

Forest pathogens with higher damage potential due to climate change in Europe¹

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Abstract: Most atmospheric scientists agree that climate changes are going to increase the mean temperature in Europe with increased frequency of climatic extremes, such as drought, floods, and storms. Under such conditions, there is high probability that forests will be subject to increased frequency and intensity of stress due to climatic extremes. Therefore, impacts of climate change on forest health should be carefully evaluated. Given these assumptions, several fungal diseases on trees may become more devastating because of the following factors: (i) abiotic stresses, such as drought and flooding, are known to predispose trees to several pathogens; (ii) temperature and moisture affect pathogen sporulation and dispersal, and changes in climatic conditions are likely to favour certain pathogens; (iii) migration of pathogens triggered by climatic change may increase disease incidence or geographical range, when pathogens encounter new hosts and (or) new potential vectors; and (iv) new threats may appear either because of a change in tree species composition or because of invasive species. If infection success is dependent on temperature, higher mean temperatures may lead to more attacks. Pathogens that have been of importance in southern Europe may spread northward and also upward to mountains. Pathogens with evolutionary potential for greater damage should be identified to estimate the magnitude of the threat and to prepare for the changing conditions. A review of the above-mentioned cases is presented. Some priorities to improve the ability to predict impacts of climate change on tree diseases are discussed.

Key words: review, drought, water stress, temperature, global warming, pathogenic fungi, opportunistic fungi, predisposition, global change, epidemiology, forest diseases.

Résumé : La plupart des atmosphéristes s'entendent sur le fait que, en Europe, les changements climatiques provoqueront des augmentations de la température moyenne, ce qui aura pour effet d'accroître la fréquence des phénomènes extrêmes comme les sécheresses, les inondations et les tempêtes. À cause de telles conditions, il est fort probable que les forêts seront soumises à des périodes de stress plus intenses et plus rapprochées. Par conséquent, les impacts des changements climatiques sur la santé des forêts devraient être minutieusement évalués. À la vue de ces hypothèses, plusieurs maladies fongiques des arbres provoquées par les facteurs suivants devraient causer de plus en plus de dommages : (i) les stress abiotiques tels que les sécheresses et les inondations prédisposent les arbres à plusieurs infections pathogènes; (ii) la température et l'humidité influencent la sporulation et la dissémination des agents pathogènes et, en conséquence, les changements climatiques sont susceptibles de favoriser certains de ces agents; (iii) la migration des agents pathogènes provoquée par les changements climatiques peut accroître l'incidence ou l'aire de distribution des maladies lorsque ces agents contaminent de nouveaux hôtes ou de nouveaux vecteurs potentiels; et (iv) de nouvelles menaces peuvent surgir soit à cause des variations se produisant au sein des essences

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colonisant un territoire ou de l'apparition d'espèces envahissantes. Si le succès de l'agent infectieux dépend de la température, des températures moyennes plus élevées risquent de provoquer de plus en plus d'attaques. Les principaux agents pathogènes qui à ce jour ont été limités au sud de l'Europe pourraient non seulement déferler sur le nord, mais également envahir les hauteurs, c'est-à-dire les montagnes. Il faudrait identifier les agents pathogènes qui présentent les plus grands risques quant à leur potentiel évolutif afin de se préparer aux conditions changeantes. L'article présente un bilan des cas mentionnés ci-dessus. De même, on y discute de certaines des priorités qui permettraient d'améliorer nos méthodes de prédiction relativement aux effets qu'ont les changements climatiques sur les maladies des arbres.

Mots-clés : bilan, sécheresse, stress hydrique, température, réchauffement planétaire, champignons pathogènes, changement à l'échelle planétaire, épidémiologie, maladies des forêts.

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Effects of climate change on health trends of trees

In general, it is considered that field crops and other annual or short-lived vegetation reflect weather changes, whereas trees and other perennial flora also reflect climate changes. A severe outbreak is a rare removal by weather of obstacles that ordinarily restrain the pathogen (Hepting 1963).

Based on the accumulated evidence of modelling studies, the global temperature will rise by >2.5 °C over the next century (Jones and Henderson-Sellers 1990; Wang and Schimel 2003; Easterling and Apps 2005). A recent Intergovernmental Panel on Climate Change (IPCC) United Nations (UN) report, which was written by 600 of the world's leading climate scientists and reviewed by another 600, states that temperatures will rise by 2–4.5 °C, with a "best estimate" of a 3 °C rise by 2050, assuming that carbon dioxide levels are stabilized at about 45% above current levels. Such an increase has been termed "dangerous" by the IPCC, which traditionally is a conservative cautious body whose findings are viewed as trustworthy (IPCC 2007).

The mean precipitation should decrease; however, more rain is expected to fall in winter, whereas summers will become drier. The sea level should rise 20–50 cm. Increased winter rainfall may raise water tables enough to kill roots, thereby reducing effective rooting depth and making trees more vulnerable to summer droughts (Redfern and Hendry 2002; Solberg 2004).

Storms may possibly become more frequent (Lassing and Močalo 2000), and their consequences for the main European forest tree species are expected to be quite severe (Schutz et al. 2006). One unsure parameter is the thermohaline circulation in the North Atlantic Ocean (Adkins et al. 1997); if this is reduced, northern Europe will have a colder climate (Tank and Konnen 1997). In the last 10 years, several studies have been carried out to predict and estimate the effect of globally rising CO₂ and temperature on phenology, biochemistry, photosynthesis, and other physiological traits of European forest trees (Jarvis 1998; Saxe et al. 2001; Asshoff et al. 2006). Less effort has been directed to identifying host × pathogen interaction systems that can be modified under the new forecasted global environmental conditions. Several plant diseases are observed to be more severe after mild winters or during warmer temperatures, which suggests that directional climate warming alters plant disease severity (Harvell et al. 2002).

However, these changes are not easily determined, and consequently, forecasting changes in the occurrence or impact of diseases under altered growth conditions is not simple (Von Weissenberg et al. 2005). In addition, forecasting forest pathogen impact under such changing conditions suffers from limitations because of absence of long-term records and of standardized manner of disease variables detection (Schermer 2004). One method to predict plant disease is the use of climate change forecasts derived from global-change models, opportunely downscaled, that are analogous to general circulation models used for weather forecasts (Seem 2004).

Assuming that the rise in temperature takes place, *Picea abies* (L.) Karst. (Norway spruce) and other conifers are predicted to become quite unsuitable for forestry in the central regions of Europe (Fanta 1992; Breymeyer et al. 1996) and at lower elevations (Lexer et al. 2002), and so, the present large spruce forests will be subject to severe stress (Redfern and Hendry 2002). At the same time, there will also be a shift in altitude of spruce in the Alps and other European mountains (Carcaillet and Brun 2000). Several scenarios were hypothesized where dramatic changes in the distribution of potential forest types were modelled. In these models, fir, spruce, beech, maple, aspen, and birch (in order of intensity) were greatly reduced (Iverson and Prasad 2001). Under the global warming hypothesis, several other species will respond in similar ways, and the effects will be more severe also because of the extremely rapid rate of the expected change. The increased temperatures, increased evapotranspiration, and extreme weather events brought on by this rapid change will increase the frequency and severity of stress factors, which may lead to more frequent forest declines (Sturrock 2007). Moreover, population reduction and habitat destruction due to human activities will prevent many species from colonizing new habitats when their old ones become unsuitable. The synergy between climate change and habitat destruction threatens many more species than either factor alone (Peters 1990).

Other authors claim that species adapted to a more Atlantic climate would then be relevant. *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), *Picea sitchensis* (Bong.) Carr. (Sitka spruce), and *Abies grandis* (Doug.) Lindl. (grand fir) are the suggested species. Oaks and birches are expected to benefit from a temperature increase, whereas beeches and other broadleaf trees should be unaffected, unless summer droughts become more frequent (Larsen and Raulund-Rasmussen 1997). In Fennoscandia, birch will be at a clear

advantage compared with pine and spruce, and a natural increase of this tree species will take place (Prentice et al. 1991). In Russia, the limit of taiga will move about 200 km northward, followed by gradual spread of forest into the tundra (Zavelskaya et al. 1993).

In the Mediterranean region, which is expected to become considerably drier, the low forest of marquis type will be at an advantage compared with high forests of pine, fir, and chestnut. As a result, the natural vegetation should evolve towards more thermophilous and sclerophyllous types. In some parts of the Mediterranean area, expansion of desertification in rangelands is expected (Le Houerou 1992).

In spite of this, the effects of climate change in the next few years will hardly be perceptible as measured by changes in tree health and species composition. Some of the changes for the next decades that will be described below are in very early stages and hardly distinguishable from presently known trends and annual fluctuations due to a range of factors including local weather conditions, disease outbreaks, and management practices. However, some signs suggesting effects of general climate change may be inferred on several tree diseases.

The rise in sea level will have implications on gravitational drainage of low lands. In turn, this will cause trees to grow in more waterlogged and wetter areas than hitherto. Waterborne diseases, such as those caused by some species of *Phytophthora*, will become more frequent (Jung and Blaschke 1996; Woodward et al. 2005), and diseases that benefit from poor tree health, such as *Gremmeniella abietina* (Lagerb.) Morelet on pines (Barklund and Rowe 1983), will become more prevalent. Within the time span, such changes will hardly be distinguishable from “background noise.”

Range retractions will be proximally caused by temperature and precipitation changes, increases in fires, changes in the ranges and severity of pests and pathogens, changes in competitive interactions, and additional effects of nonclimatic stress such as acid rain and low-level ozone.

The databases

Despite the recognized importance of the long-term data set in forest diseases (Jeger and Pautasso 2008), Europe does not have any specific database for tree health. The United Nations Economic Commission for Europe (UNECE) annual report on forest conditions in Europe (Lorenz 2004) reported on defoliation and discoloration as general indicators of vitality (Klemola and Söderman 1993) but did not specify the causes very exactly, although concerted efforts have been made in this direction since 2004 (<http://www.icp-forests.org/WGbiotic.htm>). Even when recorded, the trends in these causes (e.g., pollution, physiological disorder, fungi, and insects) cannot yet be discerned over the 1984–2006 period of data presently available. The database does not include all European countries for an equal number of years and with similar sampling intensity. For these and other reasons, this database will remain less satisfactory for the time being (Klemola and Forsius 1998). However, in spite of its shortcomings, it is the best available, even though the scientific community recognizes the need for a consistent pan-European long-term integrated

monitoring of terrestrial systems programme (Parr et al. 2002).

The overall European trend shows evidence of continued decline (Elvingson 1996) with a slow increase in defoliation and discoloration for both conifers and broadleaves but with quite large variation in these trends regarding tree species, region, and country. The proportion of damaged trees has increased continuously since 2001 but has not reached the peak of the mid-1990s. *Pinus sylvestris* L. (Scots pine) is the only tree species with improved crown condition during 1997–2005 period (<http://www.icp-forests.org/pdf/ER2006.pdf>). In particular in southern Europe, cases of obvious decline related to environmental factors are well described (Bussotti and Ferretti 1998). According to Klemola and Forsius (1998) for regional samples of common species, the percentage of damaged trees (>25% defoliation) increased from 22% in 1992 to 25% in 1997. For the two most abundant species in the common tree sample (*Pinus sylvestris*, and *Picea abies*), pine showed an overall trend of recovery from 32.1% damaged trees in 1994 to 21.9% in 1997, whereas the percentage of damaged spruce trees went from 27% in 1992 to 33.5% in 1997. *Abies* spp. is similar to spruce with 32% damage. Of broadleaves, *Fagus sylvatica* L. (European beech) is the most common and shows a pronounced decrease of undamaged trees from 48% in 1992 to 32.8% in 1997. *Quercus robur* L. (pedunculate oak) (five regions) shows a similar trend: there were 35.1% undamaged trees in 1992 and only 14.3% in 1997. Data on discoloration show similar trends.

The proportion of damaged trees has increased continuously since 2001 but has not reached the peak of the mid-1990s. Being a drought-resistant species, *Pinus sylvestris* did not suffer from dry season in 2003, and it is the only tree species with improved crown condition during the 1997–2005 period (<http://www.icp-forests.org/pdf/ER2006.pdf>). Recovery has occurred especially in eastern Europe. From 1990 to 2005, *Pinus pinaster* Ait. (maritime pine), *F. sylvatica*, *Quercus ilex* L. (holly oak), *Quercus rotundifolia* Lam. (holm oak), *Q. robur*, and *Quercus petraea* (Matt.) Liebl. (sessile oak) show an increase in defoliation, whereas defoliation of *Picea abies* varies. Defoliation increased from 2003 to 2004 for *Picea abies*, *F. sylvatica*, *Q. robur*, and *Q. petraea* because of drought. In 2005, their crown condition recovered significantly, but the Mediterranean species *Pinus pinaster*, *Q. ilex*, and *Q. rotundifolia* showed no major changes (<http://www.icp-forests.org/pdf/TR2006bis3-3.pdf>).

The estimates described in this paper are based on knowledge of the life cycles of specific and more serious fungal pathogens and the various factors that affect their occurrence and preferences of host species.

Changes in tree composition as affected by diseases and the possible role of climate change in these developments

Forests

Analysing the impact of the current forest disturbance causes in the United States (insects, pathogens, fire, hurricane, tornado, ice, landslide, and drought), it has been calculated that insects and pathogens account for most of the

impact in terms of both area affected (88%) and economic costs (41%) (Dale et al. 2001). However, it is difficult to generalize about the effects of climate change on forest pathogens in North America because the effects are likely to be different for different pathosystems in different locations (Sturrock 2007).

In the 1900s, several major changes in species composition due to diseases have occurred. In North American, white pines (*Pinus strobus* L., eastern white pine; *Pinus monticola* Dougl. ex D. Don, western white pine; and *Pinus lambertiana* Dougl., sugar pine) have been severely depleted by the blister rust pathogen *Cronartium ribicola* Fisch. (Von Weissenberg 1990; Ekramoddoullah 2005). Native and introduced insects, vectors, and pathogen fungal species, such as *Lymantria dispar* L. (gypsy moth), chestnut blight (caused by *Cryphonectria parasitica* (Murr.) Barr.), and Dutch elm disease (DED) (caused by *Ophiostoma ulmi* (Buism.) Nannf., and *Ophiostoma novo-ulmi* Brasier) have consistently altered European and US forests (USDA 1977). Chestnuts have been nearly extinct because of chestnut blight, and elms have been reduced to shrubs because of DED (Mittempergher 1989; Ayres and Lombardero 2000). In the early phases of these epidemics, the devastation has usually been fast and dramatic; however, with passing of several decades, the rate of spread has been reduced because of lack of host material, improved management, and active control as well as a natural selection in favour of more resistant individuals remaining within the natural range of the species. Similarly, in Europe, the use of the exotics *Pinus strobus* and *Pseudotsuga menziesii* was discontinued in the late 1800s or a more resistant subspecies was chosen. In addition, elms and chestnuts have been dying since the 1920s and 1940s, respectively. Presently, a widespread decline of oaks in Europe is continuing, and an increase in alder decline is seen in some areas. Many of these are classical and well-known examples of major forest epidemics; some are still going on and affecting species composition more or less permanently (Tainter 2003). Alien pathogens, such as *Mycosphaerella pini* Rostrup, *Mycosphaerella dearnessii* M.E. Barr, *Diplodia pinea* Kickx (syn. *Sphaeropsis sapinea* Dyko and Sutton), and *Cyclaneusma minus* (Butin) Dicosmo (syn. *Naemacyclus niveus* (Pers.:Fr.) Sacc.), have recently appeared in northern Europe. The northward spread of these fungi, known before as southern colonizers, is supposed to be related to the increasing climate warming (Märt Hanso, Estonian University of Life Sciences, Tartu, Estonia, personal communication, 2008). Sometimes, the introduced pathogen may show higher virulence than the indigenous or already-established one because of the favourable climatic conditions in the new environment. The replacement of *O. ulmi*, which is responsible for the first pandemic of DED in Europe, by the closely related *O. novo-ulmi*, which caused the second pandemic, is a good example of this competitive ability in relation to invasive species (Desprez-Loustau et al. 2007a). Also, the American strains of *Heterobasidion annosum* (Fr.) Bref. that were introduced approximately 60 years ago in central Italy will likely predominate over the endemic strains (Gonthier et al. 2007; D'Amico et al. 2007). The replacement of the local and saprophytic species *Cryphonectria radicalis* (Schwein.:Fr.) M.E. Barr in Europe

by the alien pathogenic *Cryphonectria parasitica* has also been hypothesized (Hoegger et al. 2002).

In the cases where the pathogen is strictly spread by active insect vectors, temperature is affecting either the survival of the insects that are active during the cold period or the synchronization mechanism between the insect vector and the pathogen. An increase of temperature may alter the mechanism by which the insects adjust their cycles to the local climate (diapause), resulting in faster development and higher spread of the pathogen (Battisti 2008). Epidemic development of cypress canker was also shown to be associated with a shift in the fungal load of *Orsillus maculatus* Fieber (cypress bug) from the endemic *Pestalotia funerea* Desmaz. to the invasive *Seiridium cardinale* (Wagener) Sutton & Gibson (Battisti et al. 1999).

Landscapes

Landscape pathology is an increasingly important interdisciplinary field that has emerged from the incorporation of landscape ecological concepts (interactions of spatial patterns and ecological processes over multiple scales) and methods into the science of forest pathology. Landscape pathology studies fill a significant research gap in the context of our understanding of sustainable forest management: the introduction of exotic organisms and how climate change might affect the spread of disease (Holdenrieder et al. 2004). In addition, host landscape patterns are influenced by landscape connectivity and abiotic patterns, which also affect pathogen spread and population dynamics directly. Rapid climate change might trigger the onset of disease by intensify this lack of synchronization (Hennon and Shaw 1994; Ayres and Lombardero 2000).

Climate warming will not only act on pathosystems already present in a certain landscape but will favour the emergence of new diseases both because the distributional range, temporal activity, and community structure of pathogens will be modified (Desprez-Loustau et al. 2007a) and because the phenology and conditions of the hosts will be altered (Lonsdale and Gibbs 1996). Add to this the introductions of exotic pathogens as a result of the increasing of trade, and the situation becomes extremely complex. Where only a few species have dominated the landscapes and one or more of these are depleted, the effect can be drastic. Elms in the English landscape nearly disappeared in the 1940s and 1950s and further in the 1970s (Richens 1983). *Pinus strobus* in North America nearly disappeared because of the blister rust (*Cronartium ribicola* J.C. Fisch) epidemic over a full century (Kinloch 2003). In the dramatic early stages of these epidemics, dead standing elms and pines were constant reminders of the disaster. Over the years, other hardwoods, often pioneer species, have taken their place and forest cover has been restored in the landscape. Cypress (*Cupressus* spp.), the most typical tree of the hilly Tuscanian landscape, was seriously reduced by the cypress canker pathogen (*S. cardinale*), which epidemically spread in the 1970s (Graniti 1998; La Porta et al. 2005a). The recent dieback known as sudden oak death (SOD) has reached epidemic proportions along hundreds of kilometres of the Californian coast. It occurred following the apparent introduction of *Phytophthora ramorum* Werres, DeCock, & Mann in't Veld into stands of *Quercus agrifolia* Née (coastal live

oak), *Quercus kelloggii* Newb. (black oak), and *Lithocarpus densiflorus* (Hook. & Arn.) Rehd. (tanoak) (Rizzo et al. 2005). It causes rapid canker development that leads to girdling and “sudden” death of the tree and can be spread via sales of infected material (Stokstad 2004). However, the pathogen is known elsewhere only from Europe, where it remains so far quite rare, except on *Rhododendron* spp. and *Viburnum* spp.

Urban trees and amenity trees

Elms (*Ulmus* spp.) have traditionally been rather important amenity trees in urban areas in the Atlantic regions of Europe (Richens 1983). When DED struck the stately elms along boulevards, along canals and in parks, the effects were dramatic. Between 1930 and 1973, it was estimated that 9×10^6 elms died in England because of the disease (Gibbs and Brasier 1973), and well over 25×10^6 elms (out of the originally 30×10^6) had died by 1990 (Brasier 1996). In the Netherlands during 1930–1946, approximately 30 000 elms were lost in Amsterdam and 1.3×10^6 in the whole country (Went 1954). However, Heybroek (1962) reported that, in 1920, there were over 0.5×10^6 trees in Holland belonging to the clone *Ulmus xhollandica* Mill. ‘belgica’ selected in Belgium in 1694 and particularly susceptible to the disease. The latest event in this ongoing epidemic is the dying and removal of an estimated 8500 elms (out of some 10 000) in Copenhagen after 1994. Before the late 1960s, resistant cultivars were available; however, after the appearance of the virulent species *O. novo-ulmi*, resistant cultivars were also attacked, and new cultivars have only recently been released in Italy. Linden, plane tree, maple, bird cherries, ash, and other species are being planted in their place, but restoration of the amenity value will take decades. Plane trees in southern and central European cities are presently threatened by *Ceratocystis platani* (formerly *Ceratocystis fimbriata*) f. sp. *platani* (J.M. Walter) Engelb. & T.C. Harr. (Engelbrecht and Harrington 2005). Recently, a new disease has emerged on *Fraxinus excelsior* L. (European ash) in Poland, the Baltic countries, Sweden, Denmark, and Austria. The cause of this ash dieback is considered to be a newly described fungus *Chalara fraxinea* T. Kowalski (Kowalski 2006). Much valued columnar cypresses in the Mediterranean area are continuously threatened by the cypress canker. For details, see below.

Many of the above examples are not due to general climate changes but, rather, to actions of man (transport of infected material to areas previously free of the diseases); however, in the most recent cases (oak and alder declines), all contributing factors may not yet be well understood. Changes in climate and water tables may be involved. Increasing heat and drought in the south and east can be expected to increase losses, particularly among newly established trees and mature trees in hedgerows and urban environments (Redfern and Hendry 2002).

Many of the most important forest diseases, such as root diseases, stem decays, and declines, require a stressed host before infection or disease expression occurs. When a tree is stressed, less energy is available to sustain the physiological processes critical to disease resistance, because more energy is allocated to life-sustaining processes (Wargo and Harrington 1991). Diseases respond to stress in plants in

various ways, such as increased incidence or severity. When stressed, a normally resistant tree species may become susceptible to a certain disease, which broadens the host range of the pathogen. Stress caused by an increase in the number and severity of catastrophic weather events, especially drought, may increase disease susceptibility, especially where plants are not physiologically adapted to a site or are near the limits of their range (McDonald et al. 1987).

Specific cases

In this section, we try to consider multiple scales of host \times pathogen interactions and review factors that contribute to determining how and when climate change could have important effects on plant disease.

Heterobasidion spp. root and butt rot

Species in the genus *Heterobasidion* are the major root and butt-rot pathogens of conifers in the northern hemisphere. In the European Community, losses caused by *Heterobasidion* spp. add up to €400 million/year (Woodward et al. 1998). The spore production of *Heterobasidion* spp. is known to increase markedly at temperatures above 5 °C (Otrosina and Cobb 1989), and a climate change towards milder winter with prolonged periods with temperatures above 5 °C would increase sporulation and infection frequency by these fungi. Warmer temperatures have been shown to be highly correlated with sporulation rate (La Porta et al. 2001; Gonthier et al. 2005) and incidence rate of *Heterobasidion* spp. (Moykkynen et al. 1998; Thor et al. 2005; Mattila and Nuutinen 2007). Based on 5998 sample plots of the ninth National Finnish Forest Inventory, it was observed that, in the northern regions, a shorter period with snow cover would also benefit the life cycle and spore dispersal of this serious decay-causing fungus (Mattila and Nuutinen 2007). Thinning operations and timber extraction during longer snow-free periods provides fresh stump surfaces for establishment of *Heterobasidion* spp. but results also in root damage to the standing trees, which function as infection routes for these fungi. In addition, thinnings together with the spread of the pathogen may amplify the risk of the increasing storm damage to the forest (Thomsen 2005).

Drought conditions are also known to predispose conifers to *Heterobasidion* attack through the reduction of the endogenous defence mechanisms of trees (Lindberg and Johansson 1992), and prolonged periods of drought, particularly in the southern and eastern European conifer woodlands (Arefjew 1999), predispose trees to several pathogens, including *Heterobasidion* (Bendz-Hellgren and Stenlid 1998). In *Picea abies*, the combined stresses, drought and *H. annosum*, gave larger host responses and earlier changes in gene transcripts than for the two stresses separately (Fossdal et al. 2007). In the Mediterranean region, drought conditions were found to be significantly correlated to disease spreading rate in *Abies alba* Mill. (European silver fir; Puddu et al. 2003). Although this host tree is common in the Mediterranean area, its cultivation is menaced by *Heterobasidion abietinum* Niemelä & Korhonen particularly in new plantations exposed to climatic stress. Increased summer temperatures may also affect the relative frequency

of the different *Heterobasidion* species: in particularly warm years, *H. abietinum*, which is the most temperature-adapted species in the genus, grows better in species outside its natural host range (La Porta et al. 2005b). If this tendency is confirmed, we can expect further spread of *H. abietinum* on *Abies*, but also on *Picea* in central and eastern Europe. On the other hand, a warmer climate should be beneficial to the *Heterobasidion* antagonist *Phlebiopsis gigantea* (Fr.) Jülich, if this fungus is used for biological control (Thor et al. 1997). In the future, stump treatments (Korhonen et al. 1994) will be increasingly necessary, and more attention will have to be paid to replace susceptible conifer species with more resistant broadleaved trees.

Chestnut blight

This disease, caused by an ascomycetous fungus *Cryphonectria parasitica*, came from the Far East to the United States, where it was first reported in the 1904 in the Bronx Zoological Park of New York. From there, it went on to devastate chestnut (*Castanea* spp.) plantations and forests throughout the Northern Hemisphere. From the United States, it probably spread to Europe in the 1920s, but the first official record was near Genova, Italy, in 1938. From there, it spread rapidly to the neighbouring countries, causing a rapid decline in chestnut cultivation in many regions (Heiniger and Rigling 1994). Many of the chestnut plantations and solitary trees died or declined. Presently, however, hypovirulent strains of the fungus spread naturally in Europe, and the epidemic is declining in some areas, allowing infected trees to recover and causing new infections to be less severe (Fulbright et al. 1988). In general, time-series analysis of ascospore dispersal showed a positive association of the daily number of ascospores with increasing temperature (Guerin et al. 2001). Despite the fact that both virulent and hypovirulent strains have a wide temperature range of growth (21–32 °C) and of optimum growth (27–32 °C) (Anagnostakis and Aylor 1984), it has been shown that higher temperatures can help the exchange of double-stranded RNA (the cause of hypovirulence); consequently, if the climate becomes warmer, this may contribute to a further decrease in the epidemic (Friese et al. 1992). Some authors suggest that the impact of this emerging disease under the climate change conditions is underestimated (Anderson et al. 2004) and that increasing temperature can also give more advantage to the chestnut endophytes antagonistic to *Cryphonectria parasitica*, leading to the systemic acquired resistance of the host tree (Wilhelm et al. 1998). However, even if the disease is currently spreading northward (e.g., in France since 1980; De Villebonne 1997) and in other central European countries (Turchetti and Maresi 1999; Robin and Heiniger 2001; Wulf and Schumacher 2005), a dangerous loss of chestnuts is not very likely to occur in Europe. In contrast, the severe epidemic continues in North America where the hypovirulent strain cannot infect the virulent ones (Milgroom and Cortesi 2004).

Dutch elm disease

In theory, warmer summers could mean two or even three yearly generations of *Scolytus* beetles, vectors of the ascomycetous fungus, *O. novo-ulmi*, causing the wilt disease called DED. This higher reproductive rate, which is

also due to relaxing overwintering restrictions (Hansen and Somme 1994), may occur more often and in larger geographic ranges, which will extend the spread of the disease (Lonsdale and Gibbs 2002). In addition, the smaller size beetle species (i.e., *Scolytus kirschi* Skal., *Scolytus multistriatus* Marsh., and *Scolytus pygmaeus* Fab.) will get an advantage over larger ones because of the host's coppicing habit, thus accelerating the disease (Webber and Kirby 1983; Basset et al. 1992). However, DED is already widespread in central Europe and has spread to the northern latitudes of Oslo, Stockholm, and St. Petersburg in the 1990s, and most elms will probably be destroyed long before any climate change is evident (Dunn 1999). In field trials over many years, it was observed that the amount of wilting caused by the Eurasian race of *O. novo-ulmi* increased when mean air temperature exceeded 17 °C (Sutherland et al. 1997). These results were also confirmed in a 14-year field study in England, where the fungus caused greater wilting in warmer years (Harvell et al. 2002). An unfavourable condition is facing especially *Ulmus glabra* L. (mountain elm) in northern Europe and in the Alps. As a matter of fact, this elm species appears to be partially protected by the fungus because there is not enough vector pressure in the cooler places where it normally lives. This condition may change under the assumption of climate warming (Hansen and Somme 1994). From several prediction analyses that have been carried out based on ecological and mathematical models over short as well as long time spans (Swinton and Gilligan 1996, 1999), a wide variety of outcomes ranging from pathogen extinction to substantial elm loss have been proposed. The main unresolved problem is posed by the aggressive species of the fungus and its continuing evolution (Brasier 2001), to which no hybrid elm so far produced in breeding programs has proved sufficiently and durably resistant. A possibility of selecting and spreading a hypovirulence factor is presently being investigated (Brasier 1983a, 1996; Doherty et al. 2006). Even regeneration of dead and dying large trees by coppicing will not be of much help because the disease will attack coppice trees as soon as they attract the beetles (Mittemperger 1989). This change from tree to understorey is seen in countries where the disease has occurred in successive epidemics, such as in England, Holland, and Belgium (Brasier 1983b, 1996). At present, the role of elms in forestry is relatively small, and the biggest value of the species is as amenity trees in urban areas and parks using patented resistant clones developed in several countries. The current breeding programme dealing with selections of new DED-resistant hybrids adapted to Mediterranean climate conditions is potentially a source of outcome clones adapted also to central European countries that are challenged by the climatic warming trend (Santini et al. 2008).

Honey fungus (*Armillaria* spp.)

Several *Armillaria* species are present in Europe (Guillaumin et al. 1993). Distinctions should be made among *Armillaria mellea* (Vahl:Fr.) Kummer, *Armillaria ostoyae* (Romagnesi) Herink and *Armillaria gallica* Marxm. & Romagn. The two first species are already strong pathogens but will further benefit from a situation where trees be-

come more stressed because of climatic effects (Szynkiewicz and Kwasna 2004) or by risks posed to storm-damaged stands (Maugard and Fraysse 2002). Hyphal growth of *Armillaria mellea* and *Armillaria gallica* appear to be greater at higher temperature (Rind and Losel 2005). The growth temperature of *Armillaria* spp. ranges between 10 and 31 °C, although the optimal temperatures for many species ranges between 20 and 22 °C (Rishbeth 1978; Keca 2005). It could mean that, under the climate warming conditions, low soil temperatures probably will not limit rhizomorph growth during winter as it normally happens in much of the north temperate zones. However, *A. gallica* will probably benefit most from trees being more stressed, both because it is quite thermophilic, as well as *Armillaria mellea*, and because it acts like a weak parasite that attacks and sometimes kills weakened trees. In addition, *Armillaria gallica* mycelium and rhizomorphs are not able to withstand temperatures above 35 °C and 37 °C, respectively (Jacobs 2005). This slight difference between mycelium and rhizomorphs may play a certain ecological role in its spread. Thus, this would be a good candidate for an opportunistic pathogen becoming problematic because of climate change if climate change means increased stress to trees because of temperature and drought (Wargo 1996; Hasegawa 2003; Popoola and Fox 2003; Guillaumin et al. 2005). The coexistence of *H. annosum* and *Armillaria* will increase root and butt rot, particularly on many conifers, and prompt the change to other tree species (Cermak et al. 2004). However, few resistant tree species are available and suitable for the range of sites where the present species are growing. In fruit tree orchards, *Armillaria* will become more common as well.

***Rhizina undulata* Fr.: the tea break fungus**

In the present conditions, this ascomycetous fungus causes root rot and death of mature conifers in the vicinity of soils and sites heated by local or larger fires, which have become more frequent in several Mediterranean countries (Neves et al. 1986). Gaps are commonly found in forests around such places. The fungus has been found also on chestnut and other broadleaves. The transmission is by ascospores through the soil after they have been activated by fire or exposure to temperatures of 35–45 °C in the neighbourhood of pine roots (Booth and Gibson 1998). However, it has been proven that the fungus can usually occupy discrete territories also because of its clonal propagation (Lygis et al. 2005). Following a sudden outbreak, the fungus attacks pines over several years, causing extensive dieback. Afterwards, intensiveness of the disease gradually declines. After replanting, the disease centres with a new generation of conifers, *R. undulata* proved to be unable to attack the next generation of trees (Vasiliauskas 1999). However, in Fennoscandia, the fungus is known only as a cause of mortality of young conifer seedlings (Solbraa and Brunvatne 1994; Von Weissenberg 1997). It is not known if this bimodal lifestyle is due to climate, weather, or soil conditions, but a shift in Fennoscandia towards a climate with central or Atlantic European characteristics may cause this fungus to become devastating to mature coniferous forests if the practice of using prescribed burning for site preparation continues in Fennoscandia. Drier conditions may also

lead to more frequent forest fires, and the activity of this fungus may hinder reforestation. Avoiding the problem by postponing planting is not a viable option because of high risk of nitrate leaching and weed proliferation. In England, the habit of tea-break fires in the forest have been discontinued because of this fungus (Hardison 1976). However, in Fennoscandia, such a potential change of behaviour will hardly be perceptible within the time span.

Oak decline

Since last century and over the past several decades, a decline of oak forests has been seen throughout Europe (Delatour 1983; Oleksyn and Przybyl 1987; Spiecker and Gottschalk 1998; Lorenz et al. 2006; IPCC 2007). In most cases, it has been associated with climatic events, especially drought (Brasier and Scott 1994; Siwecki and Ufnalski 1998). Many plant pathogens are favoured by the stress on the trees induced by drought, but separating the role of drought per se from the role of several species of pathogens and insects has not always been possible (Schoeneweiss 1986; Cattaneo et al. 1992). A special role can be attributed to root diseases such as rot of large roots (by *Armillaria* spp. and *Collybia fusipes* (Bull.:Fries) Quélet) and destruction of fine roots (*Phytophthora* spp.), because their effect interacts directly with the trees' water use (Brasier and Scott 1994). Laboratory and field studies indicate that the fungus causing Mediterranean oak decline, *Phytophthora cinnamomi* Rands, is favoured by warm temperature and limited by frost, and this partly explains the current distribution of damage in Europe (Marçais et al. 1996; Lonsdale and Gibbs 2002; Marçais 2005; Desprez-Loustau et al. 2007b). Other studies indicate that this pathogen causes more severe root rot at higher temperatures than the current Mediterranean mean (Harvell et al. 2002). Increasing temperatures could move damage to the north and east (Brasier et al. 1996; Bergot et al. 2004). Although other *Phytophthora* species could also be favoured by climate change (Jung et al. 1996; Woodward et al. 2005; Hansen 2008), *Phytophthora cinnamomi* was the most resistant to osmotic stresses (Turco et al. 2005).

The strong climate × pathogen interaction (Bussotti and Ferretti 1998) is illustrated by the fact that (i) mature oaks are primarily affected by the decline; and (ii) *Q. robur* is more diseased than *Q. petraea*. Indeed, mature trees have less adaptation capacities when the water regime changes, and *Q. petraea* is more thermophilic and xerophilic than *Q. robur*. Climate change may favour *Q. petraea* over *Q. robur*.

Also, endophytic fungi have been associated to oak decline. In fact, among the 27 endophytic species identified on three Mediterranean *Quercus* spp., four of them that are known to be pathogenic showed a colonization frequency statistically higher in declining trees compared with the healthy ones (Ragazzi et al. 2003). One of these species, *Discula quercina* (Westd.) Arx, is usually viewed as a symptomless colonizer of healthy *Quercus cerris* L. (Turkish oak) in an unstable equilibrium between transient mutualism or neutralism and latent pathogenesis. It is suggested that climatic factors can change the endophytic nature of *D. quercina*, turning it into a weak pathogen or an opportunistic invader of senescing trees (Moricca and

Ragazzi 2008). Experimental trials carried out in controlled environmental chambers with this endophyte showed stronger infection rates when using higher temperature and lower humidity on seedlings of several oak species (Ragazzi et al. 1999). In conclusion, oak decline has many symptoms and causes and is spreading in many parts of Europe. The UNECE (1998) report describes increases in defoliation (percentage of trees with >25% loss of leaves) for the category in “all (relevant) regions” from 1992 to 1997 of 23%–43% for *Quercus robur*, 7%–29% for *Q. ilex*, and 20%–31% for *Q. petraea* (the 1997 report). In Portugal, defoliation of *Quercus suber* L. (cork oak) peaked in 1991 at 53% of trees with some recuperation after that. Of several causes (in Portugal) mentioned in the report, drought is of interest in the present context.

Charcoal disease caused by *Biscogniauxia* in oaks and beech

Opportunistic pathogens of the *Fagaceae* are numerous. Beech and oak trees under water stress can become affected by *Xylariaceae* fungi, which cause necrosis and cankers on branches and stems (Nugent et al. 2005). Among them is *Biscogniauxia* (*Hypoxylon*) *nummularia* (Bull.: Fr.) O. Kuntze., which specifically colonizes beech. This pathogen has frequently been observed in progressive group death in coppices in southern Italy (Granata and Whalley 1994; Paoletti et al. 1996; Luchi et al. 2006; Granata and Sidoti 2004).

When oaks are subject to drought stress, another ascomycete, *Biscogniauxia mediterranea* (De Not.) Kuntze. (*Hypoxylon mediterraneum* (De Not.) Mill.), seems to be at an advantage on several oak species: *Q. suber* (Luque et al. 2000; Schiaffino et al. 2002; Evidente et al. 2005), *Q. cerris* (Capretti and Mugnai 1987; Luchi et al. 2005), *Q. rotundifolia* (Martin et al. 2005), *Quercus pubescens* Willd. (downy oak; Luchi et al. 2005), and *Q. ilex* (Collado et al. 1999, 2001; Luchi et al. 2005). Insect defoliation combined with drought clearly promote fungal colonization also in case of moderate water stress (Capretti and Battisti 2007). In recent decades, the impact of this pathogen has clearly increased in the Mediterranean area on several oak species in connection with exceptionally dry years (Desprez-Loustau et al. 2006). In addition, *B. mediterranea* is often associated with low water potential values and relatively high temperatures (Vannini and Valentini 1994; Hendry et al. 1998, 2002). The fungus causes bark and xylem necrosis and, eventually, the death of trees of *Q. cerris*, *Q. ilex*, and *Q. suber* in the region. The main symptoms of the disease are black carbonaceous stroma on dead branches or stems and brown exudates from cortical lesions. The incidence of the disease by both these *Hypoxyla* is greater in areas where water availability is poor and the trees are more stressed (Desprez-Loustau et al. 2006). *Biscogniauxia mediterranea* is reported also from Africa, Central America, Europe, the United States, and Russia. Besides the above-mentioned oak species, *B. mediterranea* has also been recorded on several broadleaves, including *Carpinus betulus* L. (European hornbeam), *Corylus avellana* L. (common hazel), and *F. sylvatica*. Both *B. mediterranea* and *B. nummularia* spend most of their life cycle as endophytes in the aerial plant organs, but they may become pathogenic

in the woody organs of the declining trees. These fungi generally behave as saprophytes in the northern Mediterranean basin where the climate is more temperate (Malençon and Marion 1952; Vannini and Scarascia-Mugnozza 1991; Granata and Whalley 1994; Natercia and Santos 1995; Paoletti et al. 1996; Vannini et al. 1996).

Alder decline

The first record of a previously unknown and lethal disease of *Alnus glutinosa* (L.) Gaertn. (black alder) was found in 1993 in southern Britain (Gibbs 1995). However, it quickly became clear that the pathogen was an entirely new species, *Phytophthora alni* Brasier & S.A. Kirk, with several subspecies obtained by complex events of autopolyploidization and further hybridization (Ioos et al. 2006).

Most records of the alder *Phytophthora* have come from the *Alnus glutinosa*, but the pathogen has also been detected in *Alnus incana* (L.) Moench (grey alder) and *Alnus cordata* (Loisel.) Desf. (Italian alder) (Santini et al. 2003). This *Phytophthora* disease is now widespread in Europe and, in addition to the United Kingdom, has been reported from several countries: Austria, Belgium, Czech Republic, Denmark, Finland, France, Germany, Hungary, Ireland, Italy, Lithuania, the Netherlands, Norway, Poland, and Sweden (Streito 2003; Webber et al. 2004). Very high losses have occurred in some localities (such as parts of France and Germany), whereas the disease impact has been relatively small in others. Environmental factors may also play an important role in the occurrence of the disease, and it seems probable that distinct waves of infection can occur, which may be associated with flooding episodes (Webber et al. 2004). Recently, another species called *Phytophthora polonica* L. Belbahri, E. Moralejo & F. Lefort sp. nov., which could not be assigned to other taxa including *Phytophthora alni*, has been described and associated with alder decline in Poland (Belbahri et al. 2006).

The new two *Phytophthora* species are characterized by optimal growth rate of colonies on carrot agar at 30 °C, but they can grow up to 38 °C (Belbahri et al. 2006). *Phytophthora alni* disease has been observed to be increased with the mean summer temperature of the river water (Thoirain et al. 2007).

Several cases of dieback of *Alnus viridis* (Chaix) DC (green alder) were observed in the southern Alps (Maresi and Ambrosi 1999) and on the northern slope of the Alps (Steyrer et al. 2002) associated with microfungi (*Valsaceae*) developing in bark necroses. In both cases, these symptoms have been related to drought stress because of a shortage of snow cover.

In the last decade, somewhat similar signs of declines have been noted in *Alnus glutinosa*, and bacteria (Surico et al. 1996; Scortichini 1997) as well as mycoplasma-like organisms (Marcone et al. 1997) seem also to be associated with alder declines. A spread of and possible trends in this new development are poorly known at this time.

Canker stain of planetree

The plant pathogenic fungus *Ceratocystis platani* (*C. fimbriata* f. *platani*) attacks *Platanus* species (*Platanus acerifolia* Willd., London plane; *Platanus orientalis* L., ori-

ental plane; and *Platanus occidentalis* L., American sycamore) and has killed tens of thousands of plantation trees and street trees in the eastern United States, California, and southern Europe. With regard to Europe, after the first recorded appearance of *Ceratocystis platani* in Italy in 1972, it spread to neighbouring states (France in 1974, Spain in 1977, and Switzerland in 1986). In Italy, the disease spread especially northward but also to the south, severely affecting street trees, particularly those in the larger cities (Panconesi et al. 2003). In 1986, as we had feared, there was a first report of *Ceratocystis platani* having invaded a natural forest of *Platanus orientalis* in Sicily, Italy, and in southwestern Greece more recently (Tsopelas and Angelopoulos 2004). According to genetic studies (Engelbrecht et al. 2004), it seems that this pathogen was introduced in Europe and in California from the eastern United States. In fact, its genetic variability, especially in Europe, is very limited, suggesting that this population has gone through a recent genetic bottleneck, perhaps from the introduction of a single genotype. It is usually transmitted through pruning or via other wounds. The fungus kills the bark and cambium and stains the wood (ink disease) of affected trees. Infected trees may die after 3–6 years (Butin 1995). Because plane trees are important amenity trees, especially in cities, spread of diseased plants and wood is prohibited by European Union directives. Natural spread of the disease can be prevented by destroying infected trees, even though the persistence of living fungus in dead stumps can be longer than 5 years (Maire and Vigouroux 2004; Matasci and Gessler 1997). Mycelium growth occurred between 10 and 35 °C, with optimum growth at 25 °C. Viability was lost after 48 h at 40 °C. Germination of conidia and ascospores was maximal at 25 °C (Mancini and Scapin 1981). Whether the fungus is influenced by climatic conditions is unknown, but the possibility of the disease spreading farther north cannot be ruled out at the present.

Cypress canker

Caused by the imperfect fungus *Seiridium cardinale* (Wagner) Sutton & Gibson, this dramatically effective shoot and stem canker disease has spread to all areas of the natural range of *Cupressus sempervirens* L. (Italian cypress) around the Mediterranean basin in recent decades. Of the three species of *Seiridium* that cause canker diseases on cypress (including *Seiridium cupressi* (Guba) Boesew., and *Seiridium unicorne* (Cooke & Ellis) B. Sutton.), *Seiridium cardinale* is the most pathogenic and the most thermophilic. Conidia can germinate, and colonies can grow in vitro, up to 35 °C. However, the disease may occur at temperatures up to 30 °C, although infection is optimal at about 25 °C (Graniti 1998). This disease affects the landscape and amenity value of cypress; in forest areas, it is also severely decimating in scattered and small stands (La Porta et al. 2005a). Introduced from California where it damages *Cupressus macrocarpa* Hartw. ex Gordon. (Monterey cypress) and *Cupressus arizonica* Greene (Arizona cypress), it is now widespread from Turkey in the east to Portugal (Neves et al. 1986) in the west. In certain areas, 50%–90% of the cypresses have died. Frost, winds, and cork-borer insects contribute infection courts (Graniti 1993). On the other hand, if temperature increases, fewer incidents of frost damage are

expected. These damages, especially bark microwounds, are normally associated as high access points to *S. cardinale* spores that will reflect in low infection incidence.

The canker fungus can also intensively colonize seed cones of *C. sempervirens* and is associated with seed insect vectors *Megastigmus wachtli* Seitner and *O. maculatus*. Both insects and fungus are known to respond positively to temperature increases, and warmer climate may speed up insect colonization and fungus development (Zocca et al. 2008).

The disease attacks several Mediterranean species of *Cupressus* and variation in resistance among species is evident. Within the time span of this report, species composition is rapidly changing in the areas affected. In the same climatic situation, *Leptographium* spp. can contribute to the death of trees that are stressed as well. *Leptographium* spp. are pathogenic fungi associated with root-collar rot diseases of conifers (*Pinus* spp. and *Pseudotsuga* spp.) and are associated with insects (Webber and Hansen 1990; Baker et al. 1994).

Shoot blight caused by *Sphaeropsis sapinea*

Several species of pines in areas frequently stressed by drought before and during flushing have recently been attacked by the opportunistic fungus *Sphaeropsis sapinea* (Fr.) Dyko & Sutton, also known as *Diplodia pinea* (Desm.) Kickx, and trees may die in a few years. This parasitic fungus has been studied in Italy since the early 1900s and, normally, has been proven to be a weak pathogen (Moriondo 1978). In presence of water stress, it is considered to be responsible for different kinds of symptoms and may affect different parts of the plant: branch or crown dieback; bark necrosis; blue stain of the sapwood, with resin flow; death of cones (economically valuable for *Pinus pinea* L., (Italian stone pine); and canker. Despite a study that tends to minimize the role of drought (Paoletti et al. 2001) on the colonization by *Sphaeropsis sapinea*, the fungus has been found quite commonly on pine plantations in association with drought in Europe (Desprez-Loustau et al. 2006) on the following pine species, in order of damage: *Pinus nigra* Arnold (Austrian pine), *Pinus pinea*, *Pinus sylvestris*, *Pinus halepensis* Mill. (Aleppo pine), *Pinus radiata* D. Don (radiata pine), and *Pinus pinaster* (very rare). In the northern parts of the Mediterranean basin, where droughts are less frequent, trees show discoloration and browning (death) of needles in the lower two-thirds of the crown but do not die. Severe loss of seed production also occurs since the fungus attacks the cones (Capretti 1999). Recently, the fungus has been found in Estonia as an invasive species (Märt Hanso, Estonian University of Life Sciences, Tartu, Estonia, personal communication, 2008). Also, in the Southern Hemisphere where *S. sapinea* was probably introduced, this pathogen has been associated with global change scenario (van Staden et al. 2004). Naturally occurring inoculum of *Sphaeropsis sapinea* was highly tolerant of heat in laboratory tests and remained viable after 6 weeks at 55 °C (Jacobs 2005). In particularly hot years, the pathogen can cause severe damage also in central Europe (Jankovsky and Palovcikova 2003; Juhasova et al. 2006; Hanisch et al. 2006). If climate change causes increasingly frequent droughts in the areas affected by the disease, then changes in species

composition because of this fungus are already an evident consequence.

Silver fir decline

Since the first observations in the early 19th century in Germany, *Abies alba* Mill. decline has been increasingly studied especially from the 1970s (Schutt 1977; Von Schuck et al. 1980.). The previous studies attributed air pollution, especially indicated as high concentrations of sulphur dioxide, as the main cause of *A. alba* decline (Wentzel 1980; Zawada and Widera 1980), even though there were several concerns about this explanation (Kandler 1992). However, further analyses and investigations have failed to confirm that forests are dying or are even declining over large areas of central Europe, i.e., Germany, southeastern France, Switzerland, Austria, and the Czech Republic. Foliar injury by air pollutants and mortality, have occurred but is generally restricted to specific locations in the Czech Republic and in eastern Germany (Kandler and Innes 1995). The symptoms of decline include crown "thinning," "stork's-nests," epicormics, wetwood, and root damage, and they occur over large areas in Europe (Krehan 1989). In some regions, such as Bavaria, *A. alba* has lost more than 75% of its area over the last 200 years (Eichenseer 1997). In southern Europe, the damages were relatively limited (Moriondo and Covassi 1981). The possible primary causes of fir decline have been recognised as a complex of mutually interdependent factors, such as sulphur emissions and other pollutants (Elling 1993), soil acidification, management methods, lack of genetic variability, epidemics, severe recurrent frost events, and especially, even with different sensitivity among different fir species, dry periods and drought (Becker et al. 1989; Guehl et al. 1991). It is hypothesized that the principal features of *A. alba* distribution on a continental scale are determined by the macroclimate. Simulations of future distributions, also accounting for CO₂ trend climate scenarios, suggest that this species may suffer a substantial range and population reduction (Huntley et al. 1995).

Gremmeniella abietina

The disease is also called brunchorstia dieback (caused by *Brunchorstia pinea* (Karst.) Hönh.) in Europe and scleroderris canker (caused by *Scleroderris lagerbergii* Gremmen) in North America. In the United States, the fungus arrived from Europe, where it is indigenous, and was first recorded in 1962. In Europe, it attacks mainly *Pinus nigra*, *Picea abies*, and *Pinus cembra* L. (Swiss pine) at high altitudes in the Alps (Tomczek 1985), whereas it is less serious on *Pinus sylvestris* as well as *Pinus contorta* Dougl. ex Loud. (lodgepole pine) and *Pinus banksiana* Lamb. (jack pine) in the United States (Laflamme et al. 2006).

In southern Europe, *Pinus halepensis*, *Pinus pinea*, and *Pinus pinaster* have also shown high susceptibility to this pathogen (Moriondo 1978; Barbacovi et al. 1979; Capretti and Dorworth 1989; Santamaria et al. 2006). Where *Pinus nigra* is currently planted as an introduced species (e.g., in the United Kingdom), higher temperatures in summer may reduce the risk of *G. abietina* damage, enabling the trees to

be planted more widely in the uplands in the future (Redfern and Hendry 2002).

The disease is typified by death of the leaders and the apical needles of the lower branches of pine and spruce. Under severe conditions, all the foliage of the host may be affected and die. It is most damaging to species that are grown towards the limit of their range, and attacks are favoured by shaded conditions; by dense, badly aerated plantations, in which humidity is high; and by weather damage, such as temperature oscillations during shoot elongation. The disease may kill young trees as well as reduce growth and cause distortion of older trees. It can also cause serious nursery loss. Mycelial inoculations cause cankers in the dormant period but not in summer. During the dormant period, the host cannot actively defend against the fungus.

Several works suggest that the distribution of scleroderris canker is strongly influenced by climate (Venier et al. 1998). Climatic conditions such as wet springs and cool summer months, high precipitation, high RH, and fog are reported to favour serious outbreaks of the disease (Butin and Hackelberg 1978; Uotila 1988). Serious epidemics needs rainy and cloudy summers or a serious summer frost for 2 years consecutively. Mild winters enhance the growth in canker but, alone cannot cause epidemics. Cold winters delay the start of growth in spring, enhancing the infections (Uotila and Petäistö 2007). In northwest Denmark (Jutland), the epidemics are initiated when both spring and late summer are wet and cold (Thomsen unpublished data).³ Both May and August or September must have precipitation/temperature ratios (mm rain/°C) >8 before symptoms become severe the following year. In Japan, the epidemic of 1970 is thought to have been favoured by unusually low air temperatures from late September to early October and a subsequent long period of deep snow (Yokota 1975).

In the Mediterranean region, the pine trees can be affected by the disease, particularly from winter or late-season frost (Vagniluca et al. 1995). Some tested models fit very well with the mean temperature and the precipitation of the coldest quarter, with a concordance of 84% (Venier et al. 1998). Temperature sum, which is measured as degree-days, is a very important factor for fungal sporulation. Cumulative number of conidia increased linearly with logarithm of temperature sum. A binary logistic regression model with temperature sum and rainfall as variables accurately predicted the date of the first spores in the spring with an error <3 days (Petaistö and Heinonen 2003). Rain is an important factor in increasing conidia dispersal significantly, but conidia were found also in consecutive rainless days.

Red and brown band needle blight of pines

Red band needle blight is caused by the pathogens *Dothistroma pini* Hulbarý and *Dothistroma septosporum* (Doroguine) Morelet (= *Dothistroma pini* Hulbarý = *Cytosporina septospora* Doroguine) (teleomorph state *Mycosphaerella pini* Rostrup = *Scirrhia pini* Funk & A.K. Parker). Detailed observation and measurements clearly showed that distinguishing *D. pini* from *D. septosporum* is extremely difficult if not impossible, but molecular approaches were

³Thomsen, I.M. 2008. Precipitation and temperature as factors in *Gremmeniella abietina* epidemics. In preparation.

recently able to unambiguously identify the pathogens (Barnes et al. 2007).

Until recently, the disease was primarily of concern in the Southern Hemisphere where it has been a problem in commercial pine plantations, particularly on *Pinus radiata*. However, since the 1990s, there has been a continuous increase in disease incidence in the Northern Hemisphere and Europe, where it affects trees in their native ranges, mainly on subspecies of *Pinus nigra*, in addition to those planted as exotics (Bradshaw 2004), and *Pinus pallasiana* Lamb. (Crimean pine) in Ukraine (Barnes et al. 2007). In Estonia, *Mycosphaerella pini* have colonized the entire country in a few years. After the first record on *Pinus nigra*, *Mycosphaerella pini* is now a common colonizer of *Pinus sylvestris* needles thanks to the formation of anamorphic fruitbodies, dissemination of conidia, and new infections of pine needles (Märt Hanso, Estonian University of Life Sciences, Tartu, Estonia, personal communication, 2008).

Mycosphaerella pini affecting *Pinus nigra* in France in 1998 was associated with higher winter mean temperature (1.1 °C). The severity of disease is strongly affected by humidity, temperature, and light (Bradshaw 2004). Penetration of *Mycosphaerella pini* on inoculated seedlings was significantly greater under a variable than in a constant air temperature regime (Muir and Cobb 2005). Meteorological data from East Anglia suggests that, since the late 1990s, the climatic conditions appear to have been favourable to the disease, with a mean annual maximum temperature and rainfall having increased by 0.9 °C and 0.3 mm, respectively, (Archibald and Brown 2007).

A recent severe epidemic in British Columbia on *Pinus contorta* subsp. *latifolia* Engelm. ex S. Watson was shown to be clearly related to climate change (Woods et al. 2005), with higher frequency of prolonged periods of precipitation and temperatures of 18–20 °C during summer months, suggesting the disease might become more severe in the future.

Phytoplasmas

These microorganisms, simpler and smaller than bacteria, were formerly known as MLO (mycoplasma-like organisms) (Agrios 1975). Such pathogens are obligate parasites of plants and insects. Several insect species act as vectors for these prokaryotes, and these vectors play a major role in determining the type of ecological niche for a given phytoplasma (Davis and Sinclair 1998; Lee et al. 1998, 2000; Weintraub and Beanland 2006). In a few woody host species, such as some palms, sandal (*Santalum album* L.), paulownia (*Paulonia tomentosa* (Sprengel) Steud), and American ashes (*Fraxinus americana* L. and *Fraxinus pennsylvanica* Marshall) and elm (*Ulmus americana* L.), they cause death (Lanier et al. 1988; Sinclair and Griffiths 1994; Lee et al. 2000). More frequent are cases of forest broadleaved and fruit trees where the pathogens' infections localized in the host tissues are associated with serious weakening, loss of vitality, and slow growth and decline (Sinclair et al. 1994; Lee et al. 1995). The most common symptoms can be foliar chlorosis; leaves curled upward along the longitudinal axis, which also became sometimes bronzed-reddish and thick and brittle; smaller leaves; sparse foliage; interveinal chlorosis; premature spring bud break; premature autumn colour;

proliferation of buds and slender shoots with short internodes; growth of normally dormant axillary buds; dwarfism; off-season growth; deliquescent branching; tufting; phloem necrosis and dieback; and badly lignified and rubbery wood (Firrao et al. 2007). Over the last decades, more and more reports show an increase of the phenomena in many ornamental and forest species in Europe (Agrios 2005; Seemüller 1992; Bachand and Castello 1998; Mittempergher 1997) including ash (Maurer et al. 1993; Sinclair and Griffiths 1994; Sinclair et al. 1996), elm (Sinclair 1981; Pisi et al. 1981; Carraro et al. 2004), alder (Seemüller and Lederer 1988), beech (Parameswaran 1980), oak (Ragazzi et al. 1995), poplar (Seemüller and Lederer 1988; Berges et al. 1997; Cousin et al. 1998), hazel (Marcone et al. 1996a), European hackberry (Bertaccini et al. 1996), and eucalyptus (Marcone et al. 1996b). Also, several fruit trees show the presence of phytoplasmas associated with decline symptoms (Jarausch et al. 1995; Lee et al. 1995) including grapevine (*Vitis* sp.; Daire et al. 1997) and *Olea europea* L. (olive tree; Pollini et al. 1996). Phytoplasmas have been detected in forest trees belonging to ≥ 25 genera. Most of the trees are only slightly affected and tolerate the infection until other interacting stress factors (drought, salt, high or low temperatures, and pollution) cause loss of vigour and dieback (Mittempergher 1997; Juretic et al. 2002; Bertaccini 2007). Concerning the global warming, these kinds of diseases would likely increase both in terms of incidence and severity. That can be directly due to the drought stress for the hosts (Han et al. 1991; Sinclair et al. 1994) and indirectly due to the better efficiency of vectors in relation to a higher temperature (Garcia-Salazar et al. 1991; Murrall et al. 1996).

Conclusion

In conclusion, climatic conditions that give advantages to the pathogen and disadvantages to the host are often involved in creating the greater potential for damage to trees (Garrett et al. 2006). Nevertheless, the general assumption is that the effects of climate change are going to be different for each pathosystem in different locations, so that it is not possible to generalize. Models of plant disease have now been developed that incorporate more sophisticated climate predictions. Using models such as CLIMEX, Desprez-Loustau et al. (2007b) demonstrated that predicted warming would be favourable to most of the pathogens mentioned above by the end of the 21st century, especially those such as *P. cinnamomi*, for which winter survival is a limiting factor linked to low temperatures. However, most plant disease models use different climatic variables and operate at a different spatial and temporal scale than do the global climate models (Chakraborty et al. 2000). At the population level, the adaptive potential of host tree and pathogen populations (McDonald and Linde 2002) may prove to be one of the most important predictors of the level of climate change effects. Ecosystem ecologists are now addressing the role of forest disease in ecosystem processes and the challenge of scaling up from individual infection probabilities to epidemics. Interactions between climate and biotic systems are extremely complex, and understanding the potential impacts of climate change on fungi in forest ecosystems is a great challenge. Information is needed on how hosts and patho-

gens, including fungal communities, interact with each other, with the forest ecosystem in general, and with the changing global environment.

Climate change will affect plant pathosystems at several levels from genes to populations and from ecosystems to distributional ranges; and, in most aspects of epidemic trend, from environmental conditions to host vigour and susceptibility and from pathogen virulence to infection rates. Climate change is likely to have a deep impact on plant–pathogen interactions, and it will probably represent one of the biggest challenge for the ecological and functional stability of the forests in the coming years.

Stress host–pathogen relationships and interactions need to be identified. A better understanding of pathogen requirements; host adaptability; microbial diversity; and variations with site, forest composition, temperature, and moisture in forest environment will provide information needed to predict host and pathogen responses to altered environmental conditions. More information is needed also on the ecological specificity of mycorrhizas and their successional variation. This knowledge will improve our understanding of the roles fungi play in community development and ecosystem stability and can be used to develop sound forest management practices for a period of rapid climate change.

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