from forests, plantations or individual trees which provide sources of infection. Cleaning and disinfecting nurseries between crops is important too; where appropriate, soil sterilizing methods should be used prior to re-sowing nursery bed. Moreover, younger plants should be separated from older plants of the same or related species, to avoid transfer of pathogens.

As certain pathogens can be transferred in seed (e.g., Fusarium circinatum, cause of pine pitch canker), any seed for propagation should be obtained from approved sources, particularly registered seed stands, where available. Any tools used in pruning or grafting should be disinfected between plants, and cultivation tools and machinery must be kept as clean as possible. If a disease does appear, the affected plants should be removed and burned as soon as possible. In preparing beds for sowing seed, re-planting young seedlings, or in preparing substrates for potting, mycorrhizal soil, free from diseased litter, and obtained from a healthy plantation, should be used to add organic matter.

A further precaution is to avoid transfer of seedlings between production nurseries, even where the seedlings appear to be healthy.

Good forest hygiene should follow similar protocols: plant only healthy seedlings, preferably locally grown, disinfect tools between individual plants or between plantations or forest areas, including forest machinery, and treat any disease that occurs promptly before it can spread. Many silvicultural practices influence the development of diseases either directly, as in the infection of wounds, or indirectly by their effects on host vigor or persistence of pathogen inoculum. Examples which may be effective against diseases of forest trees include the removal or destruction of inoculum (i.e., stump removal for the control of root rots caused by species of Armillaria, Heterobasidion, Phellinus and Rigidoporus), the timing of pruning to coincide with low inoculum densities during dry weather (i.e., cypress canker) or with the status of the host branches (i.e., before the branches die and self-prune as in Eucalyptus spp. in Zambia and Oceania); and the partial or complete sterilization of nursery soil to eliminate soilborne pathogens such as Macrophomina phaseolina.

Biological Control

Under natural conditions, pathogens are components within the ecosystem complex, and interact with the other organisms present and with their environment. Multitrophic interactions between pathogens and the multitude of other organisms present mean that over time a balance may develop, such that outbreaks of pests or disease do not exceed rather low levels, although individual plants that lack required resistance genes, or are growing in suboptimal conditions may succumb to pathogens (Gilbert [2002\)](#page-41-0). Changes in the ecosystem, however, whether deliberate, accidental, or through natural agents can disrupt the balance, potentially stimulating the pathogen, resulting in epidemic development. This principle may be mimicked artificially in the application of biological control. Most commonly, particular fungi and/or bacteria have been used to control various fungal pathogens in agriculture, horticulture, and, to a lesser extent, forestry.

The most effective biological control used in forestry was developed in the UK in the 1960s to prevent the colonization of pine stumps by Heterobasidion annosum, a root and butt rot hymenomycete that also kills pines (Holdenrieder and Greig [1998\)](#page-41-0). Oidia (a type of asexual spore produced by fragmentation of the hyphae) of the fungus *Phlebiopsis gigantea* are applied to the fresh stump surface immediately after felling; this saprotrophic fungus rapidly grows into the stump, preventing H . annosum from colonizing. Further strains of P . gigantea are effective against *Heterobasidion* spp. in other conifers. Current work in Sumatra is examining the potential for another *Phlebiopsis* sp. to control invasion of fresh tree stumps by Ganoderma philippii (Agustini et al. [2014\)](#page-39-0).

Similar control of the root rot pathogen *Phellinus noxius* is obtained in Queensland through inoculation of hoop pine (Araucaria cunninghamii) stumps with spores of *Trametes versicolor* and a *Tyromyces* spp. (Anonymous [1988](#page-39-0)).

Commercial preparations of Trichoderma spp. spore suspensions are available for the treatment of wounds, particularly to prevent colonization of *Prunus* spp. by the silver leaf pathogen, Chondrostereum purpureum (Grosclaude et al. [1973\)](#page-41-0). This treatment is more effective than the wound paints used previously. Trichoderma spp. have also received attention as potential biological control agents in tropical forests (Prasad and Naik [2002;](#page-43-0) Sariah [2003;](#page-43-0) Widyastuti [2006\)](#page-44-0), although no commercial products are yet available.

Although a highly promising approach to disease management, biological control requires a great deal more research before it can be deployed on a wide scale in tropical forestry.

Chemical Control

Chemicals used to control plant diseases are grouped into three broad categories, depending on usage and mode(s) of action:

- (a) Sterilants and fumigants
- (b) Protectants
- (c) Therapeutants

Some chemicals can fit into more than one category, however, having both protectant and therapeutic properties. Commercial agrochemicals are formulated in a mixture of one or more active ingredient with wetting agents, stickers, emulsifiers and diluents, and are recommended for use in particular situations, on given crops. Moreover, national and international regulations control the approval and licensing of chemicals for particular purposes, in order to ensure the health and safety of users and operators and the protection of the environment.

The chemicals approved for use in nurseries and in forestry are changing rapidly, due to health and safety concerns; hence no particular manufactured chemicals are named here.

Prior to sowing seed, or to using composts as growing substrates in nurseries, inoculum of pathogens can be killed using sterilants and fumigants. Sterilant chemicals may also be used when cleaning machinery and other equipment and plant containers used during propagation to destroy inocula of pathogens; these chemicals have activity against a wide range of living organisms, usually including the plants themselves. Fumigants are used to completely or partially sterilize soil or other substrates before use.

Fumigant chemicals in particular can be dangerous to handle, and are quite expensive, being used in large quantities. Nursery soils and other substrates can also be partially sterilized using dry heat or steam, or by injection of ozone, when suitable machinery is available.

Protectants are applied prior to infection, to reduce the chances of disease becoming established in plants. These chemicals are often applied to growing plants at times of particular susceptibility, and provide protection over the whole aerial surface, provided they are applied correctly. Fungicidal chemicals vary in their effects against particular pathogens, a feature which must be taken into consideration before use. Moreover, in order to provide reliable protection, formulation of the pesticide is crucial: it must provide a uniform persistent layer over the host surface, be stable under fluctuating environmental conditions and be compatible with the equipment used for application. Timing of application is of utmost importance for good disease control to be obtained.

Most chemicals used as therapeutants are systemic, absorbed through the plant surface and translocated throughout the whole plant. On contact with infections, the pathogen may be killed or inhibited. The half-life of systemic fungicides in plants varies, but eventually activity decreases and is lost as the concentration of the active chemical is reduced below critical levels following dilution by growth of the host or inactivation by natural degradation processes.

Hypothetically, it is not necessary to ensure uniform coverage of systemic therapeutants, although good practice in formulation and application are essential to ensure effective use of these expensive chemicals. Usually, the chemicals are applied as sprays applied to foliage, but root drenches and injection into tree stems are also used under appropriate circumstances. Antibiotics produced by living organisms act systemically and are also quite selective with effects against bacteria, fungi, and various mollicutes. Choice of the appropriate type of therapeutant is therefore essential for effective disease control.

Many systemic therapeutants have specific modes of action against pathogens. Although this makes these compounds highly selective and therefore less damaging to the environment, prolonged use may result in the development of fungicide resistance pathogen populations, rendering the fungicide useless against the respective diseases. Although antibiotics used in medicine have also been applied in forestry, their use probably accelerated the development of antibiotic-resistant bacteria.

The application of man-made chemicals to manage diseases should be a last resort in any situation, used only when other methods of control, such as correct soil preparation, installation of good drainage, appropriate sowing densities for seed, have failed.

In tropical forestry, chemical controls may be used in forest nurseries. Soil sterilants are applied to nursery beds or to potting soil prior to planting to control diseases, pest, and weeds. Foliar sprays and soil drenches with protectants or therapeutants are also used to manage outbreaks of damping-off, blights and other diseases (e.g., Dothistroma needle blight on Pinus radiata and brown needle disease of Pinus caribaea). Application of similar chemicals to diseased older trees is rare because of the expense of applying the expensive chemicals using aircraft. Thus, although Gibson ([1974\)](#page-41-0) showed that application of copper-based fungicides to control Dothistroma needle blight on Pinus radiata was feasible in Kenya, the cost of the procedures and various logistical problems meant chemical control was discontinued. In subtropical areas of New Zealand, however, aerial application of copper-based fungicides is still used to control Dothistroma needle blight (Bulman et al. [2013](#page-40-0)).

Selection and Breeding for Resistance

For annual crops, such as cereals and potatoes, it has proven possible to breed hybrids showing good levels of resistance to many pathogens, such as rusts, mildews, and blights. This resistance is often mono- or oligogenic and highly specific to given races of the pathogens, leading in time to the pathogens overcoming the resistance for the reasons given in section ["Host Resistance to Infection.](#page-30-0)" This type of approach would be completely unsuitable for plants with long life spans. In the more recent past, plant breeders have focused on the more difficult task of incorporating polygenic resistance into cultivars which is likely to have much longer-lasting results. Although the resulting hybrids do not resist infection completely, the progress of disease is slowed markedly with reduced crop losses. Being polygenic, moreover, the probability of pathogen races developing that can overcome the resistance is far lower than with mono- or oligogenic resistance (e.g., Poland et al. [2009\)](#page-43-0). For trees, with rotation periods of 10–100 years in duration, the use of cultivars with polygenic resistance is likely to be a much safer option than deployment hybrids with mono- or oligogenic resistance. Forest practice has generally encouraged the use of genetic variability in the field, but in recent

times, clonal forestry has taken on much greater importance in tropical regions, particularly with very fast growing trees, such as Eucalyptus hybrids. Should diseases threaten in such plantations, it could be pertinent to plant mixtures of cultivars, or multilines, which have different disease resistance genes, although mixtures may lead to other problems in harvesting.

In practice, the selection and breeding of forest trees has taken little note of susceptibility to diseases, with the exception of poplar against canker and rust diseases (e.g., Pinon and Frey [2005](#page-43-0)). There is a gradual selection for healthy plants within the overall breeding program. Very considerable efforts have, however, been made to incorporate resistance to fusiform rust into Pinus taeda in southeastern USA with some success (Kayihan et al. [2005\)](#page-42-0). Clones of *Pinus radiata* resistant towards Dothistroma needle blight are also under development in New Zealand (Bulman et al. [2013](#page-40-0)). Many pines show quantitative variations in resistance to pitch canker caused by Fusarium circinatum (syn. Gibberella circinata) suggesting that it may be possible to manage this problem by more targeted selection, or through breeding programs (Wingfield et al. [2008b\)](#page-44-0).

Disorders

Apart from being attacked by a wide range of pests and pathogens, trees also suffer from abiotic stresses, caused by climatic, edaphic, and environmental problems. These stresses are generally termed "disorders" and have visible symptoms resulting from deviations in normal physiological processes caused by nonliving factors.

Differences from pest and pathogen attack include the tendency for the symptoms to appear uniformly amongst affected plants, without evidence of a slow spread from an infection focus, and a lack of association with particular pathogens, although affected tissues may be invaded secondarily by various opportunistic pests or pathogens. Disorders are frequently involved in complexes together with biotic diseases, such as oak decline in many parts of the temperate world (Paoletti [2000\)](#page-43-0). Many disorders can be avoided from the outset through careful matching of species (including provenance) to site, or can be cured or modified by amendments to the environment. Examples are the application of fertilizers, better drainage, or use of more appropriate spacing at planting.

Disorders in tropical countries are most commonly caused by shortage or surplus of water, insufficient soil nitrogen and/or phosphorus, and excess salinity. Deficiencies of other macro-and micronutrients and excess concentrations of toxic elements also occur occasionally at particular sites. The effects of abiotic factors can be direct, impacting on the plant itself, or indirect, where pests and diseases affect the trees secondarily due to abiotic problems. Symptoms of nutrient deficiencies vary with plant and the confounding effects of other problems and require laboratory analyses for diagnosis. Confirmation of the diagnosis obtained using chemical analyses must be backed up by a positive response in the plants to applications of the particular nutrients.

Catastrophic environmental events, including wind, hail, lightning, and fire are also common in tropical regions. The resulting damage is usually immediately obvious, but where internal tissues have been damaged by low- intensity fires, for example, may be delayed for up to a year. Frequent lightning strikes in parts of the tropics can affect groups of trees, from one to several hundred in extent, and are characterized by a sudden appearance and nonspreading habit. Some affected trees may have longitudinal strips of bark torn off or longitudinal splits at points on the bark, most of which are rapidly colonized by bark beetles. Hail storms can defoliate trees, causing extensive tearing in the foliage and damage to young stems. The damage results in numerous wounds encouraging the development of fungal infections, such as Diplodia die-back of Pinus radiata in Southern Africa (Zwolinski et al. [1990](#page-44-0)), and consequent die-back and death of large trees.

Other disorders brought on by environmental and climatic factors include basal sweep, resulting from constant, mono-directional winds. Air pollutants can cause severe damage to trees near industrial plants and escape of pollutants (excess fertilizers, pesticides) into water courses can lead to tree health issues, particularly in urban or agricultural environments. Diagnosis in these situations relies on detailed knowledge of site history; chemical analyses may be required for reliable diagnosis of problems arising from pollution (Costello [2003](#page-40-0)).

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