Endemic and Emerging Pathogens Threatening Cork Oak Trees: Management Options for Conserving a Unique Forest Ecosystem

Salvatore Moricca
Dipartimento di Scienze delle Produzioni Agroalimentari e dell'Ambiente (DISPAA),
Sezione di Patologia vegetale ed Entomologia, Università degli Studi di Firenze, 50144 Firenze, Italy

Benedetto T. Linaldeddu
Dipartimento di Agraria, Sezione di Patologia Vegetale ed Entomologia,
Università degli Studi di Sassari, 07100, Sassari, Italy

Beatrice Ginetti
Dipartimento di Scienze delle Produzioni Agroalimentari e dell'Ambiente (DISPAA),
Sezione di Patologia vegetale ed Entomologia, Università degli Studi di Firenze, 50144 Firenze, Italy

Bruno Scanu
Dipartimento di Agraria, Sezione di Patologia Vegetale ed Entomologia,
Università degli Studi di Sassari, 07100, Sassari, Italy

Antonio Franceschini
Dipartimento di Agraria, Sezione di Patologia Vegetale ed Entomologia,
Università degli Studi di Sassari, 07100, Sassari, Italy

Alessandro Ragazzi
Dipartimento di Scienze delle Produzioni Agroalimentari e dell'Ambiente (DISPAA),
Sezione di Patologia vegetale ed Entomologia, Università degli Studi di Firenze, 50144 Firenze, Italy

Cork oak (*Quercus suber*) is an evergreen oak tree native to southwest Europe and northwest Africa. The few relict areas of southeast Italy constitute the far eastern limit of the species (Beccarisi et al. 2010). Cork oak ecosystems include a mosaic of habitats spanning from open savanna-like formations to closed sclerophyll forests as a result of the long-term human presence and related activities in this area (Blondel 2006; Bugalho et al. 2011). These heterogeneous forest ecosystems cover over two million hectares in the western Mediterranean basin where they sustain a rich biodiversity of endemisms as well as representing an important source of income derived from cork production (Campos et al. 2008; Marañón et al. 1999).

Cork production is an additional source of income to farmers, supplementing that generated by traditional agricultural, silvicultural, and pastoral activities (Pinto-Correia 2000). Cork processing is a thriving industry that involves a number of small and medium sized enterprises and provides employment in less developed areas of southern Europe (Goncalves 2000). However, the progressive reduction in the market price of cork is contributing to a progressive abandonment of cork oak forests and subsequent shrub encroachment in several areas in southwestern Europe (Pinto-Correia 1993). Without proper management, these fragile ecosystems are quickly overgrown by Mediterranean matorral species, such as *Cistus* species, which in turn promote an increased risk of wildfires and loss of habitats and biodiversity (Acácio et al. 2009).

In contrast, high anthropogenic pressure, consisting of overgrazing and irregular cutting of firewood, is contributing to the degradation of cork oak ecosystems in some areas (Campos et al. 2007). Overall, the abandonment of traditional land management activities, associated with land use transformations, have led to a progressive loss in cork oak forests (Costa et al. 2011). In addition, during the last decades, tree mortality events have occurred with an increasing frequency in several cork oak forests in the Mediterranean basin, contributing to a further degradation of these woodlands (Brasier 1992; Costa et al. 2010; Franceschini et al. 1999).

Cork oak suffers from few major disease problems. In literature, more than 300 species of fungi and oomycota are reported on cork oak, of which at least 100 are pathogenic (Franceschini et al. 1993; Luque et al. 2000). Fortunately, very few are primary pathogens able to attack healthy tree tissues, the majority being opportunistic pathogens that colonize oak tissues when they have been previously weakened by abiotic or biotic factors (Luque et al. 2000). Recently, some species of opportunistic fungi have received greater attention, because they can colonize oak tissues as endophytes without inducing disease symptoms for a long time (Gonthier et al. 2006; Moricca et al. 2012). Healthy, unstressed trees normally manage to keep these endophytes under control, so that the trees do not suffer or exhibit symptoms, even though they are colonized (balanced antagonism) (Ragazzi and Moricca 2012; Schulz and Boyle 2005). However, when the trees become weakened by environmental stress factors, these fungi, initially confined, can colonize adjacent tissues, causing a progressive decline and eventually the death of the tree (Moricca and Ragazzi 2008; Saikkonen et al. 1998). There is some evidence to suggest that regional increases in the frequency and severity of droughts, combined with higher temperatures, are specifically selective for those cork oak pathogens that are most thermotolerant, and that some of these pathogens, combined with climate-driven physiological stress, then cause increasing decline and higher mortality rates in cork oaks (Desprez-Loustau et al. 2006; Picco et al. 2011).

Oak decline is commonly considered a multifactorial disease in which many interacting abiotic and biotic factors such as drought, frost, insect pests, and pathogens, variable in type, intensity, and

Corresponding author: Salvatore Moricca; E-mail: salvatore.moricca@unifi.it

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frequency even at site level are involved (Inácio et al. 2011; Linaldeddu et al. 2011; Moreira and Martins 2005; Ragazzi et al. 1995). The effects of these factors have long been synthesized in a theoretical model that hypothesizes the succession of three different types of factors predisposing, inciting, and contributing (Manion 1991). It has, however, been shown that pathogens belonging to the genera *Diplodia* and *Phytophthora* have had a prominent role in the decline and mortality of oak trees in a variety of contexts (Linaldeddu et al. 2014; Lynch et al. 2013; Perez-Sierra et al. 2013; Scanu et al. 2013).

The aim of this review is to analyze the recent advances achieved regarding the bio-ecology of the endemic and emerging pathogens that threaten cork oak trees with particular emphasis on the species more directly involved in the etiology of oak decline. Pathogens are dealt with according to the tree portions in which they mainly occur: the leaves, stems, and roots. The means to control the most deleterious agents are also discussed, with an emphasis on environmentally friendly control measures. Gaps in our knowledge of cork oak pathogens, their reproductive strategy, and dispersal ability within the cork oak range are outlined.

Leaf Pathogens

The most commonly observed leaf spot causing-agents of cork trees include *Discula quercina* (Fig. 1A), *Cystodendron dryophilum* (Fig. 1B), *Lembosia quercina* (Fig. 1C), and *Dendrophoma myriadea* (Fig. 1D). It is well known that leaf diseases can weaken trees by interrupting photosynthesis, respiration rate, and the metabolic pathways, and by impairing thermal regulation (Marçais and Desprez-Loustau 2014). However, to date, little information is available about pathogenicity, geographic distribution, oak host range, and genetic variability in any country of the main cork oak leaf pathogens. Another major gap in knowledge about cork oak-leaf pathogen interactions in natural ecosystems concerns the proximal mechanisms of leaf infection. In addition, for all these species except *D. quercina*, there are no nucleotide sequences available in public databases, and no ex-type cultures are known to exist.

The ascomycete *D. quercina* (Fig. 1A), known to cause anthracnose, shoot blight, and twig cankers on oaks in North America and Europe, is probably the species most studied (Hecht-Poinar and Parmeter 1986; Moricca and Ragazzi 2008, 2011; Ragazzi et al. 2002, 2007b). On cork oak, *D. quercina* causes dark brown-to-black leaf spots, coalescing into larger necrotic areas at the end of the growing season; sometimes it also causes twig cankers. At the physiological level, infection of *D. quercina* on cork oak modifies the normal balance of some metabolic processes, including stomatal conductance and photosynthesis (Linaldeddu et al. 2009b). *D. quercina* has been shown to produce in vitro several secondary bioactive metabolites, some of which are phytotoxic (Maddau et al. 2011). In autumn, this pathogen produces on leaves several black and erumpent acervular conidiomata, which are the main source of inoculum (Marras 1962a). The sexual phase (*Apiognomonia quercina*) develops very rarely on cork oak. In contrast, on deciduous oaks, the differentiation of perithecia is more common; in turkey oak, for instance, *D. quercina* usually overwinters as ascomata on fallen leaves, and during the growing season the sexual spores produce primary infections on the buds, shoots, and expanding leaves (Ragazzi et al. 1999). *D. quercina* also survives as an endophyte in the asymptomatic tissues of healthy and declining oak trees (Linaldeddu et al. 2011).

C. dryophilum causes characteristic, leathery-brown zonate spots with a distinct margin (Fig. 1B), whereas *L. quercina* causes typical, scab-like, dark and velvety spots (Fig. 1C). Attacks of both these fungi are reported in dense stands with an abundant overstory, where they cause a slow but gradual and sometimes total defoliation (Marras 1962a). Both pathogens differentiate their asexual reproductive structures in springtime (May-June): *C. dryophilum* on the lower leaf blade and *L. quercina* on the upper leaf blade, mainly in the center of spots. Most knowledge on the biology of *C. dryophilum* and *L. quercina* comes from Sardinia (Italy), and relatively little is known about these species in other Mediterranean countries.

D. myriadea causes a leaf-tip necrosis (Fig. 1D), mainly in autumn, when light-brown necrotic areas appear at the leaf tip; these areas have a distinct reddish-brown edge that distinguishes them clearly from the still healthy dark-green leaf. Symptomatic leaves look scorched and are easily recognized from afar. The fungus is fairly rare, but on the trees its infection may be severe. Pathogenicity tests on seedlings have confirmed the virulence of this pathogen (Luque et al. 2000).

Other leaf pathogens on cork oaks are *Erysiphe* spp. (previously reported as *Microsphaera alphitoides*), which causes powdery mildew, and the oak rust agent *Uredo quercus* (Marras 1962a). To date, there is little information on the ecological impact and role played by these leaf pathogens in the etiology of cork oak decline. All of these leaf pathogens are endemic to the Mediterranean region and do not require preventive or curative measures. Some are controlled by natural competitors. For example, the oak rust pathogen *U. quercus* is commonly controlled in nature by *Sphaerellopsis filum*, a nonspecific rust hyperparasite (Ragazzi et al. 2007a).

Stem, Branch, and Twig Pathogens

Several ascomycete fungi are reported in literature as agents of cankers and dieback of cork oak trees. These pathogens cause local infections on trunk, branches, and twigs, variable in severity and incidence. Since the early 1980s, some of these fungi have received increasing attention because they have consistently been associated

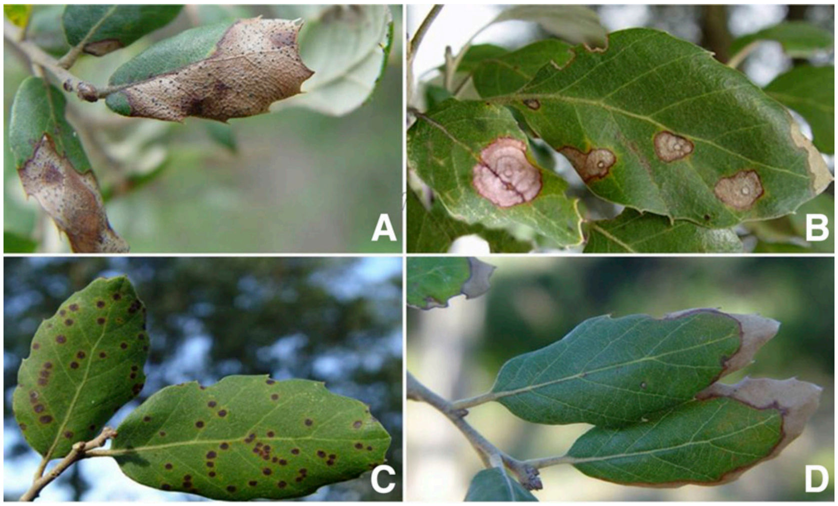

Fig. 1. Foliar diseases caused by some cork oak pathogens. **A,** leaf necroses induced by the anthracnose agent *Discula quercina*, with black acervuli that are prominent on the upper surface of the lesions. **B,** leathery-brown, necrotic leaf spots with a distinct, dark-line margin caused by *Cystodendron dryophilum*. **C,** small, scattered, black-to-velvety leaf spots with a regular margin caused by *Lembosia quercina*. **D,** leaf tip and marginal necroses, with distinct, reddish-brown edges produced by *Dendrophoma myriadea*.

with etiology of cork oak mortality in many countries (Franceschini et al. 1999; Luque and Girbal 1989).

Two species in particular, *Diplodia corticola* and *Biscogniauxia mediterranea*, were found to be the most widely distributed pathogens in declining cork oak forests; the first has been considered the most virulent cork oak pathogen (Linaldeddu et al. 2009b; Luque et al. 2000). Attacks of *D. corticola*, originally misidentified as *Diplodia mutila*, were reported on cork oak trees in Italy, Morocco, Portugal, Spain, and Tunisia (Alves et al. 2004). The pathogen also affects other Mediterranean oak species such as *Quercus afares*, *Q. canariensis*, *Q. coccifera*, and *Q. ilex* (Linaldeddu et al. 2009a, 2014; Tsopelas et al. 2010). In recent years, *D. corticola* has caused concern in the United States, where it colonized aggressively *Q. agrifolia*, *Q. rubra*, and *Q. virginiana* (Aćimović et al. 2016; Dreaden et al. 2011; Lynch et al. 2013). Despite the number of studies aimed at elucidating the taxonomy and pathogenicity of *D. corticola*, its evolutionary and geographical origins remain unresolved. Phylogenetic analyses based on ITS and *tef*1-α sequences of isolates from different countries revealed the existence of two distinct evolutionary lineages with a different geographic distribution (Linaldeddu et al. 2013). More recently, another canker-causing agent, described as *Diplodia quercivora*, phylogenetically very closely related to *D. corticola*, was reported on declining *Q. canariensis* trees in Tunisia (Linaldeddu et al. 2013) and on *Q. virginiana* in Florida (Dreaden et al. 2014a). These two taxa were accommodated in the subclade 4, a distinct group within *Diplodia* genus, which includes only species known primarily as oak pathogens (Alves et al. 2014). The two species can be distinguished from each other and from other *Diplodia* species by morphology and DNA sequence polymorphism. A PCR-RFLP-based assay has been recently developed to rapidly identify isolates belonging to *D. corticola* or *D. quercivora* without the need for sequencing (Dreaden et al. 2014b). Given the virulence evidenced by artificial inoculation experiments on oak logs, *D. quercivora* represents a new serious risk for the health of cork oak forests (Linaldeddu et al. 2013).

D. corticola infections limit both the vitality and the productivity of cork oak trees. The most common symptoms *D. corticola* causes on cork oak trees are sunken cankers on collar, trunk, and branches. These cankers often exude a dark brown sap, giving them the appearance of bleeding, which gradually dries to a blackish gluey mass on the bark (Fig. 2A). The wood becomes discolored and the vascular system necrotic. The symptoms' appearance on the foliage (wilting) suggests that phytotoxic metabolites are involved in the host-pathogen interaction (Fig. 2B). Indeed, *D. corticola* is able to produce in vitro a broad array of secondary metabolites, some of which, including diplopyrone, diplofuranones A and B, diplobifuranylones A and B, and the SS-enantiomer of sapinofuranones B, C and D, show phytotoxic, antifungal, and antibacterial activities (Masi et al. 2016).

Pycnidia of the fungus differentiate on all aerial tree organs infected, including acorns (Fig. 2C). Conidia (Fig. 2D) are dispersed by wind, water, or insect vectors. However, little is known about the inoculum potential, pattern of seasonal spore release, and abiotic factors favoring *D. corticola* infections in cork oak forests. Linaldeddu et al. (2010) found that natural infections of *D. corticola* on cork oak seedlings, exposed monthly for one year to the natural inoculum pressure of the pathogen in a declining cork oak forest, were variable during the year with two peaks of infections, one in May and one in September. Recently, it has been demonstrated that some wood-boring insects act as spore vectors for *D. corticola*. Inácio et al. (2011) found that the oak pinhole borer (*Platypus cylindrus*) is a vector of *D. corticola* which, together with some *Raffaelea* species, accounted for more than 90% of fungi present in the gut and in mycangia of this insect. More recently, Kostovcik et al. (2015) found that *D. corticola* is one of the fungi most frequently isolated from mycangia of two invasive insects: *Xyleborus affinis* and *Xylosandrus crassiusculus*, collected from various habitats across Florida. Interestingly, *X. crassiusculus* is considered a high-risk quarantine pest in Europe and has recently been reported from Italy (Pennacchio et al. 2003).

Biscogniauxia mediterranea has emerged as an opportunistic and potentially invasive fungal pathogen. The frequency of its attacks on oaks has increased significantly over the past decades in the Mediterranean area. This increase in infection is associated with high mortality rate especially of young cork oak trees and it seems directly related to the increase in exceptionally dry and warm years (Desprez-Loustau et al. 2006; Henriques et al. 2012). Although several studies have demonstrated that *B. mediterranea* is less aggressive than *D. corticola*, it is the fungal species most commonly associated with declining oak trees especially during the final stage of the disease and contributes to accelerating tree decline and eventually tree death (Martín et al. 2005). The life cycle of *B. mediterranea* on cork oak includes first a latent endophytic phase, then a parasitic phase, and lastly a saprophytic phase (Franceschini et al. 2002). This fungus can persist as an endophyte in all of the aerial organs of cork oak trees. The endophytic behavior of

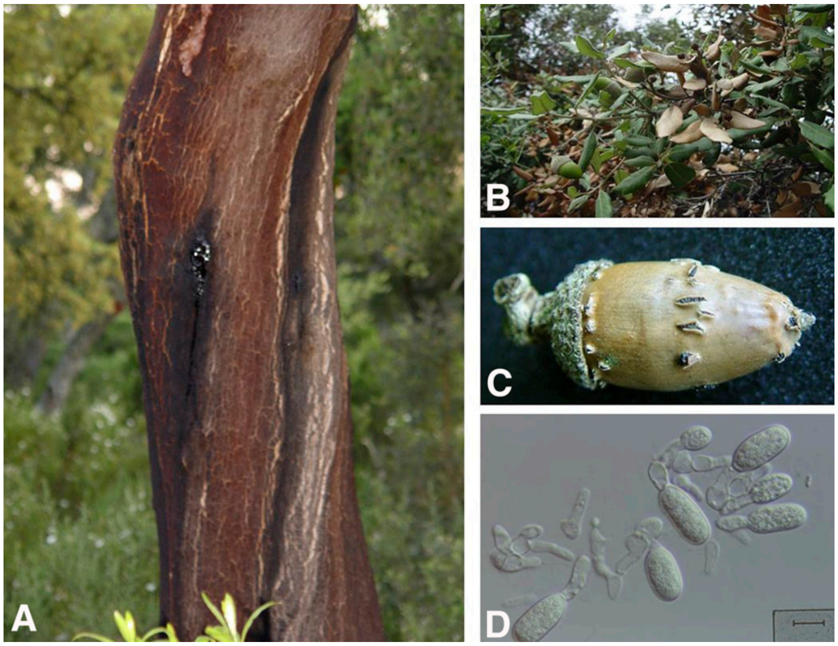

Fig. 2. Symptoms caused by *Diplodia corticola* on cork oak. **A,** trunk with necrosis and a black, mucilaginous exudate. **B,** wilting and death of shoots. **C,** acorn with erumpent pycnidia. **D,** particular of conidiogenous cells and conidia, bar = 12.5 µm.

B. mediterranea is influenced by changes in the host physiology with some stress factors, especially water stress, that can favor oak tissue colonization by this pathogen and promote its switch from an endophytic phase to a parasitic phase (Linaldeddu et al. 2011).

B. mediterranea is a necrotrophic pathogen, whose infections induce extensive inner bark and xylem necrosis associated with blackish exudation from the outer bark. *B. mediterranea* produces several phytotoxic metabolites namely biscopyran, phenylacetic acid, and 5-methylmellein (Evidente et al. 2005). However, limited information is available on the specific role of these compounds in the development of disease symptoms. On infected tissues, the fungus develops the characteristic charcoal cankers (Fig. 3A).

These cankers arise when the bark is torn by the black carbonaceous stromata exerting pressure in the ritidome. At that stage (saprophytic phase on dead tissues), *B. mediterranea* increases its biomass by producing great numbers of propagules (ascospores and conidia) that are easily dispersed by wind (Fig. 3B), water, and insects (Franceschini et al. 2002; Inácio et al. 2011). Precipitation (a period of three consecutive days with precipitation above 0.5 mm) is a crucial condition for ascospore release, whereas wind is the main way of dispersal (Henriques et al. 2014a). Several insects also contribute to the dispersal of this fungus in cork oak forests, their action being important not only as vectors of inoculum, but also because the wounds they cause can act as an infection point (Martín et al. 2005). The main insects known to be vectors of *B. mediterranea* are *Agrilus* spp., *Platypus cylindrus*, and *Tropideres* spp. (Inácio et al. 2011).

B. mediterranea has been recently expanding its incidence, geographical distribution, and host range, proving to be an invasive pathogen favored by climate change (Desprez-Loustau et al. 2007; Jurc and Ogris 2006; Mirabolfathy et al. 2011; Ragazzi et al. 2012). The high level of genetic variability of this fungus might account for its plasticity and adaptability to variable environmental conditions (Henriques et al. 2014b).

The list of invasive fungi of cork oak trees is increasing. In addition to *B. mediterranea* and *D. corticola*, new and "emerging" fungal pathogen include the canker agents *Coryneum modonium* (Bragança et al. 2013), *Neofusicoccum parvum* (Linaldeddu et al. 2007a), and several Ophiostomatoid fungi of the *Raffaelea* genus (Inácio et al. 2012).

Root Pathogens

Species in the genus *Phytophthora* (oomycetes) are arguably the most destructive root pathogens of cork oak. Since the early 1990s, *Phytophthora cinnamomi* has had a major impact in cork oak decline in Mediterranean European countries, including France, Italy, Spain, and Portugal (Brasier 1992; Robin et al. 1998; Scanu et al. 2013). Knowledge about the occurrence of the pathogen in western Africa is very scarce (Brasier 2003). The situation is in need of investigation, especially in view of the widespread distribution of cork oak in the region and of the recent report of *P. cinnamomi* on nursery plant material in Morocco (Touati et al. 2014).

P. cinnamomi infects trees growing singly or in groups (Fig. 4A), invading the roots, collars, and trunks, from which a black exudate often oozes (Fig. 4B). Infected trees show extensive loss of both lateral, small, woody roots and fine roots. Consequently, the root system is hampered in absorbing and transporting water and nutrients, and this causes plant death. Slower growth is accompanied by leaf yellowing, microphyllia, crown thinning and development of epicormic shoots, usually followed by dieback of the entire tree (Camilo-Alves et al. 2013). Depending on the site and climate conditions, trees can die suddenly in one or two seasons, or exhibit a slow decline, which may occur for several years (Camilo-Alves et al. 2013). *P. cinnamomi* thrives in cork oak woodlands crossed by water courses, in lowlands with stagnant water, and wherever water abounds (Moreira and Martins 2005). Its successful propagation and dissemination is due to the production of a large number of zoospores, which are differentiated inside the sporangia and released in the soil water. *Phytophthora* zoospores are motile and are chemiotactically attracted to the roots, where they encyst and secrete a number of proteins that glue them to the root surface and facilitate the infection (Hardham and Cahill 2010).

Fig. 3. *Biscogniauxia mediterranea* on cork oak. **A,** characteristic, black stromata (charcoal canker) erumpent through the bark. **B**, a sporulating canker on the lower trunk: spore masses, released in the form of a tan cloud, are dispersed by air currents.

The center of origin of *P. cinnamomi* is unknown, although Papua New Guinea seems the most likely center, given the high level of genetic diversity found among isolates of *P. cinnamomi* in this tropical region (Old et al. 1984). Although *P. cinnamomi* is probably native to tropical regions, this pathogen has become invasive in many Mediterranean areas characterized by prolonged and severe drought conditions (Shearer et al. 2004). This ecological adaption is due to the production of long-term survival structures, such as stromata-like hyphal aggregations, thick-walled chlamydospores, and selfed oospores on roots and root debris, enabling the pathogen to survive over unfavorable seasons such as the long, hot, and dry summers typical of Mediterranean ecosystems (Jung et al. 2013, 2016).

Other *Phytophthora* species, namely *P. quercina*, *P. gonapodyides*, and *P. psychrophila*, have been recently associated with declining Mediterranean oaks in Italy and Spain and their pathogenicity has been demonstrated on *Quercus faginea*, *Q. ilex*, and *Q. suber* (Linaldeddu et al. 2014; Pérez-Sierra et al. 2013; Seddaiu et al. 2014).

The oomycete *Pythium spiculum* was frequently isolated from declining cork oak roots and rhizosphere in southern Iberia (Serrano et al. 2012a). *P. spiculum* is often found simultaneously with *P. cinnamomi* in oak stands in southwestern Spain and southern Portugal. Owing to their different asexual reproductive structures and therefore soil water requirements, the two pathogens may be most active in different seasons and thus vicariant in pathogenicity, with a low level of competition between them for colonization of oak roots (De Vita et al. 2011).

Other root pathogens of cork oak include *Armillaria* spp., which cause plant growth reduction, wood decay, and mortality (Marçais and Bréda 2006). The identification of *Armillaria* spp. was originally based on morphological traits and mating tests. Accurate DNA-based techniques were recently developed for identifying *Armillaria* species (Mulholland et al. 2012). Given the variable degrees of pathogenicity of *Armillaria* species (Sicoli et al. 2002), a fast and accurate identification of these taxa is crucial.

Some species of *Armillaria*, like *A. mellea*, *A. gallica*, and *A. tabescens*, were found over the years to be important factors in the decline of oaks throughout Europe and North America (Brazee and Wick 2009; Marçais and Bréda 2006). However, reports of *Armillaria* infections on cork oak are sporadic (Bragança et al. 2004; Marras 1962b), and therefore the actual contribution of these pathogens to cork oak decline and mortality remains unresolved as does the true identity of the species involved.

Cork Oak Forest Management: What to Do and What Not to Do

Management options for cork oak forests should consider the specific economic, environmental, and social context, taking into account the characteristics of the forest and its ability to produce goods. Currently, the main cork oak goods correspond to the production of cork and occasionally firewood and acorns. Cork is extracted for the first time when the tree is 25 to 30 years old and about 60 cm in circumference at breast height, and thereafter usually at intervals of 9 to 10 years, though it can take up to 14 years for the cork on the trees to reach industrial size (Carvalho and Graça 2009). The effect of cork stripping on tree health has always been a concern for the sustainable management of cork oak forests (Correia et al. 1992). In addition to great water loss, cork stripping often causes dangerous wounds that represent the pathway for many fungi. In particular, extraction wounds act as a significant entry way for *Diplodia corticola* (Luque and Girbal 1989).

Two studies conducted recently in Spain showed the effectiveness of benzimidazole fungicides (thiophanate-methyl and carbendazim) in reducing the incidence and severity of *D. corticola* cankers under field conditions (Luque et al. 2008; Serrano et al. 2015). However, the increasing restriction of fungicides for the control of fungal diseases in agriculture and forestry prompts an effort to identify new environmentally friendly control strategies. Promising results for the control of oak pathogens have been achieved in in vivo and in vitro bioassays using mutualistic endophytic fungi of the *Trichoderma* genus (Linaldeddu et al. 2007b). In particular, one endophytic strain of *Trichoderma citrinoviride* from cork oak was found to produce in liquid culture a mix of polypeptide antibiotics (peptaibols) that were very effective against seven forest tree pathogens, including *D. corticola* (Maddau et al. 2009).

Trichoderma species have been extensively studied for their antagonistic properties (Howell 2003). However, only recently, attention has turned to endophytic *Trichoderma* species of woody plants with a high biocontrol potential (Mejía et al. 2008).

Despite research efforts to find effective fungicide-based or biological control strategies, preventive measures should take priority in maintaining the health of cork oak trees. This both because cork oak stands are largely subjected to human activities—pesticide use is in these unique agroforestry systems a source of concern for the environment and the health of livestock and people—and because most of the above options for the control of *D. corticola* and the other fungi infecting wounds lack replication in different situations/areas to allow generalization and confidence about their effectiveness in the short- to medium-long term. Appropriate preventive measures would include: the extraction of cork to be carried out only by experienced personnel; an increase in the use of specific machines; the promotion of technical courses for cork extractors on the application of the best available techniques for minimizing tree wounds (Luciano and Franceschini 2006); and, finally, the promotion of training courses for stakeholders (plant owners, nursery personnel, foresters, etc.) on an

Fig. 4. Symptoms caused by *Phytophthora cinnamomi*. **A,** sudden death of a group of mature cork oak trees. **B,** typical blackish exudates at the base of an infected cork oak tree.

integrated disease management of cork oak forests, requiring these special ecosystems a delicate balance between human needs and nature. All these strategies could help curtail infectious diseases and reduce and rationalize the use of chemical pesticides in cork oak stands.

Cork oak stands vary widely in composition and density, and these two variables directly influence the impact and spread of diseases caused by the Pythiaceae (*Phytophthora* and *Pythium*). In Sardinia (Italy) and northeastern Spain, cork oak grows in pure or mixed stands or in closed forests with a density of 600 to 1,000 trees/ha whereas in Portugal and the rest of Spain it is often found in open, savanna-type woodlands (montado/dehesa) with a density of 40 to 160 trees/ha (Acácio et al. 2007). In the closed forests, the understory is less varied than in the open woodlands (Pérez-Ramos et al. 2008). The predominant shrubs of the understory are *Arbutus unedo*, *Cistus* spp., *Crataegus monogyna*, *Erica* spp., *Myrtus communis*, *Lavandula* spp., *Phillyrea latifolia*, *Pistacia lentiscus*, *Rosmarinus officinalis*, and *Thymus* spp., while grasses include mainly species such as *Allium triquetrum*, *Asphodelus albus*, *Bellis sylvestris*, *Conopodium capillifolium*, *Galium aparine*, and *Scilla monophyllos* (Pérez-Ramos et al. 2008). Some of these plant species were found to be infected with *P. cinnamomi*, although usually without showing disease symptoms. Species like *Calluna vulgaris*, *Cistus* spp., and *Ulex* spp. sometimes die due to root infection and Moreira and Martins (2005) suggested to use these species as indicators of the occurrence of *P. cinnamomi* in active disease sites. Mediterranean shrubs and grasses may provide an important basis for the production and survival of pathogen's inoculum, thus acting as reservoirs for *P. cinnamomi* in infested sites. This was demonstrated for the leguminous *Lupinus luteus* commonly found in dehesa ecosystems in southern Spain (Serrano et al. 2010). Shrub clearing to facilitate cork extraction reduces understory composition and diversity (Pérez-Ramos et al. 2008), and this may have the indirect benefit of reducing *P. cinnamomi* attacks, as suggested for other *Phytophthora* species in Europe (Fichtner et al. 2011).

Phytophthora diseases are exacerbated in cork oak stands simultaneously exploited for agriculture and grazing, as it often occurs in the sparse montado/dehesa (Camilo-Alves et al. 2013). Since grazing animals may be important vectors of *Phytophthora* species, grazing should be prohibited wherever these oomycetes are known or suspected to occur, especially at times when the soil is wet (Li et al. 2014). The eradication of root pathogens such as *Phytophthora* and *Pythium* species once they are established in a new environment is difficult, if not impossible, to achieve (Brasier 2008). For this reason, measures to mitigate the impact of these pathogens in cork oak stands should focus essentially on prevention/management and include: keeping people, pets, and grazing animals off contaminated areas; preventing, where possible, soil and water movement out of contaminated areas by means of suitable sewage control interventions; disinfecting shoes, tools, and vehicles that may have come in contact with contaminated soils; and using healthy plant material. The above strategies could be possibly combined, in some situations, with chemical and biological control. Recently, the use of calcium amendments and soil biofumigation with *Brassica carinata* commercial pellets proved effective in the control of *P. cinnamomi* infections in the dehesa agroforestry systems (Morales-Rodríguez et al. 2016; Serrano et al. 2012b). According to Fernández-Escobar et al. (1999), oak decline can be controlled by trunk injections with potassium phosphonate, which even at low concentrations triggers resistance. Phosphonate can also be applied as a soil drench, a leaf spray, or a trunk spray (Giblin et al. 2007).

In order to provide an overview for ready and easy reference, serving also for those who are not plant health professionals, Table 1 summarizes the main preventive and/or curative measures against the most important pathogens of cork oak, grouped according to the tree organ on which they mainly occur. Readers wishing to find out more about specific topics should consult the literature cited.

Impact of Climate Change on Cork Oak Forests

Global warming has become a common driver of forest decline worldwide (Allen et al. 2010). Climate change in the Mediterranean region is mainly characterized by a gradual rise in average temperatures plus an overall reduction in annual rainfall, which also becomes more irregularly distributed across the seasons and over the years, resulting often in extended drought periods (Giorgi and Lionello 2008).

The changing climate may affect cork oak stands by modifying tree growth and mortality as well as cork production and quality (Besson et al. 2014; Carnicer et al. 2011; Oliveira et al. 2002). In particular, cork growth has been shown to be reduced by drought and high temperatures (Caritat et al. 2000). To maintain the economic and ecological value of cork oak woodlands under climate constraints, it is crucial to adopt adaptive management strategies. Palma et al. (2015) showed that adaptation of forest management by optimizing cork extraction schedule, reducing debarking surface,

Table 1. The main pathogens of cork oak, with the symptoms they cause and recommended control measures

Category and species	Symptoms	Control measures
Leaf pathogens		
Apiognomonia quercina	Anthracnose, shoot blight, and twig cankers	Cutting symptomatic branches or twigs; burning/removing infected plant residues such as fallen leaves, twigs, and branches
Cystodendron dryophilum	Zonate spots	Usually do not require control measures
Dendrophoma myriadea	Leaf tip necrosis	Usually do not require control measures
Lembosia quercina	Scab-like, dark velvety spots	Usually do not require control measures
Stem, branch, and twig pathogens		
Biscogniauxia mediterranea	Charcoal canker with carbonaceous, perithecial stromata erupting through the bark	Cutting symptomatic branches or trees; removing plant material with black stromata (charcoal cankers)
Diplodia corticola	Sunken cankers associated with wedge-shaped necrotic sectors	Minimizing bark injury during cork extraction; cutting symptomatic branches; burning/removing infected plant residues; fungicide treatments
Neofusicoccum parvum	Sunken cankers associated with wedge-shaped necrotic sectors	Minimizing bark injury during cork extraction; cutting symptomatic branches
Collar and root pathogens		
Armillaria mellea	Root and collar rot, foliar wilting	Removing infected trees, stumps, large roots, and wood residues
Phytophthora cinnamomi	Root and collar rot, bleeding cankers, sudden death	Potassium phosphonate trunk injections; calcium amendments and soil biofumigation
Pythium spiculum	Root rot	Calcium amendments and soil biofumigation

and increasing tree density could increase cork productivity under future climate change. However, given the heterogeneity of cork oak forests, the promotion of long term sustainable management practices and proactive measures based on afforestation efforts aimed at maintaining biodiversity and ecosystem services should be assessed at local or regional scale (Berrahmouni et al. 2009; Hidalgo et al. 2008).

The change in climate not only affects cork oaks, but also many of the pathogens of cork oak, and the interaction of these pathogens with their host. However, different pathogens may be affected by climate change in very different ways, and hitherto our understanding of how particular pathogens are managing to adapt to climate change is limited (Desprez-Loustau et al. 2007).

Temperature, rainfall, relative humidity, amount of light, leaf wetness, soil moisture, solar radiation, and air turbulence are just some of the variables affecting pathogen survival and infectivity. In southern Portugal and Spain, where the oomycete *P. cinnamomi* is a major factor in cork oak decline, it has been shown that the alternation of prolonged droughts and rainy periods, combined with adverse site conditions (infertile soils with lower levels of phosphorus, poorly drained soils) and a microclimate conducive to disease (e.g., stands located in south-facing hilly areas) create ideal conditions for the pathogen to thrive and deploy its virulence (Moreira and Martins 2005).

Given the current projections for climate change, with increasing mean temperatures and frequency of climatic extremes such as drought, floods, and storms in Europe, a proliferation of *Phytophthora* root rots may be expected, thus increasing the instability and vulnerability of oak forest ecosystems (Brasier 1996). It has been predicted that increasing temperatures will lead to higher annual rates of survival for *P. cinnamomi* inoculum, resulting in a potential range expansion of the pathogen along the western coast of Europe of one to a few hundred kilometers eastward from the Atlantic coast within one century (Bergot et al. 2004).

Moreover, strong physiological stress limits the vigor of trees and predisposes them to parasite attacks. Higher rates of infection by pathogenic endophytes such as *B. mediterranea* have been associated with cork oak decline when this is accompanied by persistent drought (Linaldeddu et al. 2011). The ecological impact of xylariaceous fungi has clearly increased in the Mediterranean area on several forest tree species in connection with exceptionally dry years (Desprez-Loustau et al. 2006; La Porta et al. 2008). Further research is needed to establish how higher temperatures and drought will affect the species-specific traits and population dynamics of a number of cork oak pathogens.

Conclusions

In this review, we have analyzed the role of endemic and emerging pathogens that cause cork oak decline and mortality. Overall, there is a scarce literature on cork oak pathogens compared with other forest tree species. Studies in the last few decades on pathogenic members of the *Phytophthora* genus and of the Botryosphaeriaceae and Xylariaceae families have partially filled the gap. Moreover, research conducted in different countries in Africa, Europe, and North America has contributed to expanding knowledge about the pathogenicity, epidemiology, biology, invasiveness, and management of some of these pathogens in different oak forests (Dreaden et al. 2014a; Kostovcik et al. 2015; Linaldeddu et al. 2013; Lynch et al. 2013; Morales-Rodríguez et al. 2016; Moreira and Martins 2005; Serrano et al. 2015). Detailed and modern morphological descriptions coupled with DNA sequence data currently available in public databases are facilitating the identification of taxa (Martin et al. 2014; Phillips et al. 2013). Novel DNA-based diagnostics are contributing to a more rapid and accurate detection of pathogens from symptomatic and asymptomatic oak tissues (Moricca and Ragazzi 2000).

The recent scientific evidence suggests that the theoretical model of Manion (1991) on the succession of events and factors (predisposing, inciting, and contributing) involved in oak decline cannot explain thoroughly the causes that drive the onset of the decline and mortality events. New findings emphasize how some emerging pathogens, many of which are endemic, may act synergistically to drive the rapid devastation of extensive oak ecosystems (Linaldeddu et al. 2014).

These novel decline scenarios indicate that in the future only through a combined study of all the symptoms of oak trees (and not limited to those associated with a specific group of pathogens as has often been done in the past in which agents of root rot, cankers and dieback, and leaf diseases were studied separately on the basis of the specific skills of each researcher) will it be possible to achieve an accurate diagnosis of the phenomenon and consequently develop appropriate control strategies. In the same way, it will be important to consider that primary pathogens may themselves be affected directly by climate change and indirectly by host physiology adaptations.

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Salvatore Moricca

Benedetto Teodoro Linaldeddu

Beatrice Ginetti

Bruno Scanu

Antonio Franceschini

Alessandro Ragazzi

Salvatore Moricca is an associate professor in the Department of Agri-food Production and Environmental Sciences, Plant Pathology and Entomology Division, at the University of Florence, Italy. He received his Ph. D. from the same university. He has been involved in studying the role of fungal and oomycete pathogens in forest ecosystems, the etiology of complex diseases, and the biology and life-history traits of rust pathogens, from pathogenesis to in vitro culture. His research, teaching, and outreach programs focus on pathogen detection, surveillance, and control, with an emphasis on the bio-ecology of invasive species in forest stands in relation to anthropogenic disturbance and climate change. He served as an independent reviewer for research proposals submitted to European Commission and other international research funding agencies. He serves as editor for scientific journals and as deputy coordinator of the IUFRO 7.02.05 – "Rusts of forest trees" Working Group. He is a fellow of the American Phytopathological Society, the British Society for Plant Pathology, the Italian Society for Plant Pathology, and the Mediterranean Phytopathological Union.

Benedetto Linaldeddu is a research fellow at the Department of Agriculture, University of Sassari, Italy. He graduated in agricultural science from the University of Sassari in 2001 and received his Ph.D. in plant pathology from the University of Bari in 2006. His main areas of interest focus on new or unusual plant diseases caused by invasive pathogens belonging to Botryosphaeriaceae and Diatrypaceae families. This research has led to a significant expansion of scientific knowledge about the diversity, ecological impact, epidemiology, taxonomy, and phylogeny of these pathogens, including the description of several new species and evolutionary lineages. He was awarded the Antonio Ciccarone Prize in 2006 for his research in plant pathology by the Mediterranean Phytopathological Union.

Beatrice Ginetti obtained her Ph.D. in agricultural microbial biotechnologies from the University of Florence at the Department of Agri-food Production and Environmental Sciences, Plant Pathology and Entomology Division, in 2013. She dealt with the identification and epidemiology of the introduced alder rust pathogen *Melampsoridium hiratsukanum* in the Italian Alps. She investigated the role and impact of fungal endophytes in the decline of forest tree species in urban parks and in natural areas. Her research currently focuses on the study of *Phytophthora* spp. in forests and in nurseries. She identified a number of *Phytophthora* species previously unreported from Italy, including the newly described *Phytophthora acerina*. Her current work spans from field inspection for pathogen detection and identification to accurate pathogen identification and classification in the laboratory by means of traditional and molecular methods.

Dr. Bruno Scanu received his Ph.D. in plant pathology at the University of Sassari, Italy, in 2011, and is currently working as research fellow in the Division of Plant Pathology and Entomology of the same university. His research focuses primarily on forest tree diseases with particular emphasis on those caused by the oomycete genus *Phytophthora*. His interests include the ecology, pathology, taxonomy, and phylogeny of new and unusual *Phytophthora* species, their spread and impact on natural ecosystems, plantation forestry, horticulture, and plant production nurseries. His recent research involves the management and control of *Phytophthora* diseases in Mediterranean forests.

Antonio Franceschini is professor of plant pathology at the University of Sassari. He graduated in agricultural science from the University of Sassari in 1971. He is currently coordinator of the section "oak pathogenic fungi" of the working group "Integrated Protection in Oak Forest" of the International Organization for Biological Control (IOBC), West Palearctic Regional Section. His research activity focuses on the ecology, biology, and physiology of endophytic and pathogenic fungi, with particular emphasis on the species involved in the etiology of oak decline. More recently, his research activity has been addressed to the detection and identification of *Phytophthora* species in forests and nurseries in Sardinia, Italy. His research activity is documented by more than 200 scientific papers in national and international journals.

Alessandro Ragazzi is professor of Forest Pathology in the Department of Agri-food Production and Environmental Sciences, University of Florence, Italy, and past president of the degree course in tropical agricultural sciences. He is currently responsible for the Plant Pathology and Entomology Division of the above mentioned department, and serves as editor-in-chief of the Italian Journal of Mycology. His research and extension interests are in the biology and epidemiology of pine rusts, the biology of *Botryosphaeria* spp., the study of oak decline, and the assessment of the role of microorganisms (pathogens and endophytes) in the etiology of complex diseases. Recently, his interests have turned to the study of alien pathogens and the role of climate change.

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