

Review article

***Phytophthora cinnamomi* and oak decline in southern Europe. Environmental constraints including climate change**

CM Brasier

Forest Research Station, Alice Holt Lodge, Farnham, Surrey, GU10 4LH, UK

(Received 14 December 1994; accepted 31 October 1995)

Summary — One of the most destructive of all tree root pathogens, the oomycete fungus *Phytophthora cinnamomi*, is associated with mortality and decline of *Quercus suber* and *Q ilex* in the Mediterranean region. The symptoms and distribution of this decline are described. *P cinnamomi* is a primary pathogen on a very wide range of trees and woody ornamentals worldwide, but is probably a native of the Papua New Guinea region. It is soil borne and requires warm, wet soils to infect roots. Since 1900 it has caused major epidemics on native chestnuts in the United States and Europe, and now threatens the stability of entire forest and heath communities ecosystems in some parts of Australia. Together with drought, it may be a major predisposing factor in the Iberian oak decline. Its possible role in this decline including its interaction with drought is discussed, and a generalised working hypothesis of decline is presented. The potential influence of climate warming on the activity of *P cinnamomi* is also considered. A model based on the CLIMEX program suggests that warming would significantly enhance the activity of the pathogen at its existing disease locations (such as the western Mediterranean and coastal north-west Europe), but that it would not greatly extend its activity into areas with cold winters such as central and eastern Europe.

oak decline / *Phytophthora cinnamomi* / climate change / root pathogen / drought

Résumé — *Phytophthora cinnamomi* et dépérissement des chênes en Europe méridionale : effets de contraintes de l'environnement et des changements climatiques. L'un des plus virulents pathogènes racinaires, le champignon oomycète *Phytophthora cinnamomi*, est impliqué dans la mortalité et le dépérissement de *Quercus suber* et *Q ilex* en région méditerranéenne. Les symptômes et la répartition de ce dépérissement sont décrits. *P cinnamomi* est un pathogène primaire d'une large gamme d'espèces arborescentes forestières et ornementales à travers le monde, mais est probablement originaire de Papouasie Nouvelle-Guinée. Il est présent dans le sol, et l'existence de chaleur et d'humidité est nécessaire pour l'infection des racines. Depuis le début du siècle, ce champignon a été à l'origine d'épidémies sur les chataigniers américains et européens, et menace actuellement la stabilité d'écosystèmes forestiers entiers dans différentes régions australiennes. Il peut être, en combinaison avec la sécheresse, le facteur majeur d'induction du dépérissement du chêne dans la péninsule ibé-

rique. Son rôle potentiel dans ce dépérissement, en interaction avec la sécheresse, est discuté, et une hypothèse de travail plus générale sur les mécanismes de dépérissement est proposée. L'influence potentielle d'un réchauffement climatique sur l'activité de *P. cinnamomi* est également prise en compte. Un modèle basé sur le programme Climex suggère que le réchauffement prévu pourra significativement augmenter l'activité du pathogène dans les zones où il est déjà présent (comme les régions méditerranéennes occidentales et les côtes d'Europe nord-occidentale) mais qu'il n'élargirait que faiblement son aire d'activité dans les zones à hivers froids comme l'Europe centrale et orientale.

dépérissement / *Phytophthora cinnamomi* / changements climatiques / pathogène racinaire / sécheresse

INTRODUCTION

Native oak cover in Europe is of enormous importance both ecologically and hydrologically, occupying a wide range of environments from flood plains to semi-arid hillsides. The oak forests of northern and central Europe are dominated by the deciduous forest species *Quercus robur* and *Q. petraea*, which provide a major renewable timber resource. The oak savannah woodlands and maquis of southern and Mediterranean Europe contain evergreen oak species such as *Q. suber*, *Q. ilex* and *Q. coccifera* overlapping with locally adapted deciduous species such as *Q. pyrenaica*, *Q. frainetto*, *Q. cerris* and *Q. pubescens*. These species provide cork (*Q. suber*), and fuelwood, and are often components of ancient agro-forestry systems including substantial mixed woodland-pasture areas in Spain and Portugal and mixed coppice-pasture areas in southern Italy.

Since 1900 many European oak ecosystems have shown signs of stress and some have suffered periods of considerable decline and mortality. The first part of this paper reviews the cause of these oak declines with special emphasis on the role of *Phytophthora cinnamomi* in the current Mediterranean oak decline. The second presents a theoretical analysis of the potential influence of global warming on the activity of *P. cinnamomi*, drawing strongly on recently published information.

THE CENTRAL EUROPEAN OAK DECLINES

Major periods of decline of *Q. petraea* and *Q. robur* in northern and central Europe from France to the Caucasus in the 1920s, 1940–1950s and 1980s have stimulated widespread investigations into their cause (eg, Delatour, 1983; Oleksyn and Przybyl, 1987; Anon, 1990; Siwecki and Liese, 1991; Luisi and Vannini, 1993). The frequent isolation of ophiostomatoid fungi from woody tissues of declining oaks in central Europe (Kowalski and Butin, 1989; Oleksyn and Przybyl, 1987; Siwecki and Liese, 1991) appeared to support a theory, originating in Romania and Russia during the 1940–1960s, that central European oak decline was caused by a primary disease called a vascular mycosis involving one or more fungi of the genera *Ophiostoma* or *Ceratocystis*. However, this view has been increasingly discounted in recent years (Siwecki and Liese, 1991; Brasier, 1993), and vascular mycosis is now considered unlikely as a primary cause of oak decline.

Attention has now returned to environmental influences and other biotic factors. Environmental phenomena frequently implicated in these oak declines include severe drought, prolonged flooding, rapid fluctuation of soil water levels and cold winters. There is a fairly broad consensus at present that stress resulting from episodes of severe drought, waterlogging or cold may be particularly important in initiating decline syn-

dromes, and that these stresses may lead to chronic decline, secondary attack by bark beetles, and invasion by opportunistic stem and root disease fungi. Biotic factors implicated include scale insect damage, bark beetle attack (eg, *Agrilus* spp, *Scolytus* spp), heavy defoliation by insects (eg, *Tortrix* spp), bark necroses (eg, caused by *Pezicula* spp or *Fusarium solani*), the latter sometimes in association either with cold injury or with bark beetle attack, and basidiomycete root rots (eg, *Armillaria* spp and *Collybia* spp).

Much excellent observational and chronological evidence has been accumulated (Anon, 1990; Siwecki and Liese, 1991; Luisi and Vannini, 1993), although central issues such as the role of predisposing factors and the dynamics of the decline process remain little understood. Also, while the crowns and stems of the affected trees have often been studied in detail, the condition of their roots has often been unreported. This aspect has recently been investigated, providing evidence of feeder root and small root damage (Vincent, 1991; Blatschke, 1994). Other relevant criteria such as seasonal patterns of feeder root development in healthy as opposed to stressed trees, the impact of environmental stress on feeder root production, and the effects of stress on general water and nutrient mobility within the tree have also remained largely uninvestigated until recently (see this volume).

MEDITERRANEAN OAK DECLINES

Since the early 1980s a severe decline of oaks has been reported across the Mediterranean region, though in many areas the onset of decline is thought to have been much earlier. In Spain and Portugal the oak species involved are primarily the evergreen *Q suber*, and *Q ilex*, and to a lesser extent *Q faginea* and *Q pyrenaica*. The decline of *Q suber* is also reported from Tunisia and

Morocco (Brito de Carvalho and Graf, personal communications). In Italy mainly the deciduous *Q cerris*, *Q frainetto* and *Q pubescens* are affected (Raddi, 1992). As in the central European oak declines, a wide range of associated factors have been identified including recurrent unseasonal droughts, severe summer flooding, air pollution, changes in traditional agricultural practices, attacks by wood-boring insects (*Platypus* spp), and attacks by canker and sapstain fungi such as *Diplodia mutila* and *Hypoxyton mediterraneum* (de Not) Ces et de Not (eg, see Malençon and Marion, 1952; Montoya, 1981; Torres, 1985; Ragazzi et al, 1989; Vannini and Scarascia Mugnozza, 1991; Luisi and Vannini, 1993).

The intensity of the decline is illustrated by the fact that by 1991 over 1 000 decline foci were present in the ca 2.2 million ha of oak forest and plantations across south-west Spain. This included 265 foci of average 21.4 ha in the 0.1 million ha of oak cover in the Parque Natural de Alcornocales (Cork Oak Natural Park) in Andalucía. In a typical focus, half the trees were dead or dying (Montoya, personal communication). Similar mortality has occurred in adjacent areas of the Algarve in southern Portugal. Trees either die rapidly in one or two seasons, or a more chronic decline occurs.

INVOLVEMENT OF *P CINNAMOMI* ROOT ROT IN IBERIAN OAK DECLINE

In May 1991, the author investigated the oak decline in southern and western Spain at the invitation of ICONA, Ministry of Agriculture, Madrid, with regard to the possible introduction of North American oak wilt (*Ceratocystis fagacearum*). No evidence of this organism was seen, but the decline sites first seen in Extremadura suggested the possibility of a spreading root disease, and in particular of the aggressive oomycete root pathogen *P cinnamomi* (Brasier, 1991). Sug-

gestive symptoms included sudden wilting and death of entire crowns of some affected trees in early summer or in autumn; occurrence of tarry spots on the stems of some trees and the production of epicormic shoots (possible indicators of root stress); and chronic decline over only one or two seasons (cf, Ragazzi et al, 1989). Suggestive distribution and site factors included the occurrence of dead and dying trees in large groups or foci; association of decline with river valleys or depressions, streamsides, or with seasonally lying water; and apparent association of decline with disturbed sites such as road margins and with ploughing, fire strips and areas of heavy animal trampling. Decline also appeared to progress more rapidly downhill, and to be more severe on southerly or south-westerly slopes.

Root excavations of affected trees often revealed substantial death of fine feeder roots on both *Q ilex* or *Q suber*, especially on thinner drier soils. Extensive bark necrosis of the collar and larger roots was sometimes found on trees in deeper, moister or currently wet soils. *P cinnamomi* is ephemeral and, unless lesions are fresh, is difficult to isolate (Shearer and Tippett, 1989), but this fungus was readily obtained from necrotic larger roots of a *Q ilex* at the first site sampled in Extremadura, and from necrotic larger roots of several *Q suber* at the second site sampled in Andalucia (Brasier 1991, 1992a,b). Following additional isolation attempts at decline sites across south and west Spain and in the Algarve between November 1991 and March 1992, *P cinnamomi* was obtained from either dead fine roots, necrotic larger roots and/or associated soil at 11 of 13 sites investigated (nine examined by the author and four by Spanish colleagues; see Brasier et al, 1993). Isolation frequency (positive isolations per no. of isolation attempts) at different sites ranged from 71% down to only 4%. The failure to isolate the fungus

at two sites may have been due to very dry soil conditions (Brasier et al, 1993).

In a similar survey in southern Spain, Cobos et al (1993) obtained *P cinnamomi* from the soil and fine feeder roots at 47% of all *Q suber* sites and from 26% of all individual *Q suber* trees sampled, but at only 17% of *Q ilex* sites and from only 6% of *Q ilex* individuals. Whether these differences between *Q ilex* and *Q suber* might reflect genuine differences in their susceptibility to the fungus or differences in isolation success due to their comparatively more xeric versus more mesic growing conditions remains to be investigated. Further sampling of fine roots of declining *Q suber* in the Algarve area of Portugal between October 1992 and May 1993 (Moreira et al, unpublished) produced an overall *P cinnamomi* isolation rate per tree for 88 trees tested of ca 18%. Such isolation rates are comparable to those expected for isolation of the pathogen from Jarrah dieback sites in western Australia (Old, 1979; Shearer and Tippett, 1989).

BIOLOGY, HOST RANGE AND ORIGINS OF *P CINNAMOMI*

P cinnamomi, a microscopic soil-borne fungus, is one of the world's most destructive plant pathogens. It attacks tree roots and collars mainly via its soil and water-borne zoospores. These are motile by virtue of their two flagellae and require free water and warm soil conditions for their dispersal (Crandall et al, 1945; Zentmyer, 1980; Shearer and Tippett, 1989). Attack is therefore often severe in heavy soils, but can also be devastating on sand plains with seasonal rainfall. Within a tree, attack may be repeated from year to year. Once the fungus is established its spread is mainly through the phloem and cambial tissue, and is most rapid between 25–30 °C, with a peak at ca 30 °C (Shearer and Tippett, 1989). In addi-

tion to the root necrosis, there is some evidence that the pathogen may affect host stomatal control by reducing its cytokinin production, leading to crown symptoms resembling those of drought (Cahill et al, 1985, 1986). The fungus survives dry periods either as thick-walled chlamydospores embedded in soil or roots, or deep in the soil profile (to 3 m) around infected sinker roots (Shearer and Tippett, 1989). Chlamydospores are also largely responsible for its longer distance spread in contaminated soil.

P. cinnamomi is considered indigenous to the Pacific Celebes-New Guinea region, and possibly also South Africa (Zentmyer, 1988). It is highly polyphagous, parasitising over 900 mainly woody perennial plants (Zentmyer, 1980). The fungus was probably introduced into Europe early in the nineteenth century. It had become fairly widespread by the 1940s, causing a massive epidemic on chestnut, *Castanea sativa* in southern Europe (eg, Del Cañizo, 1942; Pimentel, 1949; Moreau and Moreau, 1952) and serious disease of various woody ornamentals. It also caused a major epidemic on chestnuts and chinkapins in the south-eastern United States in the early 1900s (Crandall et al, 1945). It is particularly well known as the cause of the current Jarrah forest dieback and now also threatens the destruction of ancient, species-rich heath communities in western Australia (eg, Old, 1979; Shearer and Tippett, 1989; Wills, 1993).

Following the isolation of *P. cinnamomi* from Spanish and Portuguese oak decline sites in 1991 (Brasier, 1991), a literature search showed that the fungus was associated with death of imported *Q. suber* in North America and the Black Sea region (Mircetich et al, 1977; Giridov, 1963), and also that a warning of the potential threat of *P. cinnamomi* to cork oak forests in Portugal was given in an unpublished internal Portuguese Government memorandum by

Pimentel in 1953 (see Brasier, 1993). *P. cinnamomi* also causes aerial stem cankers on *Q. suber* (Giridov, 1963; Mircetich et al, 1977) and is a serious trunk pathogen of commercial American northern red oak (*Q. rubra*) plantations in south-west France (Moreau and Moreau, 1952; Robin et al, 1994; Marçais et al, this volume). However the primary inoculum for such stem cankers seems likely to come from root or collar infections (see also below).

PRELIMINARY CONCLUSIONS

On the bases of the close association of *P. cinnamomi* with decline sites, its occurrence in diseased roots of *Q. suber* and *Q. ilex*, tree symptoms and decline distribution, and from the known pathogenic potential of *P. cinnamomi* on woody perennials including *Quercus* spp, it was proposed that the fungus could be a major contributory factor in the rapid oak decline in southern Spain and Portugal. By analogy, it was proposed that *P. cinnamomi* may also be involved in some similar declines of *Quercus* spp in Italy, Morocco, Tunisia and other Mediterranean countries (Brasier, 1991, 1992a,b; Brasier et al, 1993).

The pathogenicity of *P. cinnamomi* to *Q. suber* and *Q. ilex* has recently been confirmed with inoculations of potted seedlings, and by direct stem inoculations of mature trees in the field.

A HYPOTHESIS OF DECLINE DEVELOPMENT

As a working hypothesis for the role of *P. cinnamomi* in Iberian oak decline, it is proposed that in consistently moister soils or periodically wet soils, necrosis of larger roots or of the collar region may sometimes occur leading to girdling and to relatively sudden death. However, on drier only seasonally moist

soils, attack may mainly be confined to the fine feeder roots. Vigorous trees may be able to tolerate an annual fine root loss to *P cinnamomi*, or indeed to recurrent drought. With less vigorous trees, however, loss of fine roots combined with factors such as drought, fluctuating water tables or moisture competition from scrub and invasive maquis, could lead either to chronic or rapid decline. As the tree canopy thins and becomes more open, higher soil temperatures may result in reduced humus levels, reduced soil microbial activity, and in damage to oak mycorrhizal systems. These factors may in turn further favour pathogen activity and development. Other site factors such as slope and drainage may also influence build-up of pathogen inoculum, and therefore local pathogen infection and dispersal rates. Secondary stress-related attacks by insects such as *Platypus* borers, and by other fungal parasites such as *D mutilla*, *H mediterraneum* and *Armillaria* spp, would further accelerate the decline of a tree, sometimes causing its rapid death. For any individual tree, decline may at some point become irreversible (cf, Houston, 1981; Manion, 1981; Griffin et al, 1993; Wargo, 1993 and see Wargo, 1996).

In addition to the above general hypothesis, an important historical feature of the current mainly *Q suber* mortality would need to be accounted for. From the observations of Pimentel (1949) and Del Cañizo (1942) on the *C sativa* epidemic in Iberia, it seems probable that the *P cinnamomi* was already widely distributed in Spain and Portugal in the 1940s (Brasier, 1993). Therefore, an explanation is needed for the much later appearance of the widespread damage to *Quercus* spp in the same areas, ie, during the 1980s. One relevant factor is that *Quercus* spp are probably in general more resistant to *P cinnamomi* than *Castanea* spp (Crandall et al, 1995). This resistance factor might initially have retained infection of *Quercus* roots at chronically low levels, equivalent to a widespread tolerance of the

disease. Indeed the inoculum for the stem cankers caused on *Q rubra* (and also on *Q robur* and *Q pyrenaica*) in south-west France seems most likely to be coming from root infections, yet no serious root disease of *Q rubra* has been observed in these situations (Moreau and Moreau, 1952; Robin et al, 1992). Hence *Q rubra*, *Q robur* and *Q pyrenaica* are presumably tolerant of this chronic root disease.

A second factor involved may be environmental stress sufficient to tip the balance from one of relative host tolerance to one of susceptibility to the pathogen. Increased susceptibility, as discussed above, would allow a greater inoculum build-up by the pathogen on affected roots, resulting in a heavier attack via zoospores on adjacent roots of the same or of nearby healthier trees. In this manner, critical thresholds of resistance could be overcome by the fungus, and pockets of severe disease could build up. Other factors, already discussed, such as the opening up of the canopy, higher soil temperatures and lower soil microbial levels, could then come into play, favouring the pathogen still further.

The most obvious stress factor during the 1980s has been drought. Successive droughts have been a recent climatic feature of most oak decline areas in the Mediterranean, and drought has frequently been proposed as the primary factor in these declines. In some situations drought alone may indeed be the primary cause of decline, and could well account for some of the fine root death observed by the author. Equally, however, *P cinnamomi* has been shown to be closely associated with most of the decline areas, at least in southern Iberia. The imposition of drought stress on oaks already exhibiting chronically low levels of root infection might critically reduce their tolerance of the fungus (cf, Griffin et al, 1993). Moreover, drought stress is already known to enhance the development of *P cinnamomi* within the infected host (Weste

and Rupin, 1975; Cahill et al, 1985, 1986; Marçais et al, 1993).

The hypothesized interaction between chronic root infection levels and drought needs to be tested experimentally, eg, through conducting artificial inoculation by zoospores followed by varying subsequent soil moisture deficit regimes. An additional possibility that the pathogen may directly influence host stomatal regulation, so mimicking the effects of drought (Cahill et al, 1985, 1986), also merits further investigation.

Lower precipitation levels, higher soil temperatures and other site conditions might account for the current decline being more advanced in the Algarve in the south of Portugal, where mortality has been heavy and the decline general, than in the Alentejo further north where sporadic pockets of severe disease occur among relatively healthier looking oak stands. Episodes of unseasonal heavy rain and flooding have also coincided with the droughts of the past 15 years. Such episodes would again favour the activity of *P cinnamomi*, providing moisture for zoospore spread and causing host stress through root asphyxia. In addition, changing land-use patterns, such as overgrazing and the neglect of once traditionally maintained oak pasture systems have also reduced tree vigour in many oak-growing areas (Montoya, personal communication).

Many critical environmental aspects of the association of *P cinnamomi* with Iberian oak decline therefore remain to be investigated.

GENERAL EFFECTS OF GLOBAL WARMING ON EUROPEAN OAK DECLINES

Attention has focused in recent years on the possible threat of a general global warming (eg, Bolin et al, 1986; Pearman, 1988). Regardless of the question of whether or

not the various global warming predictions have any validity in themselves, it is nonetheless just conceivable that some oak decline phenomena, such as the Mediterranean oak declines, might be early symptoms of warming (Brasier, 1992b). Certainly if warming did occur, all current oak decline phenomena would be likely to be influenced by it. This suggested that a risk analysis of the possible influence of global warming on European oak declines might be a useful exercise. In a theoretical assessment, Brasier and Scott (1994) have therefore summarized in general terms possible ways in which global warming and climatic disturbance might interact with oak decline phenomena. These routes, which include direct effects on tree development and distribution, direct effects on pest and pathogen activity and development, indirect effects on the oak-pathogen interaction, and ecosystem effects, will not be reiterated here. Of more immediate relevance to the present paper is the analysis made in the same publication of the possible impact of global warming on the activity of *P cinnamomi*, which will now be discussed.

THEORETICAL ANALYSIS OF THE EFFECTS OF GLOBAL WARMING ON THE ACTIVITY OF *P CINNAMOMI*

Predictions made by those proposing the onset of global warming include a possible mean temperature increase of ca 1.5–4.5 °C between now and the year 2050 in Europe (eg, Bolin et al, 1986; Pearman, 1988). Such warming is also suggested to involve not only a gradual increase in mean maximum and minimum temperatures, particularly in winter and spring, but increased levels of precipitation and greater climatic instability including more frequent and intensive rain storms and droughts. Associated effects may include increased CO₂ levels and periods of higher UV irradiation.

Since *P cinnamomi* is of world-wide economic and environmental importance, it has a relatively well-researched ecology (Old, 1979; Zentmyer, 1980; Shearer and Tippet, 1989), and is one of the few primary pathogens associated with a European oak decline (Brasier, 1992b), it was of interest to take it as an example of a specific fungal pathogen, and also of an introduced organism with a comparatively wide host range, and consider the possible influence of such a climatic change on its general biological activity across Europe (Brasier and Scott, 1994).

For a number of mainly qualitative reasons, *P cinnamomi* seems likely to become more active in Europe through global warming:

- General climatic warming may increase the northward range of this fungus.
- Warming may increase the incidence of periods favouring inoculum production and infection. This will particularly be the case if both warmer soils and increased levels of rainfall and soil moisture occur.
- Warmer seasons are likely to increase the rate of spread of the fungus in the host, leading to greater initial host damage, greater inoculum production and greater secondary infection rates.
- Warmer winters may allow increased survival of inoculum in roots or soil.
- Increased drought, waterlogging or other stress factors may reduce initial host resistance, allowing greater infection frequency, inoculum build-up and more rapid development in the host.
- The additive effects of primary drought stress, other climatic stress, and cycles of root dieback caused by *P cinnamomi* may markedly increase the incidence of host decline and mortality.
- The combined effects of stress on the ecosystem, host stress, and attacks by secondary organisms could result in increased

susceptibility to *P cinnamomi* among previously field-resistant host species.

It should be emphasized that in the case of *P cinnamomi*, or similar organisms, it may not only be an overall climatic warming alone but an increase in perturbed weather episodes favourable to inoculum production and spread that could lead to an increase in activity. Occasional periods of unusually warm weather combined with heavy rain to give warm, wet soils may be sufficient to initiate damaging and prolonged disease episodes. Also, as already discussed, drought stress following infection may greatly exacerbate root disease caused by *P cinnamomi* (eg, Weste and Rupin, 1975; Cahill et al, 1985, 1986).

The development of the CLIMEX computerized climate matching system by Sutherst and Maywald (1985; see also Sutherst et al, 1991) has facilitated the quantitative modelling of the potential response of *P cinnamomi* to global warming. A CLIMEX model was developed (Brasier and Scott, 1994) matched to the distribution of *P cinnamomi* in south-western Australia (Shearer and Tippet, 1989). The CLIMEX parameter values for temperature in the field were estimated to be 15 °C for the lower threshold for population growth, 22–27 °C for the ideal range for population growth and 31 °C for the upper threshold for population growth. The temperature ranges given in Zentmyer (1980) were used as starting values to derive the model. The parameter values for soil moisture index were estimated to be 0.5 for the lower soil moisture threshold for population growth, 0.6–1.3 for the ideal range for population growth and 2.0 for the upper threshold for population growth. The distribution of jarrah, *Eucalyptus marginata* (Abbott and Loneragan, 1986) was used to indicate starting values. The model was refined by use of a single stress factor, cold temperature, based on the absolute lower limit known for growth of *P cinnamomi* of 5 °C (Zentmyer, 1980; the fungus is also

frost sensitive, see Benson, 1982, and Marçais et al, this volume).

Figure 1 shows the predicted activity of *P cinnamomi* across Europe based on the model developed for the typical Mediterranean climate of south-western Australia, where the fungus is presently causing serious damage (eg, Wills, 1993). The activity pattern generated (fig 1) gave a reasonable fit to the European distribution for *P cinnamomi* shown on the most recent International Mycological Institute distribution map (Anon, 1984). It incorporates known *P cinnamomi* activity areas of southern Britain and Ireland, south-west France, northern Spain and in the Black Sea region. The *P cinnamomi*-associated *Q suber* decline areas of Iberia, together with other known *Q suber* decline areas of Morocco and Tunisia, are also represented.

Figure 1 was taken as a reasonable indicator of present *P cinnamomi* activity, and various comparative activity predictions were made by modifying the temperature and rainfall parameters of the computer program. An example of the predictions fitted to

a possible global warming development is shown in figure 2. A 10% increase in summer rainfall over the figure 1 'norm' (not illustrated here) added little change to predicted *P cinnamomi* activity. A 1.5 °C increase in annual minimum and maximum temperatures (also not illustrated), which is at the 'low' end of many current global warming estimates, predicted considerably enhanced *P cinnamomi* activity across the fungus' existing range, and a spread in its region of activity to south-west Germany and northwards along the Atlantic and North Sea coastal areas. A concurrent 10% increase in summer rainfall added little change to this activity. With a 3 °C increase in annual minimum and maximum temperatures (fig 2), nearer the higher end of current estimates, a significant increase in *P cinnamomi* activity was indicated, together with some spread in its activity eastward to the Danube plain (Austria and Hungary). An associated 10% increase in summer rainfall had a moderate predicted effect, and a 20% increase a more marked effect in further increasing its activity.

Fig 1. CLIMEX- generated ecoclimatic indices of climate stations in the Euro-Mediterranean region favourable for the growth and survival of *P cinnamomi* (indicated by the relative size of the dot). Crosses are climate stations predicted to be unsuitable for survival of *P cinnamomi*. From Brasier and Scott (1994).



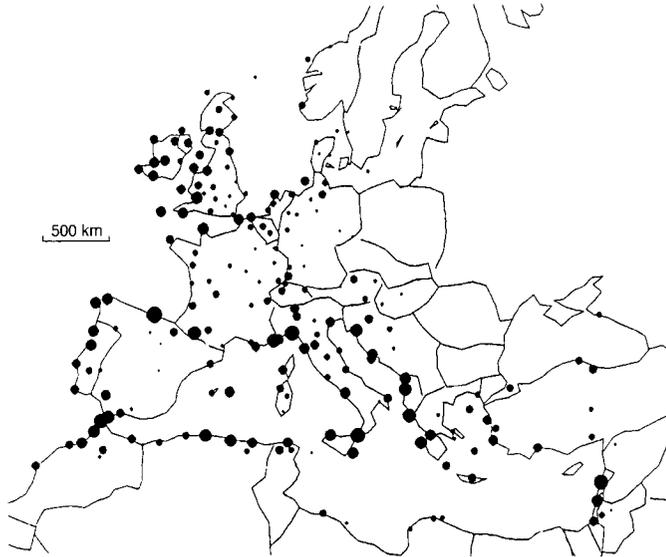


Fig 2. CLIMEX- generated ecoclimatic indices for *P. cinnamomi* in the Euro-Mediterranean region (see fig 1) with a 3 °C increase in mean annual minimum and maximum temperatures. From Brasier and Scott (1994).

In general, use of the CLIMEX program, based on an assumption that the Mediterranean-type climate in western Australia is highly suitable for the development of *P. cinnamomi*, suggests that there could be a relatively large increase in *P. cinnamomi* activity within its existing European locations, if there were a general climatic warming of between ca 1.5 and 3 °C. It also suggests some extension of its activity into the European continent, but no great extension of its activity into regions having very cold winters such as parts of Scandinavia, Russia and the central Danube. Indeed, since *P. cinnamomi* is relatively cold sensitive and can be eliminated by frost (Benson, 1982 and Marçais et al, 1996), it seems unlikely to be significantly involved in the recent oak decline phenomena in central and eastern Europe. This would not, however, rule out the possible involvement of more cold-tolerant Phytophthoras (cf, Blatschke, 1994).

Attempts to forecast an interaction of climate change with such ecologically complex and possibly even chaotic sets of processes as oak decline phenomena or the

activity of *P. cinnamomi* must obviously be treated with circumspection (Brasier and Scott, 1994). Moreover, in addition to the environmental variables examined in the model, any potential for increase in activity of *P. cinnamomi* would also depend upon other less easily quantified variables including the condusiveness of the soil type involved (Shearer and Tippett, 1989) and the availability of susceptible hosts. Limited evidence from inoculation tests suggests that *Quercus* spp are generally less susceptible to *P. cinnamomi* than the *Castanea* spp which were so severely attacked in Europe and North America in the 1920s (Crandall et al, 1945). Disease incidence in Europe also suggests that *Q. robur* is more resistant to *P. cinnamomi* than *Q. rubra* (Moreau and Moreau, 1952). By analogy, *Q. robur* may be more resistant than *Q. suber* or *Q. ilex* (Brasier, 1993). However, the relative susceptibility of different European oak species to root infection by *P. cinnamomi* needs to be more thoroughly investigated. So too does the possibility that disease levels in more resistant species might be

enhanced by climatic stress, or even that *P. cinnamomi* might adapt to more resistant hosts under some environmental conditions.

REFERENCES

- Abbot I, Loneragan O (1986) Ecology of jarrah (*Eucalyptus marginata*) in the northern jarrah forest of Western Australia. *Western Australian Department of Conservation and Land Management Bulletin* 1, 1-137
- Anon (1984) *Phytophthora cinnamomi* Rands. Commonwealth Mycological Institute Distribution Maps of Plant Diseases, Map No 302, Edition 5, Commonwealth Agricultural Bureau
- Anon (1990) Oak decline and the status of *Ophiostoma* spp on oak in Europe. *Bull OEPP/EPPO Bull* 20, 405-422
- Benson, D M (1982) Cold inactivation of *Phytophthora cinnamomi*. *Phytopath* 72, 560-563
- Blatschke, H (1994) Decline symptoms on roots of *Quercus robur*. *Eur J For Pathol* 24, 386-398
- Bolin B, Doos B R, Jager J, Warrick RA (eds) (1986) *The Greenhouse Effect, Climatic Change and Ecosystems*. SCOPE 29, John Wiley, Chichester
- Brasier CM (1991) Survey on widespread oak mortality in Spain, 13-17 May 1991 conducted on behalf of ICONA and the Dirección General de la Sanidad de la Producción Agraria (Ministerio de Agricultura, Pesca y Alimentación) Madrid, Report on isolation of *Phytophthora cinnamomi*, 4 pp
- Brasier CM (1992a) *Phytophthora cinnamomi* involved in Mediterranean oak decline. *Report on Forest Research 1991 HMSO*, London, 39 p
- Brasier CM (1992b) Oak tree mortality in Iberia. *Nature Lond* 360, 539
- Brasier CM (1993) *Phytophthora cinnamomi* as a contributory factor on European oak declines. In: *Recent Advances in Studies on Oak Decline* (N Luisi, A Vannini, eds), 49-58
- Brasier CM, Scott J (1994) European oak declines and global warming: a theoretical assessment with special reference to the activity of *Phytophthora cinnamomi*. *Bull OEPP/EPPO Bull* 24, 221-232
- Brasier CM, Robredo F, Ferraz JFP (1993) Evidence for *Phytophthora cinnamomi* involvement in Iberian oak decline. *Plant Pathol* 42, 140-145
- Cahill, D, Grant B, Weste G (1985) How does *Phytophthora cinnamomi* kill a susceptible eucalypt. *Aust Plant Path* 14, 59-61
- Cahill D, Weste G, Grant B (1986) Changes in cytokinin concentrations in xylem extrudate following infection of *Eucalyptus marginata* Donn ex Sm with *Phytophthora cinnamomi* Rands. *Plant Physiol* 81, 1103-1109
- Cobos JM, Montoya R, Tuset JJ (1993) New damage to *Quercus* woodlands in Spain. Preliminary evaluation of the possible implication of *Phytophthora cinnamomi*. In: *Recent Advances in Studies on Oak Decline* (N Luisi, A Vannini, eds), 163-170
- Crandall BS, Gravatt G F, Ryan MM (1945) Root disease of *Castanea* species and some coniferous and broadleaf nursery stocks caused by *Phytophthora cinnamomi*. *Phytopathology* 35, 162-180
- Delatour C (1983) Les dépérissements de chênes en Europe. *Biologie et Forêt* 35, 265-282
- Del Cañizo J (1942) A new method of controlling ink disease of the European chestnut. *Int Bull Pl Protection* 16, 2M-3M
- Giridov DY (1963) Causes of the infection of cork oak by ink disease. *Bot Zh* (Saint Petersburg) 48, 72-77
- Griffin DH, Manion PD, Kruger BM (1993). Mechanisms of disease predisposition by environmental stress. In: *Recent Advances in Studies on Oak Decline* (N Luisi, A Vannini, eds), 123-138
- Houston DR (1981) *Stress Triggered Tree Diseases. The Diebacks and Declines*. USDA Forest Service NE-INF, 41-81
- Kowalski T, Butin H (1989) Taxonomie bekannter und neuer *Ceratocystis* - Arten an Eiche (*Quercus robur* L). *J Phytopathol (Berl)* 124, 236-248
- Luisi N, Lerario P, Vannini A (eds) (1993) Recent Advances in Studies on Oak Decline. Proc Int Congress, Brindisi, Italy 13-18 September 1992
- Malencon G, Marion J (1952) *L'Hypoxylon mediterranean* (DNtrs) Ces et DNtrs et son comportement éphiphytique dans les chênaies nord-africaines. *Revue de Mycologie Supplement Colonial* 27, 49-73
- Marçais B, Dupuis F, Desprez-Loustau ML (1993) Influence of water stress on susceptibility of red oak (*Quercus rubra* L) to *Phytophthora cinnamomi* Rands. *Eur J For Pathol* 23, 295-305
- Marçais B, Dupuis F, Desprez-Loustau ML (1996) Modelling the influence of winter frosts on the development of the stem canker of red oak, caused by *Phytophthora cinnamomi*. *Ann Sci For* 53, 369-382
- Manion P (1981) *Tree Disease Concepts*. Prentice Hall, Englewood Cliffs, NJ
- Mircetich SM, Campbell RN, Matheron ME (1977) *Phytophthora* trunk canker of coast live oak and cork oak trees in California. *Plant Dis Rep* 61, 66-70
- Montoya R (1981) Silvicultura mediterranea de los suelos de pseudogley. *Bol Estac Cen Ecol* 10, 3-10
- Moreau C, Moreau M (1952) Étude mycologique de la maladie de l'encre du chêne. *Rev Pathol Vég Entomol Agric Fr* 31, 201-231
- Old K M (ed) (1979) *Phytophthora and Forest Management in Australia*. CSIRO, Melbourne
- Oleksyn J, Przybyl K (1987) Oak decline in the Soviet Union-Scale and hypotheses. *Eur J For Pathol* 17, 321-336

- Pearman GI (ed) (1988) *Greenhouse: Planning for Climate Change*. CSIRO, EJ Brill, Leiden
- Pimental AAL (1949) A *Phytophthora cinnamomi* (Rands) um outro agente extremamente virulento da 'doença da tinta' do castanheiro. *Agron Lusit* 9, 181-191
- Raddi P (ed) (1992) *Mediterranean Forest Tree Decline in Italy*. Consiglio Nazionale delle Ricerche, Italy
- Ragazzi A, Fedi I D, Mesturino L (1989) The oak decline: a new problem in Italy. *Eur J For Pathol* 19, 105-110
- Robin C, Desprez-Lusteau, ML, Delatour C (1992) Spatial and temporal enlargement of trunk cankers of *Phytophthora cinnamomi*. *Can J For Res* 22, 357-366
- Robin C, Dupuis, F, Desprez-Lustan, ML (1994) Seasonal changes in northern red oak susceptibility to *Phytophthora cinnamomi*. *Plant Dis* 78, 369-374
- Shearer BL, Tippett JT (1989) Jarrah dieback: the dynamics and management of *Phytophthora cinnamomi* in the Jarrah (*Eucalyptus marginata*) forest of south-western Australia. Department of Conservation and Land Management, western Australia, Research Bulletin No 3, 1-76
- Siwecki R, Liese W (eds) (1991) *Oak Decline in Europe*. Polish Academy of Sciences Institute of Dendrology, Kornik
- Sutherst RW, Maywald GF (1985) A computerised system for matching climates in ecology. *Agric Ecosyst Environ* 13, 281-299
- Sutherst RW, Maywald GF, Bottomley W (1991) From CLIMEX to PESKY, a generic expert system for pest risk assessment. *Bull OEPP/EPPO Bull* 21, 595-608
- Torres JJ (1985) El *Hypoxyylon mediterranean* (De Not) Mill y su comportamiento en los encinares y alcornoques andaluces. *Bulletin Sanidad Vegetal Plagas* 11, 185-191
- Vannini A, Scarascia Mugnozza G (1991) Water stress: a predisposing factor in the pathogenesis of *Hypoxyylon mediterranean* on *Quercus cerris*. *Eur J For Pathol* 21, 193-201
- Vincent JM (1991) Oak decline: alteration of the fine root biomass with the progress of the disease (preliminary results). In: *Oak Decline in Europe* (R Siwecki, W Liese, eds), Polish Academy of Sciences Institute of Dendrology, Kornik, 173-175
- Wargo PM (1993) Multiple factors in oak decline in the United States. In: *Recent Advances in Studies on Oak Decline* (N Luisi, A Vannini, eds), 1-9
- Wargo PM (1996) Consequences of environmental stress on oak: predisposition to pathogens. *Ann Sci For* 53, 359-368
- Weste G, Ruppin P (1975) Factors affecting the population density of *Phytophthora cinnamomi* in native forests of the Brisbane Ranges, Victoria. *Aust J Bot* 23, 77-86
- Wills R T (1993) The ecological impact of *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. *Aust J Ecol* 18, 145-159
- Zentmyer G A (1980) *Phytophthora cinnamomi* and the diseases it causes. *Am Phytopathol Soc Monogr* 10
- Zentmyer G A (1988) Origin and distribution of four species of *Phytophthora*. *Trans Br Mycol Soc* 91, 367-368