

Decline of Mediterranean oak trees and its association with *Phytophthora cinnamomi*: a review

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Abstract Mortality events in cork and holm oaks have occurred in the Mediterranean basin since the beginning of the XX century, but severity of decline increased during the 1980s. By that time, the exotic soil borne pathogen *Phytophthora cinnamomi* was often recovered from declining stands and since then it has been considered the main factor associated with decline. This work analyses data concerning *P. cinnamomi* surveys in cork and holm oaks trees, pathogenicity tests carried out in controlled experiments, studies about the influence of site characteristics in tree decline and approaches to control the disease. Results of field surveys showed that the pathogen is widespread and pathogenicity tests suggested that host susceptibility to the pathogen is moderate when seedlings are in appropriate watering conditions, particularly cork oaks. Occurrence of decline is also associated with soil characteristics that interfere with root expansion and water retention. We assessed the relative importance of each factor involved in decline and revised the role of *P. cinnamomi* in cork and holm oak decline.

Introduction: Mortality events of cork and holm oak trees in Mediterranean basin

Abnormal episodes of cork oak (*Quercus suber*) mortality with unknown etiology have been reported since the end of

the nineteenth century and consistently throughout the twentieth century, in Portugal and Spain (Baeta Neves 1949, 1954; Natividade 1950; Macara 1975; Cabral and Sardinha 1992; Brasier et al. 1993; Carvalho 1993; Sousa et al. 2007). Natividade (1958) refers that in 1951 about 246,000 dead or injured cork oaks were cut down in Portugal. A diachronic analysis based on aerial photographs of the southwest Portugal indicated that between 1958 and 1987 the area of cork oak distribution remained stable, though there was a noteworthy reduction in their density (Carvalho et al. 1992). No holm oak (*Quercus rotundifolia*) mortality was referred during that period (Carvalho 1993). During the 1980s, there was another mortality outbreak in the Iberian Peninsula, increasing its severity by the end of the decade, and this time affecting both cork and holm oaks (Brasier 1992a, 1993; Cobos et al. 1992; CAMA 2001; Moreira 2001). For example, in Portugal, between 1990 and 1992, there was a substantial increase in the defoliation level of cork and holm oak trees and authorization to land owners for cutting down dead or injured cork trees increased about 70 % (DGRF 2007; Sousa et al. 2007). In France and Italy, cork and holm oak mortality was perceived after 1989 (DFCI 1991; Ruiu 2006). Following this outbreak, mortality in south Portugal and Spain was investigated with regard to the possible presence of the fungus causing North American oak wilt (*Ceratocystis fagacearum*, Brasier et al. 1993); these authors found no evidence of this disease, however, observations of decline symptoms and its distribution in the field suggested a root disease caused by a soil and waterborne oomycete organism. Affected trees were found to have undergone loss of fine feeder roots, and some showed extensive lesions on major roots. Brasier and collaborators isolated the oomycete *Phytophthora cinnamomi* in six out of the nine surveyed declining sites in Spain and suggested that the

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pathogen was a major factor in the rapid oak mortality in both Spain and Portugal (Brasier 1992a, 1993). Following Brasier et al. (1993) survey, several others' prospectives were carried out in declining stands in Portugal, Spain and France, where *P. cinnamomi* was isolated from the rhizosphere with relative success (Cobos et al. 1992; Robin et al. 1998; Gallego et al. 1999; Moreira 2001; Sánchez et al. 2002). Several other pathogens and pests have been associated with cork and holm oak decline, varying in their aggressiveness to the trees (Macara 1974, 1975; Ferreira and Ferreira 1989; Luque and Girbal 1989; Gallego et al. 1999; Riziero et al. 2002; Sicoli et al. 2002; Sánchez et al. 2003b; Santos 2003; Jiménez et al. 2005; Machado 2005; Romero et al. 2007; Sousa et al. 2007; Corcobado et al. 2010; Torres-Vila et al. 2011). Although their involvement in tree mortality may be locally relevant, with emphasis for *Botryosphaeria* ssp. in Catalonia, Spain (Luque and Girbal 1989), only *P. cinnamomi* was associated with the overall mortality outbreaks occurring in South Europe since the 1980s (Brasier 1992a; Cobos et al. 1992; Robin et al. 1998; Moreira 2001; Sánchez et al. 2002). In North Africa, a serious decline in cork and holm oak stands has also been reported, however, to our knowledge, *P. cinnamomi* was not recovered in any of the surveyed stands, and loss of vitality appears to be associated with climate, other diseases, pests and human intervention (Ben Jamâa et al. 2002; Bouhraoua et al. 2002; Chakali et al. 2002; Benia et al. 2005; Bouhraoua and Villemant 2005; Hasnaoui et al. 2005; Assali and Falca 2007; Habib 2007; Sid Ahmed 2007; Ben Jamâa and Piazzetta 2010; Ferka-Zazou et al. 2010; Ghaioule et al. 2010; Khouja et al. 2010; Linaldeddu et al. 2010; Mannai et al. 2010).

Aim of the paper

Although *P. cinnamomi* isolation was frequently recovered from declining sites in some studies (Brasier et al. 1993; Sánchez et al. 2002, 2003a; Romero et al. 2007), in other studies, pathogen detection was not so successful (Cobos et al. 1992; Robin et al. 1998; Moreira and Martins 2005). Moreover, pathogenic tests with seedlings in controlled conditions indicated that *P. cinnamomi* is only a moderate pathogen of holm and cork oak seedlings, especially concerning cork oaks (Robin et al. 1998; Moreira et al. 2000; Robin et al. 2001; Sánchez et al. 2005). It was suggested that tree mortality was occasioned after an interaction of pathogen attack with abiotic factors, with special relevance to drought events (e.g., Brasier et al. 1993; Robin et al. 1998; Gallego et al. 1999). The aim of this review is to analyze the strength of the association between *P. cinnamomi* occurrence and cork and holm oak decline. To achieve this main objective, we examined all field surveys and pathogenicity tests that were published, as well as

studies about the relation between cork and holm oak decline and other factors than *P. cinnamomi*. The specific goals were: (1) to detect which factors are more associated with cork and holm oak decline, (2) to analyze possible interactions between the pathogen and abiotic factors and (3) to classify the role of *P. cinnamomi* in cork and holm oak mortality in South Europe.

Brief description of the species

The montado system

Cork (*Q. suber*) and holm oak (*Q. ilex* ssp. *rotundifolia*, syn. *Q. rotundifolia*; *Q. ilex* ssp. *ballota*, *Q. ballota*; Lousã and Fabião 1997) woodlands are of high conservation and socioeconomic value within their areas of geographic distribution around the Mediterranean basin: Portugal, Spain, southern France, Sardinia, Algeria, Morocco and Tunisia (DGRF et al. 2007). “Montado” in Portugal or “Dehesa” in Spain is the agro-silvo-pastoral system dominated by these Mediterranean evergreen oaks mixed with pastures, forming a savannah-like landscape. It occupies approximately 5.3 million hectares of woodland in Spain (Sánchez and Garcia 2007) and 1.2 million hectares in Portugal (DGRF 2007). Diversity of production—forage, acorn, wood, cork, charcoal—is the characteristic of these systems and the long-term ecological sustainability derives from the sub-optimization of the resources for many centuries (Joffre et al. 1999). In Portugal, permissions to cut down cork and holm oaks, independently of the health status of the trees, must be granted by the “Autoridade Nacional Florestal.”

Phytophthora cinnamomi

Phytophthora cinnamomi is a soilborne oomycete widely distributed in temperate and tropical regions. It is suggested to have spread throughout Europe in the nineteenth century, when sweet chestnut (*Castanea sativa*), a highly susceptible host, was found affected by the so-called ink disease in Portugal and Spain (Brasier 1996, 2000). *P. cinnamomi* parasitizes living roots; however, it has some saprophytic ability in soils with low microbial activity, and particularly in saturated soils, where it can compete with other soil microorganisms (Zentmyer 1980; Weste 1983; McCarren 2006). It persists in soil or infected plant material, and when conditions favoring mycelium growth prevail, the pathogen enters the asexual sporulation cycle (Hardham 2005). Within 2 or 3 days in a susceptible host, sporangia will form on the plant surface and the asexual cycle may be repeated many times in quick succession, rapidly amplifying the inoculum potential in the infected

area (Hardham 2005). This pathogen is known to survive for as long as 6 years in moist soil. Moisture is the key factor in the establishment, spread and longevity of the pathogen (Zentmyer 1980). *P. cinnamomi* is primarily a root pathogen of woody species and causes rot of fine feeder roots; larger roots are only occasionally attacked (EPPO 2004). Its mycelium develops in the cortical cells, phloem and xylem of the infected roots; although the pathogen is not able to hydrolyze lignified cell walls (Davison et al. 1994). Secondary symptoms resemble those of drought: foliage becomes chlorotic, wilts and, depending on the severity of the root rot, dies back, the crown thins, and epicormic shoots formed but are wilted, turn brown and die; the pathogen may cause also stem cankers which often result in sudden death (EPPO 2004). Host susceptible reactions vary from rapid mortality following infection to field tolerance (Zentmyer 1980). *P. cinnamomi* was first described as a root pathogen of cork oak in 1944 by Lopes-Pimentel (1946), although it was first misidentified as *P. cambivora* (in Carvalho 1993). This pathogen was also isolated from cortical cankers in cork oak trees in Russia in the 1950s (Globa-Mikhailenko 1960) and in California in the 1970s (Mircetich et al. 1977). Two different populations were detected in southern Iberia following molecular studies, though there were no differences in pathogenicity between both populations when artificial inoculations were performed (Caetano et al. 2007). Although it has been reported differences in virulence of isolates from different origins to some hosts (Robin and Desprez-Loustau 1998), no significant differences between three *P. cinnamomi* isolates were found in respect of the frequency of mortality, wilting and leaf necrosis of holm and cork oak seedlings (Robin et al. 2001).

Symptoms of cork and holm oak decline

Two main types of syndromes associated with decline have been observed (Cobos et al. 1992; Tuset et al. 1996; Gallego et al. 1999; CAMA 2001; Moreira 2001; Rui 2006; Sousa et al. 2007): (1) a sudden death of the tree, characterized by the fast drying of the crown followed by tree death in one or two seasons, particularly in early summer after the winter rains and in early autumn following the dry season; yellow or brown leaves may remain attached to the tree for some time; and (2) a progressive decline and gradual loss of foliage, where the first symptoms are drying of the top of the tree, sprouting of epicormic shoots, a more intense leaf drop which may affect the whole crown or only some branches. Affected trees occur either in groups of variable size within a forest that appears to be healthy, or dispersed throughout the forest (Cobos et al. 1992; Gallego et al. 1999). Observation of the root system showed many dead fine roots, even in trees with low defoliation levels

(Moreira 2001), and particularly in affected trees in moister soils (Brasier et al. 1993). Other symptoms not so frequent are tarry exudations on trunks and inner bark lesions or cracks in the stem bark and low branches (Brasier et al. 1993; Gallego et al. 1999; Sánchez et al. 2003a). Robin et al. (1998) observed bleeding cankers at the base of some cork oak trees not severely declining and *Phytophthora* ssp. were recovered with a high frequency from canker tissue samples. Other recovered pathogens from canker or exudations in upper branches were *Brenneria quercina* and *Hypoxylon* sp. (CAMA 2001).

Sánchez et al. (2003a) refer that decline symptoms are very unspecific. Chlorosis and wilting, defoliation, branch lesions, the absence of feeder roots can be ascribed to drought, insect defoliators and pathogens like *Botryosphaeria* ssp (anamorph: *Diplodia* ssp) or *Biscogniauxia mediterranea* (de Not) Kuntze (syn. *Hypoxylon mediterraneum* (Gallego et al. 1999; CAMA 2001; Santos 2003; Machado 2005; Franceschini 2007).

Relationship between *P. cinnamomi* distribution and health status of cork and holm trees

Several field surveys were carried out in order to study the relationship between *P. cinnamomi* and cork and holm oak decline (Cobos et al. 1992; Brasier et al. 1993; Robin et al. 1998; Gallego et al. 1999; Moreira 2001; Sánchez et al. 2002), however, these prospections only focused on declining sites where tree mortality was occurring. Plant resistance to attack by *Phytophthora* ssp. may depend on the physiologic status of the host (Duniway 1983); therefore, it is possible that in declining stands some other conditions were significantly predisposing trees to attack by pathogens. Tree death often represents an arbitrary point on a continuum process with multiple contributors where the proximate causes of death (e.g., an insect or disease) may be a secondary factor, whereas the primary one (e.g., starvation) may not be obvious (Franklin et al. 1987). For this reason, the presence of a pathogen in declining trees is not sufficient to indicate causality since it may be a consequence of alterations in host resistance due to other stress factors. For example, *Biscogniauxia mediterranea*, the causal agent of the charcoal disease, is closely associated with cork oak declining stands; however, it was recurrently recovered in both declining and asymptomatic cork oak trees in north Sardinia (Franceschini et al. 2002). These fungal populations are endophytic and remain latent in healthy tissues, developing upon decrease in host defenses caused by unfavorable conditions (Franceschini et al. 2002; Santos 2003). To analyze an association between a pathogen distribution and a disease incidence, surveys should be carried out in both declining and healthy sites. Few

P. cinnamomi inspections on healthy *montados* have been published. In Portugal, an extensive survey covering 56 healthy and declining *montados*, distributed throughout the country, showed a positive relation between the tree crown defoliation and the occurrence of *P. cinnamomi* in Algarve region, whereas no relationship was found in the other regions (Moreira 2001; Moreira and Martins 2005). This significant result was only possible after analyzing separately not only regions, but also the source of *P. cinnamomi* isolations: plant roots or soil rhizosphere of each selected tree. Thus, in Algarve region, trees with low defoliation level showed a lower frequency of *P. cinnamomi* in roots and higher frequency of the pathogen in the rhizosphere than trees with high defoliation level. A similar trend was found in another study carried out in Cáceres region (Spain), where Vivas et al. (2009) found a positive relation between *P. cinnamomi* isolation from roots and crown decline symptoms of holm oak trees. However, this pattern is not consistently observed in cork oaks. In a survey carried out in Alentejo region (Portugal), the pathogen was recovered more often from root tissues of trees found in stands with average crown defoliation level lower than 25 % (Moreira et al. 2005); in this study, the pathogen was detected in almost all the *montados* surveyed, however, positive isolation from roots was infrequent in *montados* with higher crown defoliation. Possible explanations for this trend are described below.

The study of relationship between *P. cinnamomi* detection and oak canopy status raises several questions concerning: (1) pathogen isolation, (2) time delay between infection and manifestation of above-ground symptoms, (3) quantification of disease symptoms, (4) use of different units in statistical analysis, (5) host species (Fig. 1).

1. Pathogen isolation: Although negative results are usually attributed to low soil moisture at the time of the sample collection, Robin et al. (1998) and Sánchez

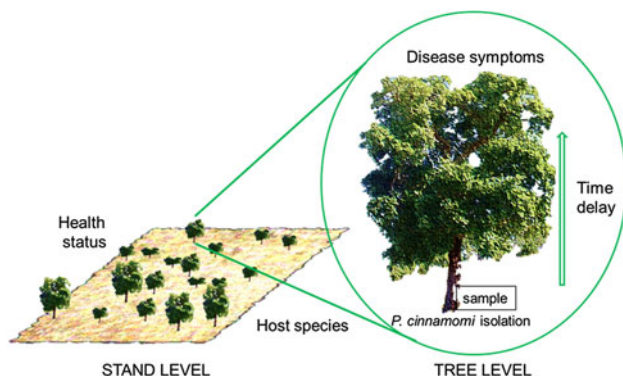


Fig. 1 Scheme of the critical steps on the studies concerning the relationship between *P. cinnamomi* distribution and health status of cork and holm trees

et al. (2003a) observed that isolation success was not significantly correlated with soil moisture or rainfall, and positive isolations were obtained in soils with relative soil water content as low as 6 %. The environmental factor associated with isolations success was the minimum temperature recorded in the 5-week preceding isolation attempts (Sánchez et al. 2003a). *P. cinnamomi* is a moderate temperature species and minimum temperature for growth is approximately 10 °C, with a few isolates being able to grow at 5 °C; free water is required for *P. cinnamomi* release of zoospores from sporangia and subsequent dispersal through the soil, however, water is not essential for production of chlamydozoospores and oospores, and for direct germination of the sporangia (Zentmyer 1980). *P. cinnamomi* is able to grow and reproduce in slightly drier conditions than other *Phytophthora* ssp. (Weste 1983). Negative results in pathogen isolation may be instead due to sub-optimized isolation methods. Usually a combination of baiting and selective medium is preferred; however, this procedure has several critical steps that should be adjusted, otherwise, isolation is just a matter of luck. For example, the amount of soil analyzed for *P. cinnamomi* detection mentioned in almost all the studies referred in Table 1 is about 10 g per sample, whereas it should be taken about 3–5 soil monoliths (20 × 30 × 30 cm) for analysis to increase the probability of obtaining sufficient inoculum for bait infection (Jung et al. 2000; Jung 2011). Several other precautions are required in order to avoid *Pythium* ssp. contamination, a faster growing oomycete that inhibits *Phytophthora* ssp. isolations. On the other hand, isolation success is also related to the material source. Authors usually use soil samples from the rhizosphere and fine feeder roots for *P. cinnamomi* isolation attempts and, to a lesser extent, bark tissue. Positive isolations are more frequent when using soil samples instead of root samples, since roots infected primarily by *Phytophthora* ssp. are latter invaded by other opportunistic pathogens (Jung 2011). However, the presence of the pathogen in the rhizosphere confirms that the pathogen is active but it does not present an unequivocal evidence of root infection. Some authors developed other methods than the combination of baiting and selective medium for *P. cinnamomi* detection from the soil or infected plants. ELISA-based kits for *Phytophthora* ssp. are not species specific and may show cross reactivity with some species of *Pythium* (O'Brien et al. 2009), but new developed molecular techniques appear to be sensitive and species specific, though it requires specialized equipment (Cooke et al. 2007; O'Brien et al. 2009; Williams et al. 2009; Langrell et al. 2011).

Table 1 Occurrence of *Phytophthora cinnamomi* in *Quercus suber* and *Q. ilex* recovered by the baiting method and selective medium

Host	Unit	Date	Region	Health status criteria	Sample type	Total stands	Total trees	Healthy units		Declining units		Reference
								Positive for Pc	Negative for Pc	Positive for Pc	Negative for Pc	
<i>Q. suber</i>												
	Tree	Sept to Dec 91	SW Spain	Decline symptoms ^a	Roots, soil	30	78			20 (26 %)	58 (74 %)	A
	Tree	May, Nov 91 March 92	SW Spain, S Portugal	Decline symptoms ^a	Roots, soil	5	13			5 (38 %)	8 (62 %)	B
	Stand	2003–2005	SW Iberia	Declining stands ^b	Roots, soil	31	62			19 (61 %)	12 (39 %)	C
	Stand	Sept to Dec 91	SW Spain	Stands with mortality	Roots, soil	30	78			14 (47 %)	16 (53 %)	A
	Stand	Spring 99 to spring 00	W Spain	Stands with mortality	Roots, soil	4	3–5 per stand			0 (0 %)	4 (100 %)	D
<i>Q. ilex</i>												
	Tree	Sept to Dec 91	SW Spain	Decline symptoms ^a	Roots, soil	53	162			10 (6 %)	152 (94 %)	A
	Tree	May, Nov 91 March 92	SW Spain, S Portugal	Decline symptoms ^a	Roots, soil	5	9			3 (33 %)	6 (67 %)	B
	Tree	Jan 98	SW Spain	Crown defoliation	Soil	3	28			20 (71 %)	8 (29 %)	E
	Tree	Jan 98	SW Spain	Crown defoliation	Roots	3	28			27 (96 %)	1 (4 %)	E
	Tree	Dec 99	W Spain	Crown defoliation	Soil	1	25			19 (76 %)	6 (24 %)	F
	Stand	2003–2005	SW Iberia	Declining stands ^b	Roots, soil	70	140			30 (43 %)	40 (57 %)	C
	Stand	Sept to Dec 91	SW Spain	Stands with mortality	Roots, soil	53	162			9 (17 %)	44 (83 %)	A
	Stand	Autumn 91 to spring 92	W Spain	Stands with mortality	Roots, soil	21	63			9 (43 %)	12 (57 %)	D
	Stand	Spring 99 to spring 00	W Spain	Stands with mortality	Roots, soil	17	3–5 per stand			3 (18 %)	14 (82 %)	D

Table 1 continued

Host	Unit	Date	Region	Health status criteria	Sample type	Total stands	Total trees	Healthy units		Declining units		Reference
								Positive for Pc	Negative for Pc	Positive for Pc	Negative for Pc	
<i>Q. suber, Q. ilex</i>												
Tree		Jun, Nov 95 96	SE France	ACD of 4 trees	Roots, soil, bark	24	96			28 (29 %)	68 (71 %)	G
Tree		Sp. Au 95–98	C Portugal	Crown defoliation	Roots	20	65	0 (0 %) ^c	4 (100 %) ^c	7 (11 %) ^d	54 (89 %) ^d	H
Tree		Sp. Au. 95–98	C Portugal	Crown defoliation	Soil	20	65	0 (0 %) ^c	4 (100 %) ^c	3 (5 %) ^d	58 (95 %) ^d	H
Tree		Sp. Au. 95–98	S Portugal	Crown defoliation	Roots	30	192	3 (14 %) ^c	19 (86 %) ^c	29 (17 %) ^d	141 (83 %) ^d	H
Tree		Sp. Au. 95–98	S Portugal	Crown defoliation	Soil	30	192	4 (18 %) ^c	18 (82 %) ^c	21 (12 %) ^d	149 (88 %) ^d	H
Stand		May, Nov 91 March 92	SW Spain, S Portugal	Decline symptoms ^a	Roots, soil	9	22			6 (67 %)	3 (33 %)	B
Stand		Jun, Nov 95 96	SE France	ACD of 4 trees	Roots, soil, bark	24	96			7 (29 %)	17 (71 %)	G
Stand		Spring 00	SW Spain	ACD in 4 ha	Soil	8	196			6 (75 %)	2 (25 %)	I
Stand		Autumn 91 to spring 92	W Spain	Stands with mortality	Roots, soil	9	21			3 (33 %)	6 (67 %)	D
Stand		Spring 99 to spring 00	W Spain	Stands with mortality	Roots, soil	6	3–5 per stand			4 (67 %)	2 (33 %)	D

Pc, *P. cinnamomi*; ACD, average crown defoliation; Sp, springs; Au, autumn; A, Cobos et al. (1992); B, Brasier et al. (1993); C, Romero et al. (2007); D, Molina et al. (2003); E, Sánchez et al. (2002); F, Molina et al. (2005); G, Robin et al. (1998); H, Moreira and Martins (2005); I, Sánchez et al. (2003)^a

^a Crown defoliation, exudations, branch dieback

^b Not specified

^c Trees with defoliation inferior to 10 %

^d Trees with defoliation superior to 10 %

2. Time delay between infection and above-ground symptoms: Root pruning precedes crown dieback since a tree can tolerate a great loss of its rootlets or feeder roots without showing visible above-ground symptoms (Tsao 1990). Tests showed that sweet chestnut seedlings, a highly susceptible species to *P. cinnamomi*, tolerate a loss of 90 % of the rootlets before exhibiting alterations in water status as measured through plant hydraulic conductance and leaf water potential (Maurel et al. 2001a). This indicates that expression of above-ground symptoms might be a quantitative rather than a qualitative problem affecting the root system (Jung et al. 1996). On the contrary, failure in detection of *P. cinnamomi* in the rhizosphere of declining plants is not unusual, because of the decrease in the fungal population due to antagonism and interference of fast-growing-associated secondary microflora (Tsao 1983).
 3. Quantification of disease symptoms: In studies concerning oak decline, some authors evaluate above-ground symptoms as a visual and subjective measure of the percentage of crown defoliation (e.g., Jung et al. 2000; Sánchez et al. 2002; Vettraino et al. 2002; Jönsson et al. 2003; Sánchez et al. 2003a; Moreira and Martins 2005). Although cork oaks are considered evergreen trees, they have short-lived foliage and a late flushing pattern; average leaf longevity is about 12 months whereas holm oak leaves last 1–3 years, and both leaf shedding and leaf birth occur during spring (Escudero et al. 1992; Sá et al. 2005; Caritat et al. 2006). Overlapping between different leaf cohorts is very low, and leaves should be classified as overwinter, rather than true perennial (Mediavilla and Escudero 2008). Therefore, caution should be exercised while taking measurements of cork oak crown defoliation during spring. Moreover, cork oak has been described as an extremely polymorphous species with many overlapping morphological attributes, mainly distinguishable by certain traits of the leaves, fruits, and cupules (Natividade 1950; Coelho et al. 2006b). Thus, density of the canopy may be influenced by factors other than health status, like phenological variability, effect of tree competition or artificial pruning. Some authors considered additional criteria to infer on the tree health status, like dieback of the tip of branches (e.g., Hansen and Delatour 1999; Balci and Halmschlager 2003). Oak trees undergo self-pruning of lower branches under the shade, but dieback of high branches is a reliable symptom of stress. However, after the collapse of dead branches, trees may present enough vigor to be considered asymptomatic, rendering unreliable evaluation of their health status (Ribeiro 2006). Nevertheless, dieback or lower leaf density in the upper part of the canopy can be related with water stress.
 4. Use of different units in statistical analysis: In studies of the association between *P. cinnamomi* distribution and oak decline, researchers analyzed data at tree level or at stand level. Usually, at tree level, the independent factor is the presence of the pathogen in the tree rhizosphere and the dependent factor is the degree of the tree crown defoliation, whereas at stand level, a set of trees are analyzed; the stand is positive for the pathogen if at least one soil or root sample yields the pathogen and decline symptom is calculated as average tree crown defoliation of part or of all the trees from the set (Table 1). Analyses at tree level may be hampered by eventual difficulties when isolating the pathogen or when evaluating disease symptoms, and by time delay between infection and above-ground symptoms, but at stand level one can use average values, thus avoiding great variation of data. Moreover, studies based on data obtained from nearby trees often display spatial autocorrelation, in that locations close to each other exhibit more similar values of independent factors than those further apart, increasing the chance of a type I error (incorrect rejection of a null hypothesis Legendre 1993). On the other hand, analyses at stand level pose some subjectivity in relation to the methodology applied to select the area of the stand units and to calculate its health status, where different authors use their own criteria (Table 1). Tomé (2007) demonstrated that different criteria to infer the health status of the stands lead to different results and highlighted the importance in the implementation of standard and systematic methodology. In addition, stand units should be as homogeneous as possible, at least in relation to topographic characteristics that may influence *P. cinnamomi* distribution, like slope and orientation (Moreira and Martins 2005). Additionally, the absence of the pathogen in a stand should be based on more than two samples analyzed for *P. cinnamomi* detection; otherwise, the number of negative locations would be overestimated (Pryce et al. 2002).
 5. Host species: Several studies encompassed cork and holm oaks and both species are usually analyzed together (Brasier et al. 1993; Molina et al. 2003; Sánchez et al. 2003a; Moreira and Martins 2005). However, pathogenicity tests reveal that they exhibit differential susceptibility to *P. cinnamomi*, holm oak being more susceptible than cork oak (Maurel et al. 2001b; Moreira 2001). Thus, pooling both species in the same analysis may lead to inaccurate results.
- Different methods for classifying the health status of the trees, the use of different units and problems in *P. cinnamomi* detection pose difficulties in evaluation studies. Declining stands positive for *P. cinnamomi* varied between 0 % (cork oak *montados*) and 61 % (cork oak *montados*; Table 1). At tree level, symptomatic trees positive for

P. cinnamomi also showed great variation, from 6 to 96 % (both extreme values observed in holm oak *montados*). In two studies where both asymptomatic and symptomatic trees were surveyed, there was no strong relation between the presence of the pathogen and decline symptoms (Table 1), contrarily to other susceptible hosts like sweet chestnut (Vettraino et al. 2005) and Fraser fir (*Abies fraseri*; Griffin et al. 2009) as well as with susceptible hosts to other *Phytophthora* ssp. (Hansen 1999; Jung et al. 2000; Balci and Halmschlager 2003; Jönsson et al. 2005) where the pathogens were frequently isolated from declining stands and/or trees and less frequently from healthy ones. For example, *P. cinnamomi* was isolated in 96 % of declining sweet chestnut stands and only in 21 % of asymptomatic ones (Vettraino et al. 2005). *P. quercina* was isolated in 63 % of declining pedunculate oak (*Q. robur*) and sessile oak (*Q. petraea*) trees and only 23 % in asymptomatic trees (Jung et al. 2000). This result was consistent, irrespective of the unity level, evaluation methods for health status estimation and inherent difficulties in *Phytophthora* isolations. In USA, little leaf disease in shortleaf pine (*Pinus echinata*) affects 1/3 of the stands; *P. cinnamomi* seemed to be associated with both healthy as well as affected stands; however, careful, quantitative surveys showed that not only declining stands were infected in higher number than healthy ones, but also declining trees were, on average, more infected than nearby healthy trees in affected stands (Hansen 1999).

Although *P. cinnamomi* has been isolated from declining cork and holm oak stands, its prospection in healthy stands using an adequate method is essential to evaluate the status of the stands or of the trees. At stand level, units should be uniform concerning topographic characteristics and an index of mortality relating dead (or highly damaged) trees with the total number of trees should be used to evaluate health status. At tree level, preference should be given not only to crown defoliation, but also to dieback of branch tips and spatial autocorrelation should be considered.

Pathogenicity of *P. cinnamomi* in cork and holm oak seedlings

Along with surveys in declining stands, experimental host inoculations with *P. cinnamomi* were carried out in nurseries under controlled conditions using 6 months up to 2 years old seedlings (Tuset et al. 1996; Robin et al. 1998, 2001; Gallego et al. 1999; Moreira et al. 2000; Maurel et al. 2001b; Sánchez et al. 2002; Tapias et al. 2008a). The most evident result from these studies is the finding in differential susceptibility between holm and cork oak seedlings to infection. In the studies where both cork and holm oak

seedlings were tested, the latter always showed more symptoms and mortality rates than cork oak seedlings (Table 2). Although both species showed necrosis in tap roots and a reduction in root and in foliar biomass, symptoms were much more severe in holm oak seedlings except in the study conducted by Sánchez et al. (2002). Cork oak mortality was barely observed whereas holm oak mortality occurred in half of the studies and varied between 1 and 67 %. This result is in agreement with histological studies showing that *P. cinnamomi* is able to invade vascular cylinder in newly emerged plants of both species, however, progress is more rapid and severe in the holm root cortical parenchyma than in cork oak (Moreira 2001; Pires et al. 2008). However, comparatively to other susceptible species, like the sweet chestnut, holm oaks exhibit more tolerance; in a comparative study, all the sweet chestnut seedlings died compared with 10 % of the holm oak seedlings (Maurel et al. 2001b). In most of the experiments with seedlings in appropriate watering conditions (usually field capacity), there was only slight or even no root or leaf symptoms (Moreira et al. 2000; Maurel et al. 2001b; Sánchez et al. 2002) and no physiological alterations related to transpiration and photosynthesis (Tapias et al. 2008a). Furthermore, inoculated seedlings even presented better performances than the controls in some experiments. For example, inoculated holm oak plants had better water use efficiency (Maurel et al. 2001b) and cork oak plants had better hydraulic conductance and photochemical efficiency (Tapias et al. 2008a) and showed higher root biomass than controls as a response to infection by *P. cinnamomi* (Moreira 2001). In relation to leaf water potential and stomatal conductance, results were contradictory; Tapias et al. (2008a) observed that the decrease in cork oak leaf water potential was not accompanied by changes in stomatal conductance, whereas Robin et al. (2001) and Maurel et al. (2001a, b) observed marked decrease in stomatal conductance of cork and holm oaks even at high values of water potential. Causality observed in these physiologic parameters may have different implications in the mechanism of infection. Decrease in stomatal conductance associated with leaf water potential is probably related to hydraulic signals acting in the stomata but decrease in stomatal conductance independent of leaf water potential may be related to non-hydraulic signals like an increase in abscisic acid concentrations, associated with root pruning caused by *P. cinnamomi* infection (or drought), as it was found for the susceptible sweet chestnut (Maurel et al. 2004).

In relation to interaction between water regime and *P. cinnamomi* infection, it was observed that both waterlogging and water shortage altered the host symptomatology to infection. Waterlogging treatment resulted in more mortality, more necrosis and less root and foliar biomass

Table 2 Morphologic and physiologic differences between *Quercus suber* and *Q. ilex* seedlings inoculated with *Phytophthora cinnamomi* in relation to non-inoculated controls. Experiments were subjected to three different watering regimes. Each line refers to the effect of inoculation in relation to non-inoculated seedlings, according to the respective water regime

Host	Treatment	Duration (months)	Dead plants	Taproot necroses	Foliar sympt	Root BM	Foliar BM	Length	g_s	Ψ	F_v/F_m	N, P K	Reference		
<i>Q. suber</i>	Flooding	1		>	=								Sánchez et al. (2002)		
		9	0	>		<							Moreira et al. (2000)		
		3	0/10	>	>								Romero et al. (2007)		
	Watered ^a	4	2.5 %											Tuset et al. (1996)	
		5	3/74	>			<			<	< ^d			Robin et al. (2001)	
		9	0	>			<							Moreira et al. (2000)	
		6		>	>									Sánchez et al. (2002)	
		5		>	=									Sánchez et al. (2005)	
		5								=	=			Robin et al. (2001)	
		9	0	=(0)			>							Moreira et al. (2000)	
		5	0	>			<			<	< ^d			Robin et al. (2001)	
		4	0/135							=	<	>		Tapias et al. (2008a)	
		2,5	0/25	✓ ^b							=			Robin et al. (1998)	
		2	1/3						< ^c	<		<		Luque et al. (1999)	
		Drought	5	1/?							=	=			Robin et al. (2001)
9	0		>			=							Moreira et al. (2000)		
<i>Q. ilex</i>															
<i>Q. ilex</i>	Flooding	1		>	=								Sánchez et al. (2002)		
		9	25 %	>		<							Moreira et al. (2000)		
		4	64.3 %										Tuset et al. (1996)		
	Watered ^a	5	67 %	>			<			<	<			Robin et al. (2001)	
		9	0	>			<							Moreira et al. (2000)	
		6		>	=									Sánchez et al. (2002)	
		5		>	>									Sánchez et al. (2005)	
		5								=	=			Robin et al. (2001)	
		10	1 (10 %)	>			<	<	<	<	=		<N, <P, =K	Maurel et al. (2001b)	
		9	16.7 %	>			<							Moreira et al. (2000)	
		5	20 %	>			<			<	<			Robin et al. (2001)	
		2,5	25 %	✓ ^b							<			Robin et al. (1998)	
		Drought	9	0	>			=							Moreira et al. (2000)
			10	1	>			<	=	=	=	>		<N, <P, =K	Maurel et al. (2001b)
			5	6/32							=	=			Robin et al. (2001)
F/D	8	8/18	>	>				<					Gallego et al. (1999)		

Seedlings were 6 months to 2 years old. All *P. cinnamomi* inoculations were applied in the substrate, except in Luque et al. (1999), where the pathogen was applied in a wound made on the host

>, significantly more symptoms than controls; <, significantly less symptoms than controls; =, no significant differences between control and inoculated plants; sympt, symptoms (wilting, yellowing, necrosis); BM, biomass; length, seedling length; g_s , stomatal conductance; Ψ , predawn stem water potential; F_v/F_m , photochemical efficiency; LHC, hydraulic conductance; N P K, leaf nitrogen, phosphorus and potassium; F/D, alternating flooding and drought

^a According to soil type and plant needs

^b Not specified symptoms

^c Diameter of the stem

^d There was no effect on Ψ until 92 days after inoculation

for both cork and holm oaks compared to controls. A global data analysis shows a synergistic effect between excess water and infection by *P. cinnamomi* on the severity of the disease (Moreira et al. 2000; Robin et al. 2001; Sánchez et al. 2002), since waterlogging by itself did not cause major symptoms in the seedlings. Waterlogging caused some root necrosis (Moreira et al. 2000) and root weight losses (Robin et al. 2001), but waterlogging combined with *P. cinnamomi* increased disease symptoms exponentially and was related to major mortality. It is considered that waterlogging increases the severity of diseases caused by root pathogens, primarily by adversely affecting host physiology while increasing the mobility of the pathogen through the soil (Schoeneweiss 1975; Zentmyer 1980). The observed synergistic effect could be attributed to a strong increase in the pathogen population causing multiple infections on the host (Moreira et al. 2000; Robin et al. 2001; Sánchez et al. 2002) acting together with higher host susceptibility after root hypoxia caused by excess water (Jacobs et al. 1996). This author observed that levels of defense barrier compounds (e.g., polymerized phenols) in cork oak roots changed at near-anoxic oxygen conditions.

Contrasting to excess water, the effect of the pathogen was reduced in plants subjected to drought. In cork oaks subjected to water shortage, the pathogen did not affect root biomass (Moreira et al. 2000) and though holm oak root biomass decreased, infection did not alter root collar diameter and aerial biomass (Moreira et al. 2000; Maurel et al. 2001b). Inoculation of both cork and holm oaks subjected to water stress had no effect on stomatal conductance (Maurel et al. 2001b; Robin et al. 2001) and in leaf water potential (Robin et al. 2001), except in one study where inoculated holm oaks had leaf water potential values as well as plants in good watering conditions (Maurel et al. 2001b). This may happen if stomatal closure following root infection reduces water losses. In relation to midday-stem-water potential, decreases were only related to water shortage and not to inoculation (Turco et al. 2004). Water stress also limited necrosis length caused by the pathogen when comparing to necrosis length in cork oaks plants subjected to good watering conditions (Luque et al. 2000). When subjected to water shortage, inoculated plants may not suffer from water stress since they already reduced water absorption and water losses as a consequence of *P. cinnamomi* infection (Maurel et al. 2001b). Physiological responses to infection like stomatal closure, better water use and photochemical efficiency, observed in plants infected by *P. cinnamomi* in good watering regimes, may enable trees to tolerate some water stress, at least temporarily. However, when irrigation is reduced long enough to significantly decrease soil moisture, there is an indication that the combination of water stress and infection increases severity symptoms (Moreira et al. 2006). Long-term

experiments under water shortage are necessary to understand the relationship between drought and infection.

Other studies, concerning germination and survival of newly emerged plants, showed high damping-off in artificially inoculated soils, with holm oaks being more affected; damping-off in naturally inoculated soils was very low and eventually attributed to low inoculum values or to the presence of antagonistic factors (Tapias et al. 2006, 2008b; Moreira 2001). On the contrary, other experiment showed high holm oak damping-off in naturally inoculated soils; however, part of the samples were subjected to alternation of flooding and drought conditions (Gallego et al. 1999) which may affect plant tolerance and pathogen aggressiveness. In relation to open field experiments in soils naturally infested with *P. cinnamomi*, damping-off occurred in 12.3 % of the germinated cork oak seedlings (Moreira et al. 2007) and in 19.6 % of the planted holm oak seedlings after the first year of experiment (Molina et al. 2005); however, authors considered that not all mortalities could be ascribed to the pathogen. Finally, studies regarding selection of more resistant seedlings detected some differential resistance/tolerance to *P. cinnamomi* infection among new emerging cork and holm oak seedlings from different origins (Moreira et al. 2007; Tapias et al. 2008b). The possibility of using plants more tolerant or resistant to *P. cinnamomi* infection can be an important tool to the reforestation of highly infested areas (Moreira et al. 2007); however, older seedlings from diverse origins had similar physiologic responses to infection (Tapias et al. 2008a).

In general, authors considered reactions shown by inoculated oaks very similar to the response usually observed in trees subjected to drought. Both pathogen infection and water stress may reduce root biomass and leaf water potential. Although in some circumstances, major roots and the lower stem may be infected (Shea et al. 1982; Dawson and Weste 1984). It is considered that the main effect of *P. cinnamomi* is the destruction of fine roots; therefore, reducing water absorption capacity and causing water stress symptoms. Exceptions were found on silvertop ash (*Eucalyptus sieberi*), a susceptible host that suffers from water stress when only about 1/6 of the roots are infected; thus failure in water transport cannot be due directly to decay of the root system (Dawson and Weste 1984). Likewise, in jarrah (*E. marginata*), there was a reduction in cytokinins before significant reduction in root tips (Cahill et al. 1986). The authors suggested that changes in the balance between this phyto hormone and abscisic acid could cause water transport failure and symptoms of drought. In holm and cork oak trees, there are no studies concerning hormonal changes after infection, but there are indications that the water absorption deficit is related to root pruning (Robin et al. 2001). *P. cinnamomi* invades

Table 3 Abiotic factors associated with *Quercus suber* and *Q. ilex* decline

Species	Scale	Region	Health status criteria	Abiotic factors										Reference						
				Stand					Soil											
				Tree age	Cultural practices	Structure	Orientation	Texture or type	Depth	Topography	OM	P	N		K ₂ O	Perm	SC			
<i>Q. suber</i>	Tree	N Portugal	Crown defoliation	-					Slope (-)	+	-	-					Martins et al. (2006)			
				S Portugal	Crown defoliation						+	-	-						Martins et al. (2006)	
	Stand	C Port SW Portugal	Dead/alive % defoliation	+ ^b		NS ^d	NS		Clay (+) Silt (-)	-	Slope: NS	-	-	-	-			Ribeiro (2006) Bernardo et al. (1992)		
				Sardinia Italy	Average defoliation	NS	Pasture > Shrub clearing	NS ^d	NS	NS ^f									Ruiu et al. (2005a)	
	Tree	SW Portugal	5 dead trees/ha															Ribeiro and Suroy (2007)		
					% of dead Trees													Usually < in plains	Costa et al. (2010)	
	Tree	W Spain	Crown defoliation			Shrub.> Agrosil.> Wood. ^e	South (+)		Leptosols > Luvisols > Arenosol											
					30 % wilted															
	Stand	Sardinia Italy	Average defoliation		NS	NS ^d	NS		Gravel > Sand = Clay > Silt											
					Symptomatic: 30 % wilted															
								Clay NS Sand NS Clay > Sand												

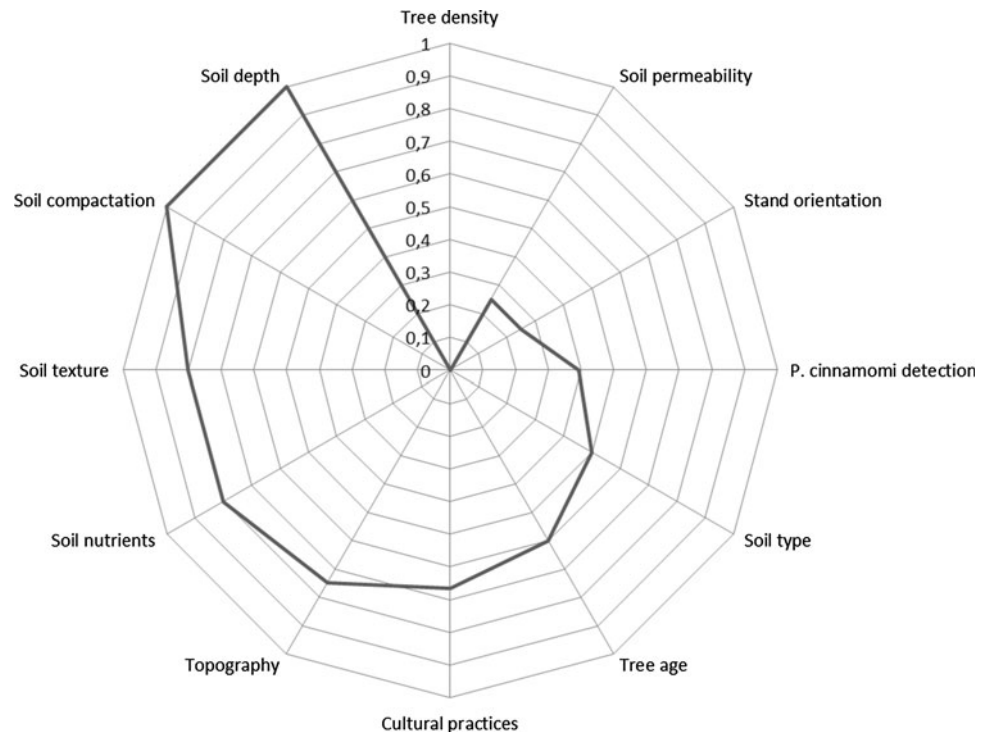
Table 3 continued

Species	Scale	Region	Health status criteria	Abiotic factors		Soil											Reference			
				Stand	Tree age	Cultural practices	Structure	Orientation	Texture or type	Depth	Topography	OM	P	N	K ₂ O	Perm		SC		
																			Soil	
<i>Q. suber Q. ilex</i>	Stand	W Spain	Symptomatic trees ^a	–	Cork harvest > Pruning > No activity = Harrowing = Shrub clearing					Schist > Rock > Clay = Sand								Valleys > Slopes > Plains		Perez et al. (1993)

OM, organic matter; K₂O, potassium oxide; P, phosphorus; N, nitrogen; perm, permeability; CEC, cation exchange capacity; SC, soil compaction; C port, Center Portugal; +, positively related with mortality; -, negatively related with mortality; NS, non-significant; >, category more associated with decline than the next one; =, both categories equally associated with decline

- ^a Symptoms not specified
- ^b Related to tree size
- ^c Pasture, shrub clearing
- ^d Density
- ^e Shrubland, agro-silvo-pastoral system, woodland
- ^f Substrates: basalt, trachyte, granite, schist, sedimentary
- ^g Analysis made in trees located in slopes
- ^h Analysis made in trees located in streams

Fig. 2 Relative significance of each independent factor associated with cork and holm oak decline in the studies referred in Tables 1 and 3



holm oaks roots more rapidly than cork oak ones, but penetration and intra- and intercellular progression of the pathogen through the cortical parenchyma and vascular cylinder are similar in both species (Pires et al. 2008). Both species respond with accumulation of phenolic compounds close to the hypha, which are not able to prevent root invasion (Pires et al. 2008). However, histological examinations of other resistant species showed that their root tissues were also invaded by the pathogen; nevertheless, those species were able to restrict colonization and necrosis (Cahill et al. 1989; Jang and Tainter 1990). The authors observed deposition of phenolic compounds in infected roots, as well as granulation of the cytoplasm, shrinkage of the protoplast and cell-wall distortion and disruption, regardless the species was considered resistant or susceptible. No specific change has been consistently associated with resistance, though deposition of phenolic compounds, lignification of cell walls and formation of papillae are observed more often in resistant ones (Cahill et al. 1989; Cahill and Weste 1983; Cahill et al. 1993). For example, resistant sweet chestnut hybrids increase production of leaf phenolic compounds after infection, whereas in the susceptible sweet chestnut no difference in leaf phenol content was observed (Dinis et al. 2011). Numerous plant species considered resistant to *P. cinnamomi* exhibit horizontal resistance, opposed to vertical resistance where disease does not occur (Erwin and Ribeiro 1996; Irwin et al. 1995). There are no reports of species being able to block pathogen ingress. It is thought that field-resistant plants are able

to restrict colonization, sealing the lesions off by the periderm and shedding them (Tippett et al. 1985; Irwin et al. 1995; Cahill et al. 2008). When an infected plant can prevent further spread of the pathogen determines the severity of infection (Cahill et al. 2008).

In conclusion, the pathogenicity tests indicate that holm and cork oak seedlings present some susceptibility to *P. cinnamomi* infection, particularly in conditions of excess water, with holm oaks being more susceptible. Both cork and holm oaks have limited capacity in preventing *P. cinnamomi* progression, particularly in new root tissues, but in appropriate watering and nutritional conditions, infected cork oak seedlings may replace necrotic roots (Moreira 2001), thus avoiding water stress caused by the reduction in water absorption following root destruction.

Relationship between cork and holm oak mortality and site characteristics

Cork oak mortality events have been usually empirically ascribed to complexes involving abiotic stress factors related to soil properties, particularly hydromorphic and shallow soils, and drought, inadequate silvicultural practices and secondary attacks by insects and fungi (Natividade 1958; Cabral et al. 1992; Diniz 1994). Studies attempting to statistically relate abiotic factors and mortality are shown in Table 3. Results varied from region to region. Since trees are subjected to several local abiotic

factors that interact between them, the relative effect of each one depends on that of the others. Thus, a negative effect in one region may be positive or neutral in another. For example, the presence of understory is associated with increase in mortality of cork oak trees in SW Portugal (Costa et al. 2010), but in Sardinia, unshrubby stands do not affect trees vitality (Ruiu et al. 2005a). Diniz (1994) and Cabral et al. (1992) observed that the shrub gum rockrose (*Cistus ladanifer*), present in some severely affected areas, may compete for limiting water sources in shallow and sun-exposed soils. In areas with no water limitations or with other shrub species, competition may be absent. Moreover, shrub clearing may alter soil properties, exposing them to sunlight, temperature oscillations, erosion and lixiviation, which may increase tree mortality (Macara 1975). As a consequence, the effect of the understory in tree vitality depends on plant species that are involved and on water availability, which, in turn, may depend on other stand characteristics like orientation or topography. Additionally the effect of shrub clearing in tree vitality depends also on the method applied. Shrub removal with soil mobilization causes disturbance in the root system of the trees and may increase tree vulnerability to adverse conditions. Concerning orientation, it was reported higher mortality values in south facing slopes (Costa et al. 2010; Moreira and Martins 2005; Brasier 1996; Cabral et al. 1992) but in some studies this pattern was not observed (Table 3). It is expected that plants growing in south facing slopes are more subjected to drought conditions, though in some regions the absolute humidity values may not be low enough to be reflected in tree vitality and no significant pattern is observed.

Although the relationship between site characteristics and tree decline varied among studies (Table 3), we estimated the relative significance of each independent factor in tree decline as the proportion of the number of studies where the factor was significant in relation to all the studies where it was analyzed; we also included the relative significance of *P. cinnamomi* in tree decline, calculated as number of declining stands positive for the pathogen in relation to the total of declining stands (Fig. 2). Since there are mixed cork and holm oak stands and little information concerning separate species, we analyzed both species together. Cork and holm oaks are moderate susceptible to *P. cinnamomi* and are also affected by the same abiotic factors. Although the strength of association between each factor and the health status of the trees may vary between species, for a general screening, we opt to group both species. It is possible to observe in Fig. 2 that soil compaction and depth were the characteristics most associated with decline, whereas *P. cinnamomi* was detected in 40 % of declining stand; however, the presence of the pathogen is probably underestimated, since false negatives are

common when using the baiting method for *Phytophthora* spp. detection (O'Brien et al. 2009). Factors limiting vertical root expansion such as compact or shallow soils may limit root access to deep groundwater tables during the dry season (Otieno et al. 2006) and, on the other hand, expose the roots to disturbances caused by soil management, waterlogging events and root pathogens. As a consequence, weakened and predisposed trees may not be able to regenerate the reduced fine-root capacities and will suffer extreme drought stress during the dry season and/or after drought episodes, as it was observed in beech and in silver-top ash decline (Cahill et al. 2008; Jung 2009). Reduced soil compaction associated with high percentage of gravel increases soil infiltration capacities favoring holm oaks decline caused by water stress (Solla et al. 2009). Other factors like orientation, topography, soil texture or understory are usually associated with mortality and all affect water availability, either limiting or in excess. Shrub competition, south orientation or soils with high gravel content may reduce water availability to values below the appropriate range, thus imposing drought conditions to the trees. On the other hand, topographic depressions, soils with high clay content and shallow soils have poor drainage, contributing with excess water to root hypoxia, toxicity and tree decline (Bernardo et al. 1992; Natividade 1958; Cabral et al. 1992; Diniz 1994). Nutrient availability was also related to tree decline, though cork and holm oaks are adapted to nutrient-poor soils. Bernardo et al. (1992) observed that soils with deficient internal drainage and with low effective thickness for root expansion have less accessible nutrients. Cork oak trees growing on these stands showed less vitality and their leaves exhibit nutrient imbalanced concentrations. Tests carried out in sandy and schistose soils during four sequential years showed an

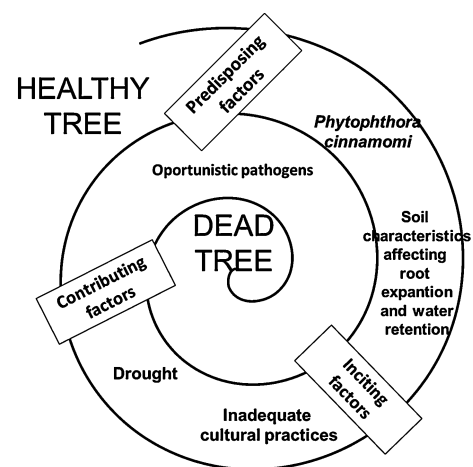


Fig. 3 Adaptation of Manion's (1981) disease spiral with main interacting factors associated with cork and holm oak decline classified according to their role in decline

overall cork oak vitality recovery after fertilization treatments, however, the response was only observed during the first year after the first fertilization (Sousa et al. 2005).

Site characteristics may act directly in the health status of the trees but also they affect *P. cinnamomi* survival acting in synergy with the pathogen. In particular, factors influencing soil moisture levels and microbial populations are factors governing the growth, reproduction and inoculum potential of the pathogen (Weste and Marks 1987). Soil compaction was reported to yield more *P. cinnamomi* inoculum (Vivas et al. 2009), though this relation may interact with water condition (Rhoades et al. 2003). Nevertheless, mortality associated with *P. cinnamomi* is usually much more severe in compact or shallow soils (Weste and Marks 1987; Fonseca et al. 2004). South-oriented stands and soils with high percentage of clay are both favorable to *P. cinnamomi* survival (Moreira and Martins 2005; Vivas et al. 2009) and unfavorable to cork oak vitality. Pathogenicity test (Table 2) indicated a synergism between waterlogging conditions and infection by *P. cinnamomi* and these results should be considered in the studies concerning mortality in the open field. Soils retaining high levels of moisture provide conditions to the increase in *P. cinnamomi* inoculum causing multiple fine-root infections and, in addition, negatively affect cork and holm oak roots and the overall health status of the trees. Although pathogen preferences for high levels of moisture, it was preferentially recovered in the driest side of the hills (Moreira and Martins 2005). This pattern was also found in Australia, and it was suggested that those soils may also have a low level of microbial antagonism (Newhook and Podger 1972). Soil dryness inactivates most of the suppressive microorganisms before affecting *P. cinnamomi* (Weste and Marks 1987), which may explain the preferential occurrence of the pathogen in south facing slopes. Furthermore, the occurrence of susceptible species like the shrub *Cistus ladanifer* in sunlight-exposed slopes can provide an important basis for inoculum production and survival, thus acting as reservoirs for *P. cinnamomi* (Moreira 2001). Regardless of sites with south orientation yielding high amount of *P. cinnamomi*, the relation between drought and infection by root pathogens in tree decline in those sites is unclear, given that pathogenicity tests showed that the symptoms of the infection are limited when plants are also subjected to moderate water stress (Table 2). Supporting this assumption is the result obtained in a *montado* at Extremadura, Spain, where trunk injections with potassium phosphonate, which have been used successfully to control *P. cinnamomi*, had no effects on holm oaks shoot growth and acorn production (Solla et al. 2009). In this study, water stress was more likely to contribute to decline than *P. cinnamomi*.

Drought has been considered a factor associated with mortality (Macara 1975; Cabral et al. 1992). In Spain, there was synchronism between exceptionally dry years and holm oak mortality (LLoret and Siscart 1995; Peñuelas et al. 2001; Sánchez and Garcia 2007) and recovery occurred after long periods of rain (Tuset and Sánchez 2004). (Cabral and Lopes 1992) also refer to a synchrony between atypical dry years (1943–1945, 1975–1976, 1980–1993) in Portugal and cork oak mortality events referred in bibliography; however, this pattern was not found in the study of Pereira (2007), which was also carried out in Portugal, though with no information concerning the period analyzed. On the contrary, in the southern regions of Portugal, there was a positive relationship between higher mortality and average annual precipitation (Ribeiro and Surovy 2007). The exception was found in the driest region, where lower values of precipitation presented more mortality values. These patterns might suggest that usually holm oaks are more susceptible to drought events and cork oaks to excess water.

Approaches to prevent decline

Development of infection is usually explained with a disease triangle, a general concept in plant pathology. The three main factors that must operate in concert to produce the disease are the presence of the pathogen, a susceptible plant host and environmental conditions favoring infection. Methods of disease control can be thought of as modifying the disease triangle by reducing or eliminating one of the three factors. Researchers have been trying to reduce host susceptibility through selection of resistant varieties to *P. cinnamomi* with promising results (Moreira et al. 2006, 2007) and studies about the mechanism of pathogenesis of *P. cinnamomi* on cork oak have been carried out with potential implications for disease control via resistance breeding (Coelho et al. 2006a; Horta et al. 2008; Maia et al. 2008). The initial approach to reduce the presence of the pathogen in the field was through application of the fungicide Metalaxyl (Coffey et al. 1984), however, some resistance has been found in some *Phytophthora* spp. (Cohen and Coffey 1986) and prolonged use of Metalaxyl reduces its efficacy (Darvas and Becker 1984). The fungicide may slow *P. cinnamomi* tissue infection but it does not eliminate the pathogen from infected plants (Marks and Smith 1992). Potassium phosphonate is other fungicide believed to have fungistatic activity and to stimulate the defense mechanisms of the fine roots (Guest and Grant 1991). Its application successfully improved vegetative growth of cork and holm oak seedlings in controlled situations (Navarro et al. 2004) as well as in adult holm oak trees in open field (Fernandez-Escobar et al. 1999);

however, other studies on treated trees have reported a lack of effectiveness of the fungicide (Porras et al. 2007; Solla et al. 2009). In order to suppress the pathogen, greenhouse experiments have been successfully realized with extracts from native plants (Neves et al. 2007), vegetable composts (Moreira et al. 2010) and calcium fertilizers (Serrano et al. 2011). The latter are not indicated to cork oak due to its preference for soils free of calcium carbonate. These experiments were conducted with seedlings in controlled situations and for the moment there are no curative treatments that can be carried out in adult trees, despite potassium phosphonate applications. Finally, restriction of human access to undisturbed sites is recommended to prevent further dispersal of the pathogen (Dawson and Weste 1985); however, these guidelines are not feasible to these human-made agro-silvo-pastoral systems. Other approach to reduce pathogen dispersal is through the control of nursery stocks used to reforestation, since there is strong evidence that *Phytophthora* dispersal and infested nursery stock are linked (Brasier and Jung 2003). Approaches described above present some limitations: selection of resistant hosts is a long-term run since it will take time to replace susceptible with resistant varieties or to improve resistance through genetic manipulation. *P. cinnamomi* suppression through products application would be demanding since the species is widespread in the Mediterranean region and will probably widen its distributions with the expected climatic alterations (Brasier and Scott 1994; Brasier 1996). Data from Tables 1, 2 and 3 indicated that cork and holm oaks appear to be moderately susceptible to *P. cinnamomi* infection. For this reason, and considering disease triangle, the occurrence of infection is strongly dependent on environmental characteristics that not only favors pathogen survival, but also reduce host resistance. Figure 2 shows that cultural practices were one of the factors associated with decline. Moreover, management practices affect soil properties in its chemical, biotic and physical characteristics (Vacca 2000; Soru et al. 2006; Moreno and Obrador 2007; Moreno et al. 2007; Azul et al. 2011; Schnabel et al. 2011), including alterations in soil compaction and effective depth. A recovery from decline after long periods of rain was referred in some holm oak stands when management practices that cause root damage, soil degradation, and lack of natural regeneration were minimized (Tuset and Sánchez in 2004; Solla et al. 2009). Diniz (1994) also point out that soil management could increase decline in stands sub-optimal for cork oaks vitality, thus cultural practices should be adapted to site characteristics. Stand management offers several possibilities in the control and prevention of cork and holm oak decline, since it interferes with several other site characteristics associated with host vitality and pathogen survival and is

one of the factors associated with decline that we effectively control.

Final considerations

Forest declines are considered a complex multifactorial phenomenon involving the combination of several factors. It is challenging to identify a cause that overcomes others, either because it may be related to other factors or because the proximate cause of death may mask the primary one. Following Manion's (1981) disease spiral concept, *P. cinnamomi* appears to act as a predisposing stress factor that, combined with other predisposing factors such as soil compaction, shallow soils, reduces cork and holm oak trees resilience, thus increasing their susceptibility to inciting and contributing stress factors, like drought or excess water events and other diseases (Fig. 3). The effect of *P. cinnamomi* appears to be a chronic root pruning, more severe in holm than in cork oaks, forcing the trees to expend more energy in the production of more fine roots. To succeed, trees should be located in soils favoring root expansion and with adequate nutrient and hydric conditions. Otherwise, trees may not be able to replace necrotic roots and, moreover, the use of limited resources for the defense system and for root reposition may limit their response to other adverse situations. The main difference between cork and holm oaks and highly susceptible species is probably a higher dependence of other unfavorable conditions to occur decline. Despite this, the role of *P. cinnamomi* in oak decline should not be ignored.

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