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REVIEW

Climate change and forest diseases

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As climate changes, the effects of forest diseases on forest ecosystems will change. We review knowledge of relationships between climate variables and several forest diseases, as well as current evidence of how climate, host and pathogen interactions are responding or might respond to climate change. Many forests can be managed to both adapt to climate change and minimize the undesirable effects of expected increases in tree mortality. We discuss four types of forest and disease management tactics – monitoring, forecasting, planning and mitigation – and provide case studies of yellow-cedar decline and sudden aspen decline to illustrate how forest diseases might be managed in the face of climate change. The uncertainties inherent to climate change effects can be diminished by conducting research, assessing risks, and linking results to forest policy, planning and decision making.

Keywords: forest management, forest pathogens, plant disease management, plant pathogens, sudden aspen decline, yellow-cedar decline

Introduction

Forests provide critical refuges for terrestrial biodiversity, are a central component of the earth's biogeochemical systems, and are a source of ecosystem services essential for human wellbeing (Shvidenko *et al.*, 2005). Forests also have the potential to mitigate global climate change by serving as net carbon sinks (IPCC (Intergovernmental Panel on Climate Change), 2007). Global forest area has been reduced by 40% over the last three centuries, primarily as a result of human activities, particularly the conversion of forested land to agricultural usage (Shvidenko *et al.*, 2005). Today, less than one-third of the earth's land area is covered by forests (FAO, 2001). Disturbance agents such as pathogens, insects and fire can decrease the ability of forests to provide goods and services, especially when the natural disturbance patterns or regimes of these agents are altered by human activities (Lewis & Lindgren, 2000; Bentz *et al.*, 2010).

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Climate has always shaped the world's forests (Bhatti *et al.*, 2006), but today the world's climate has become warmer and will change further and at an unprecedented rate (Pachauri & Reisinger, 2007). For example, for the next two decades a warming of about 0·2°C per decade is projected for a range of emissions scenarios (Nakicenovic & Swart, 2000; Pachauri & Reisinger, 2007). Recent extensive tree death events in North America have been associated with climate change (Kurz *et al.*, 2008; van Mantgem *et al.*, 2009). Climate change has the potential to initiate multiple, interacting processes that affect forests (Williamson *et al.*, 2009), some positive and others negative. For example, higher atmospheric CO_2 concentrations can result in increased growth rates and water use efficiency of trees (Rogers & Dahlman, 1993), or there may be a reduced effect of carbon fertilization on tree productivity over time and in older trees (Boisvenue & Running, 2006). Elevated CO_2 was shown to increase host resistance to two forest diseases in the southern USA (Runion *et al.*, 2010). Because responses to CO_2 enrichment may differ among species and locations, a wide range of responses to increased atmospheric CO_2 should be expected worldwide.

The purpose of this paper is to improve understanding and management of forest tree diseases under a changing climate. We do this by reviewing knowledge of relationships between climate variables and several forest pathogens and by examining current evidence demonstrating climate change, host and pathogen interactions. We also recommend and discuss forest health and forest management strategies that should be integrated to better contend with forest diseases and climate change.

The literature on climate change and forest and tree diseases has recently been synthesized (for example: Boland *et al.*, 2004; Desprez-Loustau *et al.*, 2007; Sturrock, 2007; La Porta *et al.*, 2008; Moore & Allard, 2008; Dukes *et al.*, 2009; Kliejunas *et al.*, 2009; Tubby & Webber, 2010) and some general predictions can be made:

- Because most plant diseases are strongly influenced by environmental conditions, climate change will affect the pathogen, the host and the interaction between them, resulting in changes in disease impact.
- Because abiotic factors such as temperature and moisture affect host susceptibility to pathogens and pathogen growth, reproduction and infection, changes in interactions between biotic diseases and abiotic stressors may represent the most substantial drivers of disease outbreaks.
- The distribution of hosts and diseases will change. Increases in temperature and changes in precipitation may allow the ranges of some species to expand, perhaps whilst contracting elsewhere, but models frequently predict a reduction in potential geographic distribution of tree species (e.g. Rehfeldt *et al.*, 2009) or diseases (Venette, 2009) as a result of climate change. This question has also stimulated debate with regard to infectious diseases of humans (Epstein, 2010). Pathogens may play key roles in this range reduction in forest trees.
- Pathogens that typically affect water-stressed hosts are likely to have an increased impact on forests in regions where precipitation is reduced.
- The roles of pathogens as disturbance agents will probably increase, as their ability to adapt to new climatic conditions will be greater than that of their long-lived hosts.
- Most pathogens will be able to migrate to locations where climate is suitable for their survival and reproduction at a faster rate than tree species.
- Climate change will affect the life cycles and biological synchronicity of many forest trees and pathogens, resulting in changes in the distribution and phenology of events such as budbreak in tree hosts, spore release by pathogens, and activities of insects that serve as vectors of pathogens; this may significantly alter disease incidence and severity.

Definitions

A plant disease is defined as "any malfunctioning of host cells and tissues that results from continuous irritation by a pathogenic agent or environmental factor and leads to the development of symptoms" (Agrios, 2005). Three interrelated elements result in disease: a susceptible host plant, a virulent pathogen and a favourable environment or climate and are often visualized as the 'disease triangle'.

Forest pathogens include fungi, oomycetes, bacteria, phytoplasmas, parasitic higher plants, viruses and nematodes. Native forest pathogens, which are integral components of many forest ecosystems (Hansen & Goheen, 2000), influence species richness and abundance, and forest succession, structure and composition at the stand and landscape levels (Winder & Shamoun, 2006). They also strongly affect animal populations, nutrient and water cycling, and overall ecosystem function. Native forest pathogens sometimes conflict with management objectives and the pathogens can damage valued forest resources.

Non-native or introduced forest pathogens are also widespread globally and strongly influence forest structure and composition (Dukes *et al.*, 2009). These pathogens have the potential to kill many trees, sometimes almost all individuals of a given species in a stand or landscape, because novel hosts have not coevolved with the pathogens and have limited resistance (Hansen, 2008). A similar dynamic may be observed when non-native hosts are infected by native pathogens.

Noninfectious or abiotic forest diseases are caused by persistent, nonliving factors that are directly deleterious to tree health (for example, drought, nutrient deficiency and pollution) (Boyce, 1961).

Forest decline diseases are complex and involve interacting factors (Manion, 1991; Manion & Lachance, 1992). *Predisposing factors* are long-term, static or slowly changing factors, such as soil moisture regime (a site factor), stand density (a stand factor) and precipitation (a climate factor). *Inciting factors* are short-term factors, such as defoliating insects or drought, which cause acute stress. Trees affected by inciting factors alone may recover quickly, but recovery is much slower if the trees also are affected by predisposing factors. *Contributing factors* are usually secondary pathogens or insects that kill trees already affected by predisposing and inciting factors.

Climate can be narrowly defined as the average weather, or, more rigorously, as a statistical description in terms of the mean and variability of relevant quantities (e.g. temperature, precipitation and wind), over a period of, typically, 30 years (Pachauri & Reisinger, 2007). Climate change "refers to a change in the state of the *climate* that can be identified (e.g. by using statistical tests) by changes in the mean and/or variability of its properties, and that persists for an extended period, typically decades or longer" (Pachauri & Reisinger, 2007). Climate change should be differentiated from short-term and normal decadal climate cycles, such as the El Niño-Southern Oscillation and the Pacific Decadal Oscillation.

If host susceptibility or pathogen virulence and/or aggressiveness is increased by climatic conditions, then a disease outbreak or epidemic may result (Agrios, 2005).

An epidemic is defined as a change of disease intensity in populations over time and space (Campbell & Madden, 1990), but the term is usually used to describe a widespread and severe outbreak. Plant disease epidemics may become more frequent as climate changes. Epidemics of insects and pathogens that are mobile or easily dispersed, and can kill their hosts relatively quickly, are examples of pests particularly likely to increase in frequency (Ayres & Lombardero, 2000). Many forest pathogens can take decades to spread and then to kill their hosts, yet their long-term, cumulative effects can be serious. Rates of spread of these agents and rates of tree mortality may be significantly altered by climate change.

Case studies

Climate influences the dynamics of host–pathogen interactions, so it is likely that climate change will have strong effects on the distribution (Pearson & Dawson, 2003) and behaviour of plant species and pathogens. In this section we review knowledge of relationships between climate variables and several forest diseases, as well as current evidence of how hosts, pathogens and pathosystems are responding or might respond to climate change. Currently, there are several models available to project future distribution of forest trees using climate variables (e.g. Hamann & Wang, 2006; Rehfeldt *et al.*, 2006), but relatively few specifically designed for making such projections for forest pathogens. CLIMEX, a dynamic simulation model developed in Australia (Sutherst *et al.*, 1999) for predicting the potential geographical distribution of a given species, and widely used for weeds (e.g. Goolsby, 2004), has been used to investigate the potential distribution of several pathogens (e.g. Brasier & Scott, 1994; Scherm & Yang, 1999; Venette & Cohen, 2006). Also, in Portugal, under the PHRAME (Plant Health Risk and Monitoring Evaluation) project, there has been progress made on prediction modelling for expression of pine wilt disease (Evans, 2007). For Swiss needle cast, Manter *et al.* (2005) developed a temperature-based disease prediction model in combination with geographical information systems-linked climate databases to estimate disease levels for areas in the Oregon Coast Range of the USA.

We have divided diseases and their causal pathogens or agents into three groups: diseases caused by pathogens directly affected by climate; diseases caused by pathogens indirectly affected by climate; and decline diseases. There is wide consensus that future temperatures will be warmer in much of the world; there is less certainty over future precipitation trends (IPCC (Intergovernmental Panel on Climate Change), 2007). Thus, in Table 1, we present predicted trends for the impacts of these forest diseases under two climate-change scenarios, the first with warmer and drier conditions, the second with warmer and wetter conditions. The effects of climate change on forest diseases and forest ecosystems will depend on the pathosystem and its location (Runion, 2003; Sturrock, 2007) and predicted changes in impact and accompanying uncertainty levels for sample diseases will vary under the two scenarios.

Pathogens directly affected by climate

This group of pathogens can cause disease in a healthy, vigorous host, if the pathogen's environmental requirements are met. Their life cycles are directly affected by temperature and moisture. For example, many pathogens causing needle diseases are sensitive to precipitation and humidity and their rates of reproduction, spread, and infection are greater when conditions are moist (Harvell *et al.*, 2002). In these cases, changes in temperature and moisture more directly affect the pathogen regardless of their effects on the host.

Phytophthora root rot

Among the various species of *Phytophthora* infecting woody plants the soilborne *Phytophthora cinnamomi* is one of the most destructive. This pathogen is present in most temperate and subtropical areas of the world causing disease in more than 1000 host species. Infection by *P. cinnamomi* and some other related species results in root rot and cankering, and often plant death. Temperature, moisture and pH all influence pathogen growth and reproduction. Floods and droughts are generally accepted as triggers of epidemics. Changes in climatic conditions in the last 60 years, i.e. increased mean winter temperatures, seasonal precipitation shift from summer into winter and a tendency to heavy rain are favouring infection by several species of *Phytophthora* in Central Europe. A proliferation of phytophthora root rots may be expected, increasing the instability and vulnerability of forest ecosystems dominated by beech and other susceptible tree species, including oak, alder, maple, fir and pine species (Jung, 2009).

For *P. cinnamomi*, Bergot *et al.* (2004) predict that increasing temperatures will lead to a potential range expansion of *P. cinnamomi* along the western coast of Europe of one to a few hundred kilometres eastward from the Atlantic coast within one century. For root rot caused by *P. cinnamomi*, CLIMEX models predict more widespread disease in the UK and much of coastal Europe; and globally, a marked increase of the disease in temperate zones of the northern and southern hemispheres, with a reduction across the tropics and subtropics (Brasier & Scott, 1994; Brasier, 1996).

Sudden oak death; ramorum blight

Phytophthora ramorum is an important invasive pathogen in both North America and Europe. In wildlands in the USA the disease is known to occur only in central coastal California and southwest Oregon, where infected *Notholithocarpus densiflorus* and *Quercus agrifolia* can die relatively soon after the onset of symptoms (crown dieback, stem bark lesions). In Europe in the late 1990s the pathogen was primarily found on ornamental plants in nurseries and gardens. However, in 2003 *P. ramorum*

Table 1 Predicted change in impact on forests of several examples of forest diseases as they respond to warmer and drier or warmer and wetter future climates (adapted from Dukes et al., 2009)

| Group | Forest disease (pathogen) | Climate change | | | |
| | | Warmer/Drier | | Warmer/Wetter | |
		Predicted change in impact[a]	Level of uncertainty[b]	Predicted change in impact[a]	Level of uncertainty[b]
Diseases caused by group-1 pathogens (temperature and moisture directly affect pathogen reproduction, spread, infection and survival)	Phytophthora root rot (Phytophthora cinnamomi)	−/0	L	+	L
	Sudden oak death/ramorum blight (Phytophthora ramorum)	−	M	+	L
	Dothistroma needle blight (Dothistroma septosporum, Dothistroma pini)	0/−	M	+	L
	Swiss needle cast (Phaeocryptopus gaeumannii)	−	M	+	L
	White pine blister rust (Cronartium ribicola)	−	L	0	M
Diseases caused by group-2 pathogens (temperature and moisture more directly affect host susceptibility to pathogen)	Armillaria root disease (Armillaria spp.)	+	L	0	M
	Sphaeropsis shoot blight (Sphaeropsis sapinea)	+	L	0	M
	Charcoal canker (Biscogniauxia mediterranea)	+	L	0	M
	Botryosphaeria canker (Botryosphaeria spp.)	+	L	0	M
	Pitch canker (Fusarium circinatum)	+	M	+	H
	Septoria canker (Septoria musiva)	+	M	0	M
Decline and abiotic diseases	Yellow-cedar decline	+	L	+	M
	Sudden aspen decline	+	L	0/+	M
	Oak decline	+	M	0	M

[a] +, increase in impact; −, decrease in impact; 0, no change in impact.

[b] The effects of climate change on pathogen/host interactions are complex and uncertain. Dukes et al. (2009) lists four types of uncertainties: those associated with (i) internal ecosystem processes, (ii) climate projections (general agreement that mean annual surface temperatures will increase but amount and nature of precipitation change is less certain), (iii) future human actions, and (iv) a lack of data on the pathogens themselves. These four types of uncertainty were considered when estimating predicted changes in impact by the case study diseases; associated uncertainty levels were estimated to be low (L), moderate (M) or high (H).

was found infecting mature *Quercus falcata* in the UK and *Quercus rubra* in the Netherlands. In subsequent years, over 20 different species of broadleaved trees (mainly mature *Betula*) were found to be infected with *P. ramorum* in the south of England (Webber, 2008). Since autumn 2009 there have been dramatic outbreaks of the disease in the UK, affecting stands of *Larix kaempferi* (Webber *et al.*, 2010) (Fig. 1) and several new host species (e.g. *Tsuga heterophylla*) (Brasier *et al.*, 2010). In the USA and Europe, eradication and containment strategies are being used. Regulations on movement of nursery stock and forest materials have been imposed in more than 50 countries (Kliejunas, 2010).

The life cycle of *P. ramorum*, an organism with optimal growth between 18 and 22°C, is similar to that of other aerial *Phytophthora* species. Sporangia produced on the surfaces of infected leaves and twigs of foliar hosts can be splash-dispersed to neighbouring hosts or conveyed longer distances by windblown rain (Davidson *et al.*, 2005). Moisture is essential for survival and sporulation, and the duration, frequency, and timing of rain events during the winter and spring play a key role in inoculum production. In *N. densiflorus* forests of central coastal California, winter rains are critical to persistence of the pathogen, whereas in coastal evergreen forests rain must fall in March, April and May. Increases in precipitation will probably produce optimal conditions for the pathogen in some areas, resulting in an increase in rates of infection. Scenarios of climate change produced by CLIMEX projected that the area favourable or very favourable for *P. ramorum* will decrease substantially in the eastern USA, but will increase in the west-coast states of Washington, Oregon and California (Venette & Cohen, 2006; Venette, 2009).

Dothistroma needle blight

Dothistroma needle blight – also referred to as red band needle blight – affects primarily pines (*Pinus* spp.), but also species of spruce (*Picea*), larch (*Larix*) and Douglas fir (*Pseudotsuga menziesii*) (Watt *et al.*, 2009). The

Figure 1 *Phytophthora ramorum* affecting a stand of Japanese larch (*Larix kaempferi*) in Plym Woods, east of Plymouth, UK.

disease is caused by the needle pathogens *Dothistroma septosporum* and *Dothistroma pini* (Barnes *et al.*, 2004). The disease causes premature defoliation and reduction in rates of growth, resulting in economic and aesthetic losses and, in some situations, mortality. Although the disease has a global distribution (Gibson, 1974; Bradshaw, 2004), until recently it was primarily considered a problem in the southern hemisphere, where it was introduced in commercial plantations of non-native *Pinus radiata*. Trees in Africa, Chile and New Zealand have suffered major damage from this needle blight since the 1960s.

The geographic range and intensity of dothistroma needle blight, particularly in the northern hemisphere, has increased dramatically since the late 1990s (Brown *et al.*, 2003; Woods, 2003; Bradshaw, 2004). In France, the impact of the disease was minimal during the late 1960s to 1980s, but has rapidly increased since, particularly on plantations of *Pinus nigra* ssp. *laricio* (Villebonne & Maugard, 1999). In Britain, an increase in the disease since 2000 has resulted in a moratorium on planting of *P. nigra* ssp. *laricio* and *Pinus contorta* var. *latifolia* in public forests. A rapid expansion of dothistroma needle blight was initially observed on *P. nigra* ssp. *laricio*, with intense infection and mortality on the extensive plantations in eastern England. Since 2006, when the disease was reported on *P. contorta* var. *latifolia* in Scotland, the distribution and intensity of the disease has increased appreciably, with mortality of approximately 90% occurring in some areas in trees aged 50 years or older. Although the disease has been observed since the early 1800s in British Columbia, Canada (Welsh *et al.*, 2009), its range and intensity have increased considerably since 2000, particularly on *P. contorta* var. *latifolia* (Woods *et al.*, 2005).

The increase in distribution and intensity of dothistroma needle blight is attributed to multiple synergistic factors. In British Columbia and the UK, the spread of the disease appears to have been facilitated by large plantations of highly susceptible species. Until recently, British Columbia's forest management policies promoted the establishment of *P. contorta* var. *latifolia*, even in areas where it was not naturally the dominant species (Woods, 2003). In the UK, *P. nigra* ssp. *laricio* was widely planted for timber as a key species in a climate-change adaptation strategy (Broadmeadow, 2002). However, climate in particular appears to be driving the disease. Climate models developed by Watt *et al.* (2009) indicated that dothistroma needle blight can survive in diverse environments, including sub-Arctic, temperate, Mediterranean, continental, subtropical and dry tropical. Rates of infection depend on temperature, including overnight minimum temperature; the period of needle wetness; and the quantity of spores present. Ten or more consecutive hours of needle wetness are usually required for infection by *D. septosporum* (Gadgil, 1974; Bulman, 1993). The suitable temperature range for infection is 5–25°C, with an optimum of 16–20°C (Bulman, 1993). Rainfall is particularly critical for infection; amount of summer rainfall and

rates of infection in the following year are positively correlated (Bulman, 2006). In British Columbia and the UK (Woods *et al.*, 2005; Archibald & Brown, 2007; Brown & Webber, 2008), an increase in disease intensity has coincided with an increase in spring and summer rainfall and increases in daily minimum temperatures during late summer since the 1990s. The positive correlation between daily minimum temperature and intensity of the disease may decrease if summer rainfall decreases.

Swiss needle cast

Swiss needle cast of Douglas fir is caused by *Phaeocryptopus gaeumannii* and symptoms include chlorosis, reduced needle retention, and reduced tree growth. Boyce (1940) reported that the native pathogen was widespread but had little impact throughout the *P. menziesii* region of western North America. However, a severe epidemic began in the coastal fog belt of Oregon in the early 1990s and has persisted since (Hansen *et al.*, 2000). In the Pacific Northwest, high levels of Swiss needle cast usually occur at low elevations (for example, in close proximity to the Pacific Ocean or Puget Sound), often in areas with summer fog and high rainfall and on sites formerly occupied and better suited to *Tsuga* and *Picea* spp. or to hardwoods (Hansen *et al.*, 2000). Occurrence of this disease in the Pacific Northwest is also positively correlated with degree-day accumulation during winter and leaf wetness hours during spring to autumn (Manter *et al.*, 2005). Winter temperatures and spring precipitation have increased by 0·2–0·4°C and 0·7–1·5 cm, respectively, per decade since 1970 in the Oregon Coast Range, suggesting that regional climate changes may be influencing the distribution and severity of the disease in the Oregon Coast Range (Stone *et al.*, 2008). Further increases in winter temperature of approximately 0·4°C per decade through to 2050 are projected for the Pacific Northwest, suggesting that the severity and distribution of Swiss needle cast also are likely to increase (Stone *et al.*, 2008).

A positive correlation between spring precipitation and relative abundance of *Phaeocryptopus gaeumannii* was found in southern British Columbia (Hood, 1982). In New Zealand, where *P. menziesii* is not native, the climate variable with the strongest positive correlation with severity of disease was winter mean temperature, which explained about 80% of the variation in infection and damage (Stone *et al.*, 2007).

White pine blister rust

Cronartium ribicola, a fungus native to Asia and causing blister rust of white pines (*Pinus* spp.), was introduced into Europe in the mid-1850s and to North America in the early 1900s. Infection by *C. ribicola* results in branch dieback, reproductive failure and tree mortality (Fig. 2). In North America, white pine blister rust has caused more damage and costs more to control than any other conifer disease (Bega, 1978). In many regions of Canada, mortality of *Pinus monticola* and *Pinus strobus* has been so extensive that the species no longer are considered commercially viable. In the western USA, the number of

Figure 2 White pine blister rust, caused by *Cronartium ribicola* on *Pinus lambertiana* (sugar pine) at Happy Camp, California, USA.

P. monticola grown for reforestation has been reduced by 95% because forest managers consider it too risky to plant (Kinloch, 2003). Synergistic effects of *C. ribicola*, drought, increasing temperatures and outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) are thought to drive extensive mortality in high-elevation *Pinus albicaulis* populations (Logan & Powell, 2001; Kegley *et al.*, 2004; Gibson *et al.*, 2008).

The environmental conditions associated with *C. ribicola* infection are well documented (Spaulding, 1922; Mielke, 1943; Van Arsdel, 1954; Bega, 1960). Infections of pine typically occur in 'wave' years, when weather conditions are ideal for the fungus. White pine blister rust is considered a cool weather disease (basidiospore germination and infection occurs from about 0 to 20°C), with spread driven largely by moisture, air temperature and air circulation (Van Arsdel, 1965). For example, *C. ribicola* basidiospore germination and pine needle infection requires 48 h with conditions of 100% relative humidity and temperatures not exceeding 20°C (Van Arsdel *et al.*, 1956). In the USA, portions of some north-central states and southern California are too warm for infection.

Changes in temperature and the frequency of 100% air humidity events will influence the epidemiology of *C. ribicola*. Since infection requires a cool, moisture-saturated environment, conditions suitable for *C. ribicola* to cause infection will decrease with fewer wet periods in spring or early summer. The probability of years when weather conditions especially favourable for new infections result in significant intensification and spread (wave years) will diminish as the climate becomes warmer and drier, resulting in less rust infection (Kinloch, 2003). Locations in which these changes are projected include the southern Sierra Nevada in California.

Cylindrocladium leaf blight

The fungus *Cylindrocladium quinqueseptatum* causes a severe leaf blight of many tree species in tropical and sub-tropical forests, primarily in Australia and countries in Southeast Asia, including Laos, Thailand and Vietnam. Severe epidemics are associated with warm temperatures and long periods of leaf wetness. Modelling suggested that small increases in temperature and precipitation can substantially increase the area in which there is a high probability of severe epidemics (Booth *et al.*, 2000). Based on weather records of the latter 20th century, the only area of China considered climatically suitable for severe epidemics is Hainan, an island off the southern coast. However, consistent with climate change projections, temperature and precipitation recently have increased in parts of China, especially the south. Accordingly, the disease has become a substantial problem in those areas (F. Zhang, Fujian Agriculture and Forestry University, Fuzhou, China, personal communication).

Pathogens indirectly affected by climate

Pathogens indirectly affected by climate tend to infect hosts that are stressed by (i) environmental factors, (ii) pathogens directly affected by climate, or (iii) insects. Such pathogens can sometimes infect a healthy host and remain latent until the host is stressed. Whilst the ability of these pathogens to sporulate, spread and infect new hosts is affected by temperature and moisture, factors that stress their hosts are often critical to their successful invasion of host tissues. For example, an increased incidence of summer drought will increase the probability that trees will be infected by pathogens whose activity is facilitated by host stresses, such as root pathogens, wound colonizers and latent colonizers of sapwood (Brasier & Scott, 1994; Lonsdale & Gibbs, 2002; Desprez-Loustau *et al.*, 2006).

Armillaria root disease

Armillaria species cause root disease in natural and managed forests worldwide (Kile *et al.*, 1991), infecting conifers and occasionally hardwoods, and also occasionally woody shrubs and herbaceous plants. Infection results in wood decay, growth reduction and mortality. *Armillaria* species can grow over a range of temperatures, from 10 to 31°C, although the optimal temperature for many species is at 20–22°C (Rishbeth, 1978; Keca, 2005 as cited in La Porta *et al.*, 2008). Some *Armillaria* species are primary pathogens and infect healthy trees in forests, whereas other species act as secondary agents, infecting after host immunity has been impaired by drought, temperature extremes, other pathogens, insects or reductions in site quality (Wargo & Harrington, 1991; Goheen & Otrosina, 1998). *Armillaria* spp. can also increase the probability that bark beetles or other insects will colonize trees. Armillaria root disease caused by *A. solidipes* (= *A. ostoyae*) is responsible for losses of 2–3 million m^3 timber per year in Canada's Pacific Northwest (Morrison & Mallet, 1996). Tree failures caused by decay are substantial hazards in recreational and urban areas. In general, losses attributed to armillaria root disease are greatest in relatively dry Mediterranean or continental climates (Kile *et al.*, 1991). The incidence of this root disease is likely to increase as temperatures increase and precipitation decreases (Shaw & Kile, 1991; US Office of Technology Assessment, 1993; La Porta *et al.*, 2008; Klopfenstein *et al.*, 2009). Klopfenstein *et al.* (2009) demonstrated that the area in which climate supports persistence of *P. menziesii*, a major host for *A. solidipes* in the interior northwestern USA, is likely to decrease by 2060, and suggested that the stressed *P. menziesii* will also be more susceptible to armillaria root disease.

Pine wilt

Pine wilt disease, caused by the pine wilt nematode, *Bursaphelenchus xylophilus*, originated in North America but is now found in parts of Europe (e.g. Portugal) and East Asia (e.g. Japan, China and Vietnam). It has long been known that, where mean July temperature is less than 20°C, the disease is rare, even though the pathogen may be present (Rutherford & Webster, 1987). Under elevated summer temperatures and seasonal moisture stress, the pine wilt nematode may cause rapid wilting and mortality (Evans *et al.*, 2008). The nematode was introduced to China via Japan in the early 1980s (Zhao, 2008) and has since caused mortality on over 80 000 ha of Chinese forests. Disease occurrence and severity in China are positively correlated with annual mean temperature and winter and spring precipitation, but negatively correlated with June precipitation (Xi & Niu, 2008; Zhao, 2008). Currently, climate restricts the area suitable for pine wilt disease to less than half of China, southeast of a line from Beijing to Yunnan Province. Warmer temperatures and increased precipitation, especially if combined with seasonal or occasional moisture stress, may increase the probability of the disease occurring in some northern and western regions of China (Zhao, 2008).

Under the PHRAME project (Evans, 2007) in Portugal, there has been progress made on prediction modelling for expression of pine wilt disease. This has been achieved by linking together models of tree suitability parameters and tree physiological responses relative to ecological and climatic conditions. This complementary modelling approach has yielded valuable predictive tools for improved future risk assessment of pine wilt disease for Portugal and probably for other parts of Europe (Evans, 2007).

Canker pathogens

Although numerous canker pathogens are capable of infecting vigorous trees, canker-causing fungi are more likely to reach epidemic levels and cause substantial damage to trees weakened by heat and drought stress (Schoeneweiss, 1975, 1981). Most canker diseases are caused by facultative parasites, such as species of *Biscogniauxia* (*Hypoxylon*), *Botryosphaeria*, *Diplodia*, *Septoria* (Desprez-Loustau *et al.*, 2006) and *Valsa*.

Biscogniauxia mediterranea causes charcoal canker in *Quercus suber* and *Quercus cerris* woodlands in the Mediterranean and has recently been found on oaks with cankers in Slovenia (Jurc & Ogris, 2006). Disease symptoms in Slovenia first appeared after severe drought and unusually high temperatures. Total rainfall before the onset of symptoms in summer 2003 was significantly below the 30-year average, whilst average monthly temperatures for the same months were 5·8, 3·6 and 5·6°C higher than the 30-year average. This fungus is expected to continue moving north as temperatures increase (Vannini & Valentini, 1994; Desprez-Loustau *et al.*, 2006; Vannini *et al.*, 2009).

Botryosphaeria dothidea causes serious damage only to weak, stressed or off-site trees (Ma *et al.*, 2001). Drought stress and winter injury have been associated with increased rates of infection and canker expansion of *B. dothidea* on apple trees (*Malus*) in the eastern USA (Brown & Hendrix, 1981). Severity of diplodia shoot blight, caused by *Diplodia sapinea*, has consistently been associated with water stress (Bachi & Peterson, 1985; Blodgett *et al.*, 1997a,b; Paoletti *et al.*, 2001). Similarly, cankers caused by *Septoria musiva* on inoculated, water-stressed trees were significantly larger than those on non-stressed trees (Maxwell *et al.*, 1997).

Cytospora canker of *Alnus incana* subsp. *tenuifolia*, caused by *Valsa melanodiscus*, is currently epidemic in the southern Rocky Mountains, Alaska, and other areas of western North America (Trummer, 2006; Worrall, 2009). In Colorado and adjoining areas, over 60% of standing stems are dead or diseased. Recent evidence suggests that warm temperatures in midsummer, even for a few weeks, are associated with explosive canker growth and host mortality (Worrall *et al.*, 2010a).

Decline diseases

Forest declines are diseases caused by a complex of predisposing, inciting and contributing factors. As these difficulties accumulate the tree gradually becomes less able to produce, store and mobilize carbohydrates. It typically develops symptoms of 'dieback', and unless the situation improves significantly the tree eventually dies. Three forest decline diseases are considered: The first – oak decline – is described below whilst descriptions for yellow-cedar decline and sudden aspen decline are included later in management case studies.

Oak decline
Decline of *Quercus* spp. worldwide is caused by interactions among environmental stressors (e.g. drought, pollution, low minimum winter temperatures, and flooding) (Brasier & Scott, 1994), insects and pathogens (e.g. *Armillaria* and *Phytophthora* spp.). In the USA and throughout Europe, episodic, extensive decline and death of oaks has been recorded since around 1900 (Wargo *et al.*, 1983; La Porta *et al.*, 2008). Additional drivers of oak decline in Mediterranean regions of Europe include changes in land use (Brasier, 1996). Studies of oak decline

in Mexico (Alvarado-Rosales *et al.*, 2007) concluded that low temperatures and water deficits cause stress and, in some cases, result in death of oaks. Furthermore, the fungus *Biscogniauxia atropunctata* is associated with some stressed trees; in other cases, *P. cinnamomi* was identified as a primary pathogen (Manion & Lachance, 1992; Thomas *et al.*, 2002).

Climate and forest tree death

Whether climate 'alone' causes tree mortality is difficult to evaluate, yet the number of reports of forest dieback, decline and mortality attributed to climatic drivers is increasing. Because the role of climate cannot be demonstrated as definitively as that of pathogens, the scientific community often must rely on circumstantial evidence. Evaluating whether climate change drives tree mortality is even more difficult. For instance, tree mortality in response to drought and heat has recently been associated with climate change, but episodic droughts have long been implicated in mortality independent of climate change. Thus, in the literature it is frequently unclear whether effects of climate are direct or synergistic. For example, mortality rates increased in 87% of 76 plots, and on average doubled, in unmanaged old-growth forests in western North American sampled over an average of 23 years (van Mantgem *et al.*, 2009). An increase in mortality occurred among trees of all sizes; warm temperatures and consequent moisture deficits were considered likely causes. A recent assessment of drought- and heat-induced mortality concluded that some of the world's forested ecosystems may already be affected by climate change, and that further increases in mortality should be expected even in environments that are rarely water-limited (Allen *et al.*, 2010).

In China, substantial tree mortality thought to be a result of climate change has been reported, but the mechanisms and biological details are unclear. In many areas of China, increases in temperature and precipitation over the past 50 years (Yang, 2008) may have increased the incidence of some forest diseases. In recent decades, the distribution of forests has changed substantially. In the Qi Lian Shan Mountain area of northeastern Qinghai Province and western Gansu Province of western China, forest area was reduced by 16·5% and the lower elevation limit of the forest increased from 1900 to 2300 m between 1950 and 1992, reportedly as a result of combined effects of climate change and local human development (Wang *et al.*, 2002). A northward shift between 1966 and 2003 in the distribution of species including *Larix gmelinii*, *Picea jazoensis*, *Abies nephrolepis* and *L. potaninii* was documented in Heilongjiang Province of northern China (Zhu *et al.*, 2007). Budbreak has occurred earlier in response to warmer spring temperatures in some areas, but has been later in other areas in response to cooler temperatures. Forest productivity increased between 1981 and 2000 because of the increased length of the growing season. Inland ecosystems have been particularly sensitive to climate change

(Zhu *et al.*, 2007). Severe droughts have led to mortality on a regional scale (Wang *et al.*, 2007).

Managing forest diseases as climate changes

Given the numerous examples of interactions between forest disease and climate change, the ecological, economic and social value of forests, and the role that forests may play in mitigating global climate change, it is valuable to conduct a comprehensive assessment of management options for forest diseases. Although trees in much of the world's forests will have to adapt to climate change without human intervention (Spittlehouse, 2009), many forested areas can be managed to minimize the undesirable effects of projected increases in tree mortality driven by biotic and abiotic phenomena. Implementation of management approaches that enhance tree species richness across forested landscapes can help minimize adverse consequences of pathogen activity when there is uncertainty about effects of climate on forest ecosystems.

Assuming that a forest unit is managed to meet a given objective, such as timber, habitat for specific animals, watershed protection or recreational use, and furthermore, that models project that within the next 70 years, the climate will no longer support many of the tree species currently present, then a gradient of potential management responses exists between two unrealistic extremes. One extreme, if confidence in the models is extremely high, is to promote the rapid transition of the species composition of the site. The other extreme is to make no changes in management, assuming that the approach can be changed if and when species distributions change. Projections about the magnitude, location and timing of climate change are highly uncertain at all spatial extents and resolutions. In some regions there is even uncertainty over the direction of changes in precipitation (IPCC, 2007) which strongly influences rates of disease incidence and severity. Indeed, the potential for forests to mitigate climate-change effects should be considered carefully, as shown by recent research suggesting that afforested sites, particularly in temperate and boreal forests, may actually contribute to local surface warming from the positive radiative forcing effect of albedo (Betts, 2000; Thompson *et al.*, 2009).

Regardless of these uncertainties, impacts of climate change on forest health must be mitigated. This will require proactive thinking and a modified suite of forest management approaches, because status quo management strategies will not protect forest values in a changing climate. Climate change is already disrupting practices and policies for managing commercial and non-commercial forests, such as forest classification systems, projections of growth and yield and subsequent models of supply for timber and other forest products, plans and projections for managing habitat for different species of animals, and cycling of carbon, nutrients and water (Graham *et al.*, 1990). That restoration may no longer be a universally useful concept or goal for forest

management, because climate is not static, must also be acknowledged. The health of forests should be evaluated in terms of how future climate may influence the overall ecology of forest vegetation and pathogens, not how forests can be maintained or returned to some current or past condition. As damage increases in a forest type, managers will need a triage or similar prioritization system to decide which tree species have a long-term future and are worthy of management, and on which sites the forest type or species may be lost and therefore should not be promoted. Increased disease activity caused by climate change will probably exacerbate the extent and impact of these disruptions and it is not appropriate to set aside forests as refugia for biodiversity or other goals without a full evaluation of the impacts of future climatic conditions.

Essential components for managing forest diseases as climate changes

We recommend four categories of management tactics: monitoring, forecasting, planning and use of mitigating strategies. Implementation of these tactics will vary, depending on the 'state of the science' to support the activities, where forests and their stewards are on the globe, what financial, human and other resources exist, and what resource-management objectives are intended. Regardless, action must begin, with the most critical first step being identification of locations suitable for the deployment of as wide a range of forest tree species that are as ecologically resilient and stress-tolerant as possible.

Monitoring
Monitoring the spatial occurrence of forest diseases relative to both the ranges of host trees and annual weather patterns will inform adaptive management. The reliability of monitoring data will be maximized if systematic surveys of tree health, mortality and growth, whether remote or ground-based, are conducted by skilled personnel, ideally at stand, watershed and landscape levels, at regular intervals. Forest inventory plots also can be used to detect trends in growth and mortality for individual species and incidence of diseases or other disturbance agents. The ability of these activities to effectively inform the long-term management of forests might be increased by coordinating with monitoring for other disturbance agents, such as insects or fire, and by monitoring across jurisdictional boundaries.

Forecasting
The profound changes in environmental conditions expected from global climate change mean that forest professionals cannot rely on historical observations and experiences to forecast and plan for the future, but instead must develop and use a variety of modelling tools (Beukema *et al.*, 2007). Models of diverse phenomena, from climate to vegetation to disturbance agents, can guide management of forests under a changing climate, especially when they are well integrated. Bioclimatic

envelope models, for example, which integrate spatially explicit historic and contemporary data from weather stations, general circulation models and other sources, can be used to correlate current tree and pathogen species distributions with climate variables or to project future distributions on the basis of understanding of species' physiological responses to environmental variables (Pearson & Dawson, 2003). Modelling pathogens' climate envelopes alongside host reactions to climate can thus enhance the ability to predict disease outcomes.

Despite their power as predictive tools, models have at least three continuing problems: model inputs may have a high degree of uncertainty (e.g. disease distribution); nonlinear relationships between climatic variables and epidemiological responses are common, which means there may be insufficient data for clear projections; and the potential for genetic adaptation by both plants and pathogens is often ignored in models (Scherm, 2004). Efforts to improve modelling of climate change and forest pests (diseases and insects), such as those outlined in a workshop report by Beukema *et al.* (2007), are underway. Whilst models cannot provide certainty, they can provide qualitative insights on the magnitude and direction of changes, give focus to monitoring activities, and aid in the evaluation of management strategies (Woods *et al.*, 2010).

Planning
Jurisdictions that already have forest health strategies must ensure that they are maintained and adequately funded. Also, they should review and revise pertinent legislation and policies to ensure that forest health problems can be responded to quickly and effectively (Woods *et al.*, 2010). The success of management intended to minimize the potential undesirable effects of climate change on forest pests on large spatial scales depends, in part, on the synergistic effects of other major disturbances, such as wildfire (Lertzman & Fall, 1998; Peterson & Parker, 1998). Climate change-induced increases in tree mortality from pathogens and insects may increase the occurrence and severity of fires (Bergeron & Leduc, 1998; Kliejunas *et al.*, 2009).

Hazard- and risk-rating systems are integral components of forest management plans and can be applied in the absence of disease epidemics, and have proven useful for projecting effects of climate change on forest pests (Woods *et al.*, 2010). Pest risk analysis processes have been established in the European Union. Nevertheless, methods are being reviewed and improved (Baker *et al.*, 2009). Rating systems for most pathogens either have not been developed or do not account for climate change.

Strategies for mitigating effects of climate change
Ecological resilience is the capacity of an ecosystem to absorb disturbance without shifting into a qualitatively different state (Campbell *et al.*, 2009). Adaptive capacity, by contrast, is a property of individuals, populations or species. The establishment and maintenance of forests with diverse species and age classes can help maintain resilience to mortality and reduction in growth rates of trees in response to diseases and climate change.

Facilitated or assisted migration of trees may be an effective and cost-effective strategy to increase the probability of persistence of populations or species (Woods *et al.*, 2010). Facilitated migration is the deliberate movement by humans of genotypes and species into areas where the projected climate is believed to be associated with high probabilities of persistence. In some cases, genotypes and species currently present in those areas are believed to be unlikely to persist as climate changes. Facilitated migration may be emphasized for species with narrow resource requirements or poor dispersal ability (Warren *et al.*, 2001). However, facilitated migration can have unintended consequences. For example, new pathogens may be introduced along with the target species. The introduced trees may have little immunity against diseases in the areas into which they are moved. Also, it is highly uncertain which pathogens will become more evident as climate changes. In British Columbia, for example, pines such as *P. contorta* var. *latifolia* that originated in wet ecosystems, where foliar diseases are relatively common, were more resistant to dothistroma needle blight diseases, and had higher levels of defensive, secondary metabolites, than pines from comparatively arid ecosystems (Wallis *et al.*, 2008, 2010).

Breeding programmes for forest trees can promote genetic diversity, disease resistance and tolerance to environmental stresses. A tree's resistance to pathogens depends on stochastic genetic variation, evolved immunity, plasticity and environmental conditions (Yanchuk *et al.*, 1988; Liu & Ekramoddoullah, 2003; Cruickshank *et al.*, 2010). Fungicides may be an effective method of controlling forest diseases in forest nurseries and in natural forests, especially in the short term, despite negative public perception.

Management case studies

Yellow-cedar decline
Since the early 1900s, there has been extensive mortality of *Chamaecyparis nootkatensis* (yellow cedar), a culturally and economically important species, over more than 250 000 ha of forests in southeast Alaska (Hennon *et al.*, 2006) (Fig. 3) and nearby British Columbia (Hennon *et al.*, 2005). Yellow-cedar decline is characterized by slow decline in tree condition over several years. These forests are composed of standing long-dead and recently dead and dying *C. nootkatensis* and other tree species. Insects (*Phloeosinus* beetles) and pathogens (*Armillaria* spp. and other fungi) are contributing factors in yellow-cedar decline, but are less aggressive against unstressed trees. Predisposing factors include landscape, site and stand conditions (Hennon *et al.*, 2008) that increase the probability that the fine roots of *C. nootkatensis* will freeze during cold weather events in late winter and early spring (Schaberg *et al.*, 2008).

Long-term climate and short-term weather events affect the probability that the roots of *C. nootkatensis*

Figure 3 Yellow-cedar decline on Chichagof Island in Alaska, USA.

Figure 4 Sudden aspen decline on the Dolores Ranger District, San Juan National Forest, Colorado, USA.

ensis roots from cold temperatures. In declining forests, salvaged wood from dead cedars is economically valuable (Hennon *et al.*, 2007) because the heartwood retains its integrity for up to 100 years after death (Kelsey *et al.*, 2005).

Sudden aspen decline

Sudden aspen decline is a recently described disease of *Populus tremuloides*. It is characterized by rapid, synchronous branch dieback and tree mortality on a landscape scale (Fig. 4), rather than on a stand scale, without the involvement of aggressive, primary pathogens and insects (Worrall *et al.*, 2008, 2010b). Typically, there is no increase in aspen regeneration as overstory cover decreases, and in smaller size classes there is a decrease in recruitment. This lack of vegetative regeneration is associated with root mortality, which in turn is correlated with crown loss. Sudden aspen decline extends from Colorado into southern Wyoming, and similar damage began around 2000 in northern Arizona and in the early 1990s in southern Utah, USA (Ohms, 2003; Bartos, 2008; Fairweather *et al.*, 2008). Declining aspen in the parklands and southern boreal forests of Alberta and Saskatchewan, Canada (Hogg *et al.*, 2004, 2008) may be part of this same phenomenon.

In Colorado, sudden aspen decline was first noticed in 2004. By 2008, it covered about 17% of the area dominated by aspen in the state, about 220 000 ha. In 2009 the expansion appeared to stop, although severity continued to increase in many affected stands. A severe drought and record high temperatures, centered in 2002, was suspected as the cause. This drought was also the driver of unprecedented levels of mortality in *Pinus edulis* associated with an outbreak of the bark beetle *Ips confusus* (Breshears *et al.*, 2005).

Spatial analysis of a moisture index provided evidence that drought was an important inciting factor. Sites with aspen mortality detected by aerial survey in 2008 had greater moisture deficits in the 2002 hydrologic year

will freeze. The cool, moist climate that developed in the late Holocene created bogs and forested wetlands in which the species became abundant. However, yellow cedar developed shallow roots to acquire nitrogen in wet soils (D'Amore & Hennon, 2006; D'Amore *et al.*, 2009). Open forest canopies in bogs create microclimatic extremes; in late winter and early spring these include rapid warming as an inciting factor that triggers cedar dehardening (Schaberg *et al.*, 2005) and penetration of cold temperatures into soils (D'Amore & Hennon, 2006; Hennon *et al.*, 2010). *Chamaecyparis nootkatensis* are tolerant of cold temperatures in autumn and early winter (Schaberg *et al.*, 2005). However, roots deharden quickly in late winter and early spring, when soil temperatures below −5°C are lethal (Schaberg *et al.*, 2008). These lethal temperatures are common in shallow soil horizons, but do not occur when snow is present to buffer soil temperature (Hennon *et al.*, 2010). The onset of yellow-cedar decline in about 1880–1900 (Hennon *et al.*, 1990) corresponded with the end of the Little Ice Age. Weather-station data indicated a trend towards warmer winters but persistent early spring freezing events throughout the 1900s (Beier *et al.*, 2008). *Chamaecyparis nootkatensis* trees are healthy where snow persists past the last cold period in spring, or where they are deep-rooted on relatively well-drained soils.

Drivers of yellow-cedar decline can be reduced to two factors for risk modelling: soil drainage and snow accumulation. Planting or thinning is often needed to ensure the initial regeneration and competitive ability of *C. nootkatensis* (Hennon *et al.*, 2009). These activities are directed at higher elevations or on well-drained soils where snow or deeper rooting, respectively, protects *C. nootkat-*

(October 2001 to September 2002) than did sites with healthy aspen (Worrall *et al.*, 2010b). Rehfeldt *et al.* (2009) showed that the mortality was consistent with projections of the effect of climate change on aspen. Annual values of an index of climate favourability for aspen were lowest in 2002. Locations where sudden aspen decline is occurring are at the edge of aspen's climate envelope. The lower elevation at which climate supports aspen in the southern Rocky Mountains is expected to increase by 250 m by 2030 and 750 m by 2090. Projections suggest that 82% of sites with sudden aspen decline will be outside aspen's climate profile by 2060. In some areas, root systems may be able to regenerate if aboveground biomass is cut or burned. Aspen less than about 40 years old appears to have greater tolerance to drought and high temperatures than older aspen (Worrall *et al.*, 2010b). Growth of aspen also might be encouraged at higher elevations, where conifers are expanding yet climate is expected to be suitable for aspen at least until 2100.

Summary and conclusions

Forests serve important ecological functions and also contribute to the economic, aesthetic and spiritual health of humans. Climate has always shaped the Earth's forests, but human activities over the past 200–300 years have led to unprecedented changes in the world's climate. Climate change will interact with forest disturbances, such as pathogens, insects and fire, to increasingly impact the geographic distribution, growth and sustainability of the world's forest tree species. Outbreaks of forest diseases caused by native and introduced forest pathogens are predicted to become more frequent and intense as drought and other abiotic stressors are amplified under climate change. However, uncertainty pervades predictions about the future impacts of these diseases, in part because the effects of climate change on host–pathogen interactions are complex. For example, under a climate-change scenario of warmer and drier future conditions, we predict that diseases caused by pathogens directly affected by climate (e.g. dothistroma needle blight) will have a reduced or unchanged impact on their hosts, but an increased impact under a scenario of warmer and wetter conditions. For diseases caused by pathogens indirectly affected by climate (e.g. armillaria root disease) and for decline diseases, in general, we predict an increased impact on hosts under a climate-change scenario of warmer and drier future conditions and a reduced or unchanged impact under warmer and wetter future conditions.

The cumulative mortality of forest trees, including tree death potentially attributable solely to climatic drivers, is a serious problem facing forest professionals and policy makers. Whilst trees in much of the earth's forests will have to adapt to climate change without human intervention, many forested areas can be managed to minimize the undesirable effects of projected increases in tree mortality. This will require proactive and 'new' thinking and a modified suite of forest management approaches. We recommend four categories of tactics for managing forest diseases under a changing climate: monitoring, forecasting, planning and use of mitigating strategies. Aspects of these tactics have been considered or implemented in the evolving management of yellow-cedar decline and aspen decline in the USA. To have the best possible chance of success in the face of global climate change, each of the four management tactics we have recommended will require, to varying degrees: the development of techniques and tools; informed discussion of research needs and integration of results when the research is done; prioritization of research needs using risk analyses; and the development of clear and solid links to forest policy.

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