



# The Involvement of *Phytophthora* Root Rot and Drought Stress in Holm Oak Decline: from Ecophysiology to Microbiome Influence

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## Abstract

**Purpose of Review** Holm oak is a relevant species, both for its distribution and ecological importance. Among the risks looming over this species, oak decline—influenced by extreme climatic events, and alien-invasive species—is considered the main factor causing the loss of holm oak in Mediterranean open woodlands. The aim of this review is to identify and summarize the effects of drought and pathogen root rot, focusing on tree physiology, and the relationship between the stressors (biotic and abiotic) and the tree response.

**Recent Findings** Symptoms of root rot are often associated with drought. However, it has been shown the presence of a differential response to root rot and severe drought is related with general defence mechanisms triggered by the plant. Soil microbiota has also been shown to be a key factor influencing health status and soil pathogen abundance. The application of next-generation sequencing techniques to forest pathology allows us to study complex relationships between soil, plant and microorganisms.

**Summary** Tolerance of holm oak against *Phytophthora cinnamomi* root rot is related to specific hydric and photosynthetic mechanisms that differ from those associated with drought. This response involves changes in the metabolism of the photosynthetic organs of the plant which can be linked with changes in functional traits. Studies of the soil microbiome have identified several pathogens, apart from *P. cinnamomi*, involved in holm oak decline, and the relevance of key fungal species in the management of this syndrome. In this regard, the presence of beneficial microorganisms such as *Trichoderma* spp. or ectomycorrhizae influences the physiological status of trees affected by root rot.

**Keywords** Climate change · Drought · Holm oak · Physiology · *Phytophthora* spp. · *Quercus* spp.

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## Introduction

### Oaks worldwide

There are few tree genera so widespread and linked to human activities as oaks. The genus *Quercus* represents the most diverse genus of the Fagaceae family in the Northern Hemisphere, comprising more than 400 species [1] present in a wide geographical and phytoclimatic range [2••]. Oaks have accompanied humans for millennia, providing a large amount of goods and services, both environmental and socio-economic and thus are integrated in the culture of different civilizations of the Northern Hemisphere as iconic trees [3]. The genus includes temperate species, such as *Quercus robur* L. and *Quercus petraea* (Matt.) Liebl, tropical species, such as *Quercus oleoides* Schldl. & Cham., and xeric ones found in semi-arid or even desertic ecosystems, such as *Quercus ilex* L., *Quercus*

*coccifera* L., *Quercus virens* Aiton or the extremely drought-adapted *Quercus mohriana* Buckley ex Rydb.

Schlerophyllous perennial and semi-deciduous species represent the dominant oaks in the Mediterranean climate zones of the Northern Hemisphere, including Mediterranean European and North-African countries and the southwest of North America [4]. Among them, the holm oak (*Quercus ilex* L.) is the most widespread species in the Mediterranean basin, accompanying human activities since the Neolithic period. Holm oak forests are currently a key element in the ecological and socio-economic sustainability of forest ecosystems in this area, occurring in very contrasting habitats throughout the Mediterranean countries. However, one thing that most of the Mediterranean oak ecosystems have in common is that their distributions lie in areas with high human population levels [5]; thus, they are of high ecological interest in the study of the effects of global change on natural ecosystems [6].

The configuration of holm oak forest in the Mediterranean basin presents a wide variety. In France, Central and Northern Italy, Northern and Western Spain, and mesic areas of Northern Morocco and Tunisia, the species can be found forming close forests of tall trees with a scarce understory layer of *Q. ilex* subsp. *ilex*, very different to the dense forests with a garrigue or maquis formation which can be found in the Eastern side of the Iberian Peninsula, north of Morocco and the south of Italy, or to the Mediterranean open woodlands of *Q. ilex* subsp. *ballota* named *dehesas* (Spain) or *montados* (Portugal), typical of the southwest of the Iberian Peninsula (Fig. 1). *Dehesas* and *montados* are defined as savannah-like ecosystems with low canopy cover accompanied by grass or shrub understory, being one of the most important agroforestry ecosystems in Europe, occupying more than 3.0 mill ha in Iberian Peninsula, of which 2.2 mill ha comprise holm oak stands [8, 9].

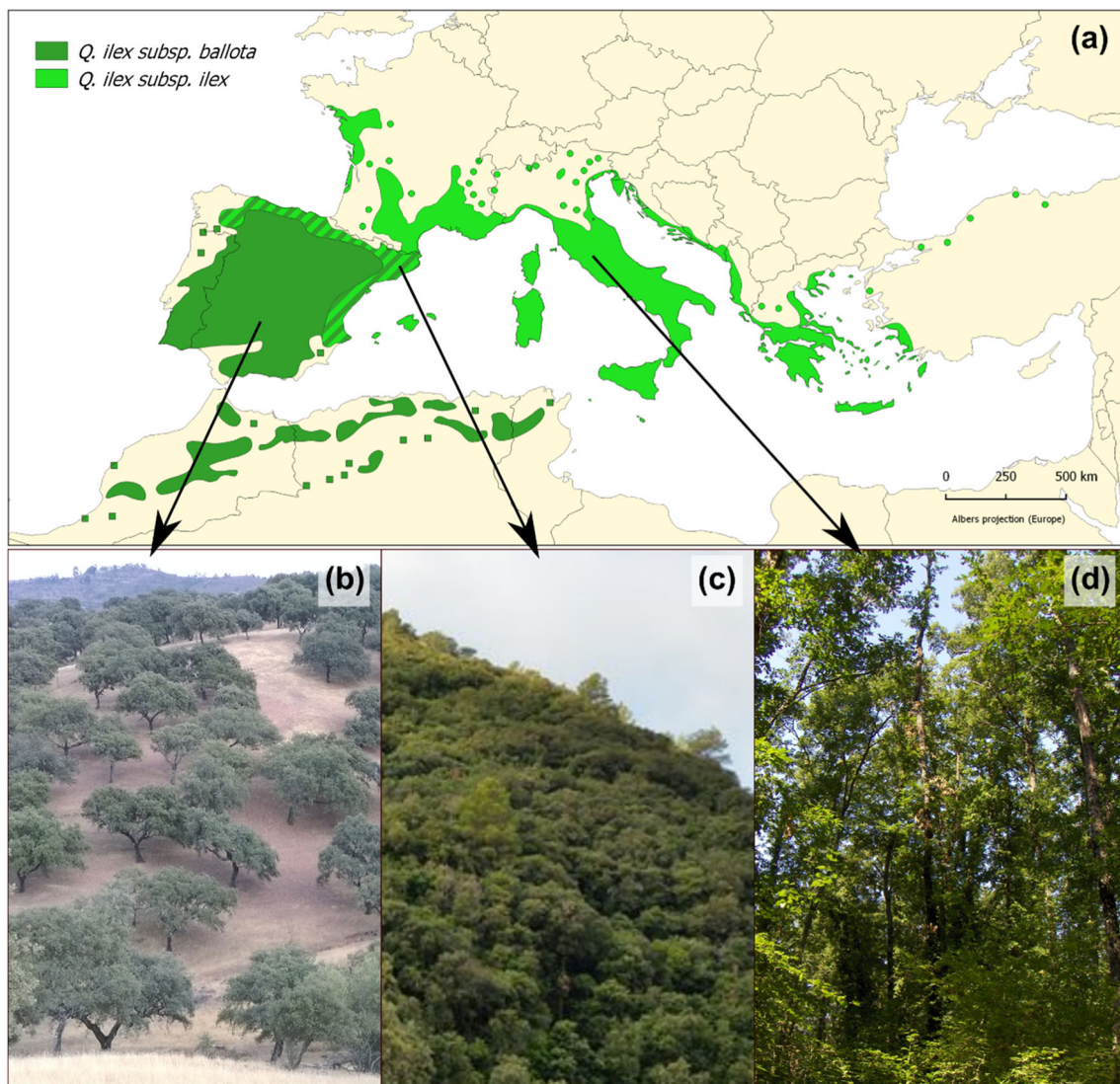
This kind of ecosystem could be found also in other Mediterranean countries as for example in Southern Italy and Greece. It represents, in all the cases, an important socio-economic ecosystem that is highly anthropized and directly related to the economic sustainability of rural areas [10]. The tree layer of *dehesas* contributes to the production of the farms (food, fuel, and livestock protection) [11] and provides shelter for a high diversity of fauna and microorganisms, soil erosion prevention, and landscape conservation, playing a key role in the conservation of biodiversity, while also acting as a first barrier against desertification—both in the southwest of the Iberian Peninsula and in the north of Morocco and Tunisia [12–14].

Thus, the ecological and economic importance of the holm oak has been recognized in several works, but the risks looming over this species today must be considered a big threat to the biodiversity and sustainability of Mediterranean ecosystems in several places [15–19]. The holm oak forests are currently threatened by climate change, land use policies

and management, and alien-invasive pathogens [13•, 20]. In this review, we pursue three main goals: (i) the outlining of the different aspects influencing holm oak decline in the Mediterranean oak woodland ecosystems, focusing on the physiology of the species related to abiotic stress tolerance and pathogen root rot; (ii) the analysis of the advances in the knowledge of the plant-pathogen interaction, paying special attention to the differences in the response of the species to drought and root rot stresses; and (iii) the identification of soil microbiota as environmental factor which can alter the physiological response of trees subjected to biotic or abiotic stress. Basic knowledge is necessary, not only to understand complex processes but also to drive scientific efforts in order to elucidate the bases of the resistance/tolerance against root rot. It is necessary to enhance the adaptation ability of the holm oak, searching for the favourable characteristics of the plant and the adequate management of the environment that, in the face of different biotic and abiotic stressors, will guarantee the preservation of the species [21]. The mechanisms of the interaction between the host and the pathogen, and the influence of other environmental factors, must be considered in susceptibility studies and in management strategies intended to mitigate tree decline.

## Holm Oak Decline

Forest decline is nowadays a major threat to the sustainability and management of forest ecosystems around the world [22]. This syndrome is affecting oak forests across the Northern Hemisphere, the oak decline being a serious problem for European oak forests since the beginning of the twentieth century [23]. Accepting the definition of forest decline as a complex multifactorial disease influenced by external biotic and abiotic stressors, including climate and land use changes [24, 25], it must be considered that extreme climatic variations, incorrect management practices, and alien-invasive pathogens are agents involved in holm oak decline [16, 26]. The environmental and economic losses due to holm oak decline are amplified in the *dehesa* rangeland ecosystem and other Mediterranean holm oak ecosystems, due to the confluence of factors affecting their sustainability, such as (i) intensification of agricultural practices and livestock farming, including overgrazing which can lead to soil erosion and compaction [27]; (ii) land withdrawal, lack of regeneration of trees and shrub invasion [8]; (iii) biotic factors such as insect pests and alien-invasive pathogens [20, 28]; and (iv) the direct effects of climate change, which can cause the displacement of holm oak and cork oak from certain distribution areas in the southwest of the Iberian Peninsula and in the north of Africa [2, 13•]. Although there are no accurate data on the incidence or the extent of holm oak decline, in the year 2010, official sources estimated the loss of holm oak stands in more than 8000 ha per year only in Spain [29]. Frisullo et al. [17] also



**Fig. 1** *Quercus ilex* distribution in the Mediterranean basin. **a** Distribution map of the species, adapted from Caudullo et al. [7]. **b** Typical *dehesa* of *Q. ilex* subsp. *ballota* in the south-west of Spain

(Huelva). **c** Coppice formation of *Q. ilex* mixed with another *Quercus* spp. (*maquis*) in the north-east of Spain (Catalonia). **d** Tall forest of *Quercus ilex* subsp. *ilex* in the region of Tuscia (Italy)

reported fast decline and mortality of holm oak in Italy related with root rot caused by *Phytophthora cinnamomi*, and in general, the climatic projection models tend to show worse scenarios for the species facing the decline [13•, 16, 20]. Therefore, the holm oak decline could be considered as an emerging complex disease that is causing significant socio-economic and environmental losses in the Mediterranean basin.

In particular, climate change projections foresee an increase in mean annual temperature and in extreme drought events, together with an increase in heavy rainfall occurrence and waterlogging periods [6, 13•, 30], affecting many forest areas, including—and especially—the Mediterranean semi-arid ecosystems. Drought events and rising temperatures are already causing species substitutions, whereas soil aridity, lower soil fertility and lower water availability are affecting

the persistence and sustainability of Mediterranean oak woodlands. Additionally, the main biotic factor threatening oaks worldwide is the root rot caused by soil-borne pathogens from the genus *Phytophthora*, considered alien-invasive pathogens in most of the cases [19••], as well as in the Mediterranean holm oak ecosystems [16].

### Holm Oak Ecophysiology and Holm Oak Decline

*Quercus ilex* is an evergreen sclerophyllous species with a deep and well-spread root system which can be 1.5-fold greater in size than the crown projection [31]. It mainly has a tree growth habit and a medium to small size, but a shrub growth habit is also common. The holm oak is thought to be among the most drought-tolerant species of the genus *Quercus* (Table 1) [8, 33]. Its fine roots are more abundant in the



**Table 1** Comparison of hydraulic characteristics for some *Quercus* species, including holm oak. Modified from Robert et al. [32]. WD, wood density ( $\text{g cm}^{-3}$ );  $D_{\text{mean}}$ , mean vessel diameter ( $\mu\text{m}$ );  $\Psi_{50}$ , waterpotential at 50% loss of hydraulic conductivity (MPa);  $\Psi_{\text{min}}$ , minimum water potential found in field trials (MPa); nd, no data available

Biome	Species	Distribution	Phenology	Porosity	WD	$D_{\text{mean}}$	$\Psi_{50}$	$\Psi_{\text{min}}$
Mediterranean/semi-arid	<i>Quercus coccifera</i>	Southern Europe	Evergreen	Diffuse	nd	48.70	-6.96	-10.30
	<i>Quercus gambelii</i>	Southwestern North America	Deciduous	Ring-porous	0.62	30.93	-0.58	-2.16
	<i>Quercus ilex</i>	Southern Europe, north-western Africa	Evergreen	Diffuse	0.75	39.47	-4.66	-3.75
	<i>Quercus suber</i>	Southwestern Europe, north-western Africa	Evergreen	Diffuse	0.77	54.5	-3.68	-2.97
	<i>Quercus wislizeni</i>	California	Evergreen	Diffuse	0.66	39.61	-1.69	-3.57
Temperate	<i>Quercus alba</i>	Eastern and central North America	Deciduous	Ring-porous	0.62	52.06	-1.37	-1.14
	<i>Quercus falcata</i>	Southeastern North America	Deciduous	Ring-porous	0.59	45.82	-0.92	-2.46
	<i>Quercus michauxii</i>	Eastern North America	Deciduous	Ring-porous	0.64	41.83	-1.70	-2.91
	<i>Quercus petraea</i>	Europe, Anatolia	Deciduous	Ring-porous	0.57	nd	-3.06	-3.17
	<i>Quercus robur</i>	Europe, west Asia	Deciduous	Ring-porous	0.57	43.12	-1.90	-2.94
Tropical	<i>Quercus oleoides</i>	From Costa Rica into Mexico	Evergreen	Ring-porous	0.86	nd	-3.03	-3.47
	<i>Quercus acutissima</i>	Southwest Asia	Deciduous	Ring-porous	0.74	72.48	-3.39	nd
	<i>Quercus serrata</i>	China, Taiwan, Japan, Korea	Deciduous	Ring-porous	0.68	27.34	-2.70	nd

superficial layers of the soil—top 20 cm—, and often more concentrated under the crown projection searching for the high soil water content [34]. These ecological characteristics make the holm oak one of the species best adapted to semi-arid Mediterranean environments and open spaces, but the management practices in the *dehesa* affect the functionality of this highly adapted root system, mainly due to the soil compaction that is a consequence of high livestock pressure and tillage practices [27]. Also, the shallow fine-root system facilitates the spread of soil-borne pathogens like *Phytophthora cinnamomi* Rands., with livestock, farming tools, or humans acting as vectors.

### Waterlogging and Root Rot in *Quercus ilex*

The increase of soil waterlogging episodes could favour the cycle and the spread of soil pathogens of the genus *Phytophthora*, which are characterized by the presence of motile biflagellate zoospores [35]. This effect in the dispersal and in the cycle of *Phytophthora*—hypoxia reduces mycelial growth and promotes sporangium production—has been found to be related with significant changes in the rate of root symptoms due to inoculation [36], but the influence of waterlogging was not identified as a factor altering plant physiology significantly in inoculation experiments carried out under controlled conditions with *Quercus ilex* subsp. *ballota* [37]. For this reason, in this review, we focused on the effects of drought on plant physiology, and their synergistic effects with the root rot.

### Drought Tolerance and Vulnerability to Climate Change

Holm oak possesses wood characteristics that confer high hydraulic efficiency and security as well as high resilience to

hydraulic system collapse or vessel cavitation, and such attributes give the species tolerance to drought conditions.

The main characteristics which provide the plant these attributes are the high wood density (WD, over  $0.75 \text{ g cm}^{-3}$ ), diffuse-porous wood, long vessels (up to 1 m), and low mean vessel diameter (below  $40 \mu\text{m}$ ), which lead to low limits for safe hydraulic conductance of the plant ( $\Psi_{50} < -4.5 \text{ MPa}$ ;  $\Psi_{\text{min}} < -3.5 \text{ MPa}$ ) [32]. It could be considered that this low limit of water potential and the high safety margin for xylem collapse under drought showed by the difference between  $\Psi_{\text{min}}$  and  $\Psi_{50}$ , confer a high degree of tolerance against the possible reduction of water availability due to climate change, an observation which agrees with the quick acclimation and tight stomatal control which holm oak showed in throughfall displacement experiments [38, 39]. Also, its response to high temperatures leads to similar conclusions: Ogaya and Peñuelas [38] found that maximum photosynthetic assimilation occurred at the highest temperatures encountered under drought conditions.

Moreover, model projections based on a moderate climate change scenario (IPCC Representative Concentration Pathway scenario RCP2.6 [40]), which implies an increase in the average global temperature of less than  $2 \text{ }^\circ\text{C}$ , did not show significant changes in the Mediterranean oak woodlands distribution area [41, 42]. However, model projections based on more severe climate change scenarios showed the vulnerability of holm oak in some areas of the southwestern Iberian Peninsula [13]. Other factors—such as undergoing consecutive intense water stress episodes within a short period, and the influence of land use or biotic stress—have a negative impact on the recovery of trees after wetter conditions return; this effect is probably linked to the carbon cycle and reduced growth rates [41, 43, 44]. Also, land use legacy and farm

management are factors that threaten the stability of holm oak *dehesas*. The intensification of silvicultural and agronomic management in these ecosystems have been found to be directly related with poorer health status of trees and lower tree regeneration rate [45•].

Despite the relevance of the biotic factors in the holm oak decline, the reviewed literature does not provide examples of niche projection models or vulnerability assessments including the influence of biotic stressors or the habitat suitability for root rot pathogens linked to climate change. Duque Lazo et al. [16] found that the distribution of *P. cinnamomi* would be increased under different climate change scenarios, agreeing with the potential invasion risk of this pathogen in the Iberian Peninsula found by Hernández-Lambrano et al. [46]. Ahanger et al. [47] made a comprehensive review of the main effects that climate change would have on the spread and aggressiveness of plant pathogens. Climate change may alter the susceptibility of hosts and the increase in temperature and in the frequency of extreme climatic events could lead to epidemic episodes triggered by pathogens with low current infection rates. Regarding *P. cinnamomi*, different projection models under different climate scenarios indicate an increase in the extent and severity of damage caused by this pathogen as a result of climate change [16].

### *Phytophthora* as Emerging Forest Pathogens

The current ease of human mobility and the increasing international trade and transport of goods, paired with climate change, are factors which contribute to the co-occurrence of host and pathogen species without a co-evolutionary past [48]. Among those, pathogens of the genus *Phytophthora* are responsible for some of the most dramatic disease outbreaks worldwide [20, 49•]. Over the last few decades, different *Phytophthora* and *Pythium* species have emerged as important invasive pathogens, considering the environmental losses they cause [49•, 50]. Some examples are *Phytophthora ramorum* Werres with sudden oak death, affecting tanoak (*Notholithoarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S.H.Oh) and several oak species in California [51], *P. cinnamomi* on eucalyptus and in Jarrah ecosystems in Australia [20] and *Phytophthora cryptogea* Pethybr. & Laff., *Phytophthora cambivora* (Petri) Buisman and *P. cinnamomi*, which cause ink disease on chestnuts worldwide [52].

Since the 1990s, *Phytophthora* root rot has been identified as one of the most relevant diseases affecting European oaks [53]. Sessile and pedunculate oaks (*Q. petraea* and *Q. robur*) from North and Central Europe are threatened by several *Phytophthora* spp. [23]. In the Mediterranean basin, *Q. ilex* and *Q. suber*, and to a lesser extent, *Q. faginea* Lam. and *Q. pyrenaica* Willd., are affected by *P. cinnamomi* root rot. In France and Italy, the decline of *Q. ilex*, *Q. cerris*,

*Q. frainetto*, and *Q. pubescens* has been also related to the presence of several *Phytophthora* spp. [54–56].

In the case of *Q. ilex*, it is considered that root rot caused by *P. cinnamomi* is the main factor in its decline [15, 57], holm oak being the species most susceptible to the attack of this pathogen when compared with Mediterranean species like *Q. canariensis*, *Q. faginea*, *Q. pubescens*, *Q. pyrenaica*, and *Q. suber* [58] and other temperate oaks such as *Q. robur* and *Q. rubra* [59]. The severity of the decline symptoms and root rot in holm oak *dehesas* has been related to water stress and *Phytophthora* spp. occurrence, mainly *P. cinnamomi* [60, 61•]; the related literature often describes the association of both tree death and intense defoliation with the lack of water and nutrient supply due to insufficient root uptake. *Phytophthora cinnamomi* invades up to 75% of the xylem vessels of fine roots [62•], being even more abundant in early stages (after 10 days) in the xylem of secondary roots [63]. However, some general defence mechanisms such as cell wall thickening or blockage of xylem vessels were detected in a histological study of the interaction [62•, 63•, 64•], suggesting that they could be a response of holm oak triggered by the presence of the oomycetes in the absorbent roots, a response which could cause adjustments of the hydric regulation and photosynthetic rates found in affected trees [19••].

*Phytophthora cinnamomi* presents a wide host range, with approximately 5000 different host species, including woody, shrub, and perennial or annual herbaceous plants [61•]. The lifecycle of *P. cinnamomi* includes both an asexual and a sexual reproductive cycle, with two mating types. In infested soils, it feeds on litter and colonizes asymptomatic hosts, persisting as oospores when mating types A1 and A2 are present [65], and growing in tissues of asymptomatic annual herbaceous plants, releasing chlamydospores and persisting as stromata into the soil after natural senescence of the plants [66]. When conditions are optimal for growth—high soil moisture and mild temperatures—pathogen structures produce sporangia, which germinate and infect new hosts through biflagellate motile zoospores. Its asexual lifecycle can be repeated several times in a short period, depending on the host, greatly amplifying the inoculum concentration in the soil after a local-scale climatic event such as heavy rainfall occurrence that affect areas of hundreds of hectares. It can survive in adverse conditions for 6 years, due to resistant structures, and interacts with plant hosts in different ways: as a biotroph in asymptomatic hosts, a hemibiotroph or necrotroph in susceptible hosts, and a saprotroph feeding on litter in wet soils [65–67]. All these conditions promote the long-term stability of the presence of the soil inoculum, even in soils with extreme moisture contents, explaining the relationships between severe symptoms in holm oak decline and extreme climatic events (severe drought or rainfall episodes), which often occur in the Mediterranean climate [60].

Apart from *Phytophthora cinnamomi*, other oomycete species have been linked with holm oak root rot. *P. quercina* T. Jung and T.I. Burgess, *P. psychrophilla* Jung and *P. cactorum* (Lebert & Cohn) J. Schröt have been isolated from declining stands of holm oak, affected by root rot, in the east of the Iberian Peninsula [18, 68•] and also have been identified through metabarcoding techniques in holm oak *dehesas* of Andalusia [69]. Additionally, *Pythium spiculum* Paul, *P. irregulare* Buisman, *Phytophthora gonapodyides* (H.E. Petersen) Buisman, and *P. cryptogea* have been isolated from declining stands in Andalusia and Extremadura, associated with very severe decline symptoms [70–72]. Mora Sala et al. [73] found that *P. quercina* was more abundant than *P. cinnamomi* in two different stands of *Q. ilex* with opposite characteristics, demonstrating their pathogenicity in a later work [74]. This hypothesis agrees with the results of Ruiz Gómez et al. [69] which found *P. quercina* as one of the main species presents in 25 declined oak stands of Andalusia, together with *P. psychrophilla* and *P. citrophthora*, all the three species presenting greater abundance than *P. cinnamomi*. These recent findings suggest that other *Phytophthora* spp. apart from *P. cinnamomi* could be involved in the holm oak decline, although in most of the inoculation tests, *P. cinnamomi* has proved to be the most aggressive species for the holm oak seedlings [74, 75].

## Mechanisms of Plant-Pathogen Interaction

Woody plants possess several mechanisms of defence against plant pathogens. There are descriptions of mechanisms of specific recognition of molecular patterns (PAMP-triggered immunity) [19••], which generally are present when the host and pathogen have co-evolved and are often mediated by specific resistance proteins. Moreover, woody plants have primary defence responses—such as cell wall thickening, accumulation of phenolic compounds in specific tissues, or callose depositions—common to a wide number of genera and species of woody plants, which are triggered by alterations in roots [76]. These responses may be triggered also by unspecific signals—for example, osmotic imbalance of plants [19••] or carbon compound deficiency [77], which can induce metabolic changes in leaves and other photosynthetic organs and are observed in several *Quercus* spp. after infection of the roots, trunk, or leaves by *Phytophthora* spp. [19••].

Holm oak seedlings exhibit an early response (e.g. 24 h after inoculation) in fine root tissues after pathogen colonization [62•, 63•, 64•], similar to other responses found in other woody species-*Phytophthora* relationships [19••, 78–81]: cell wall thickening, de-esterification of cell walls, and enlargement of intracellular spaces (even in tissues in which pathogen structures were not present) (Fig. 2). Three days after inoculation, cell wall thickening had extended to the xylem and

protoxylem cells of the central cylinder, although the percentage of infected cells was still low (9.2% of cortex and epidermis cells, without presence in the central cylinder) [62•]. Even some individuals exhibited blockage of xylem vessels at this time. Also, accumulation of phenolic compounds was observed in the contacts between the pathogen and cell walls and, inside the cells, granular compounds had accumulated around intracellular structures of the pathogen.

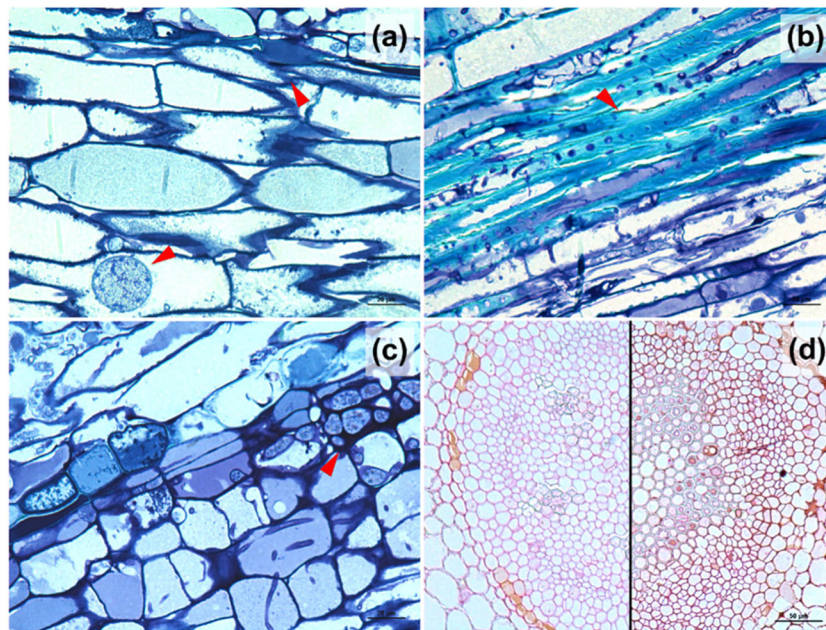
At the molecular level, there are several mechanisms by which *Phytophthora* spp. can alter the structure and composition of plant tissues. Genes encoding cell wall degrading enzymes (CWDEs) are often present in large multigene families of *Phytophthora* spp., including *P. cinnamomi* [61•]. Polysaccharide-lyases assist the penetration of host tissues by degrading cellulose, hemicellulose, pectins and glucans, and polygalacturonases secreted during the early phase of development of somatic hyphae may be related to the de-esterification of plant cell wall pectins in holm oak [62•]. Moreover, all the *Phytophthora* genus possess the ability to produce other apoplastic and cytoplasmic effectors like toxins and elicitors, unique 10-kD proteins, and Crincklers (CRN), which allows the pathogen to evade the recognition mechanism of plants, but in other cases, triggering specific responses mediated by plant resistance genes [19••]. All these reactions directly alter the transport of water and solutes and may be related to important changes in the metabolic activity of seedlings, affecting, in the long term, the net photosynthesis rate and carbon compounds translocation.

Knowledge of the events at the physiological level improves the evaluation of the interaction between holm oak and *P. cinnamomi*. It would be very advantageous to know how the decline of *Q. ilex* associated with root rot responded to changes in water availability and temperature, mainly through the physiological responses of the host.

## Physiological Response to Drought Stress and Root Rot

The stress caused by severe drought induces a complex physiological effect in woody plants, which can lead to above-ground symptoms like those caused by the effects of root rot-triggered stress, but which often produces different responses depending on the drought tolerance of the species. *Quercus ilex* subsp. *ballota* is known to have an isohydric response to water stress, which consists of quick stomatal closure to control high transpiration rates under low soil water availability, maintaining a relatively high water potential in leaves, around  $-3$  MPa and reducing the net photosynthetic assimilation reaching minimum values below  $2 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$  [32, 33] This tight control of gas exchange is the main physiological mechanism employed by oaks to prevent the risk of embolism and hydraulic failure, thereby protecting





**Fig. 2** Root sections of *Quercus ilex* seedlings inoculated with *P. cinnamomi*. **a** Cortex section 14 days after inoculation, in which cell wall thickening around hyphal structures of the pathogen and a chlamydospore inside a cortical cell can be observed (red arrowheads). **b** Central cylinder, in longitudinal section, 14 days after inoculation. Accumulation of material with dense turquoise staining in the middle lamella of the xylem, protoxylem, and metaxylem cells (red

arrowhead). **c** Central cylinder 14 days after inoculation. Hyphal cluster (stromata-like aggregations) inside parenchymatous cells of the central cylinder (red arrowheads). **d** Comparison of cross-sections of the central cylinder of fine roots from control (left) and inoculated (right) plants 7 days after inoculation, using ruthenium red staining. Differences in the colour and intensity of the cell wall stain are observed. Source: authors' archive

them during dry periods [32, 33, 53]. Moreover, the shedding of twigs from the crown is a common mechanism of adaptation to drought periods in oaks and is triggered by the activation of a specific anatomical abscission zone, as influenced by hormonal signalling [53]. Also, the cavitation of narrow vessels under severe drought conditions promotes the reduction of photosynthetic and gas exchange rates. These factors could contribute to leaf abscission after prolonged extremely dry periods [82, 83].

Probably because of the similarity of the symptoms, the damage caused by root rot is often associated with water stress, supposedly due to the loss of absorbent fine roots [19••, 61•], which reduces stomatal conductance and the rate of photosynthesis [75, 84, 85]. However, the evaluation of physiological changes in holm oak seedlings as a response to *P. cinnamomi* infection and drought has yielded widely varying results, depending on the experimental conditions. Some works found strong differences in photosynthesis and water potentials between inoculated and control plants, whereas others showed differences only due to the watering treatments, but always reporting damage to the plants as a consequence of the inoculation with *P. cinnamomi* (Table 2).

The net CO<sub>2</sub> assimilation rate (*A*) showed differences due to the water regime in all the cases in which it was evaluated, but differences due to the presence of the pathogen only appeared when plants were subjected to or influenced by hydric stress. However, the stomatal conductance was found to be

reduced by both factors in experiments performed under controlled conditions, whereas in the field it seemed to be affected only during and after a period of water stress [88•]. On the other hand, when the interaction between the two factors (biotic and abiotic stresses) was evaluated in a multifactorial experiment, it showed the independence of the influence of each factor on gas exchange parameters, but not on fluorescence [86•]. Corcobado et al. [37] found that previous differences in the physiology of seedlings, as a consequence of different watering regimes, may influence differences in post-inoculation mortality rates, but did not show physiological data after inoculation. The studies comparing plants under controlled conditions did not present clear differences in water potential due to inoculation [59, 87, 89], but when plant biomass or root traits were assessed, differences appeared in all cases. Inoculated plants showed less biomass than control plants, both in belowground and aboveground fractions, independently of the watering treatment [37, 59, 86•], and root mass fraction (RMF) decreased in inoculated plants whereas it increased due to induced-drought stress [86•]. Some of these differences suggest that there is a decoupling of hydric strategies and metabolic functioning in holm oak seedlings and plantlets subjected to inoculation and drought stress. Stomatal closure and gas exchange reduction, accompanied with the decrease of photosynthetic activity, are some of the early physiological effects in plants subjected to drought stress. However, recent works [90] found that in inoculated

**Table 2** Summary of the results of works assessing the effects of *Phytophthora cinnamomi* infection and water stress in *Quercus ilex* trees. A, net photosynthesis assimilation rate; Gs, stomatal conductance;  $\psi$ , water potential; Fv/Fm, instantaneous chlorophyll fluorescence, quantum yield

Reference	Experimental design	Inoculation	Watering	A	Gs	$\psi$	Fv/Fm	Others
Ruiz Gómez et al. [86•]	Comparison of physiological response to inoculation and severe drought in <i>Q. ilex</i>	Liquid inoculum (mycelia and chlamydo-spores) sown in pot holes	Initial flooding. Acute drought (without watering) and regular watering	Significant differences for both inoculation and drought factors without interaction		–	Significant differences only for inoculation, but influenced by drought	Significant differences in root traits and plant biomass
León et al. [87]	Comparison of <i>Q. suber</i> and <i>Q. ilex</i> , 1-year-old seedlings (inoculated and non-inoculated)	Injections of liquid inoculum (mycelia and chlamydo-spores) into the pot substrate	Flood-drought cycles: 48 h of flooding every 5 days	–	–	Differences between species	–	–
Corcobado et al. [37]	Influence of previous watering treatment on root rot symptoms. <i>Quercus ilex</i> seedlings, 2 years old	Inoculum obtained following Jung et al. 1996. Substrate mixed at 2% with inoculum.	Severe drought, flooding, and regular watering before inoculation. Regular watering after inoculation	Significant differences due to watering treatments	Significant differences due to watering treatments	–	Significant differences due to watering treatments	Plant growth and root traits were influenced by watering treatments
Corcobado et al. [88•]	Physiological comparison of declining and non-declining trees in field plots	Isolation of <i>P. cinnamomi</i> and <i>P. spicatum</i> from soil and root samples	Assessment of soil water content	Differences between declining and non-declining trees during hydric stress period, or in the recovery, but not before the stress period		–	–	–
Turco et al. [89]	Proteomic comparison of <i>Q. cerris</i> and <i>Q. ilex</i> (1-year-old seedlings), including water shortage and inoculation with <i>P. cinnamomi</i>	Millet inoculum sown in holes in the substrate	Initial flooding. Suspension of irrigation for 6 and 20 days in water-stressed plants	–	–	Differences only due to watering treatment	–	–
Maurel et al. [59]	Comparison among 5 different species (1-year-old seedlings), including water shortage and inoculation with <i>P. cinnamomi</i>	Inoculum obtained following Robin et al. 1998. Millet inoculum sown in holes in the substrate	Initial flooding and water deficit (1/4 of regular watering, not severe drought)	Lower Gs in inoculated plants and water shortage controls	Lower Gs in inoculated plants	Differences only due to water regime	–	Lower root biomass in inoculated plants



plants, net photosynthesis assimilation appeared to decrease without a significant reduction in the quantum yield of PSII. This result might be related with the increase of internal CO<sub>2</sub> concentration in leaves, which might be responsible for the stomatal closure without reduction in the photosynthetic activity. All these factors could be related with osmotic imbalance in plant, agreeing with other observations in similar host-pathogen interactions [19••].

In addition, not only drought but also waterlogging treatments have shown significant effects on the mortality of infected plants [37, 85]. Apart from the positive effect of waterlogging on the *Phytophthora* reproduction cycle, prolonged waterlogging might alter the tree physiology and health status. It has been demonstrated that oxygen deprivation in roots under flooding conditions reduces fine root growth and volume, and it causes taproot rot and the accumulation of toxic substances in other *Quercus* spp. [30]. The effect of waterlogging on plant death seems to be independent from the effect of the pathogen [36, 37]. Although to our understanding waterlogging might be considered a predisposing factor for triggering decline episodes, further investigation is necessary to enlighten the effect of the interaction between waterlogging and tree death in the holm oak decline.

Physiological assessments are necessary to reveal the nature of plant-pathogen interactions, although the characterization of the physiological response of the host is difficult, even under controlled conditions, because the underlying process of the interaction remains unknown. Non-specific immune responses have been identified in the interaction between holm oak and *P. cinnamomi* [62•] and the physiological response of holm oak to root rot indicates the existence of specific mechanisms that alter plant physiology as a response to the presence of the pathogen inside the roots. In a multifactorial greenhouse experiment with *Q. ilex* seedlings, using inoculation and drought stress as factors, physiological responses were identified that confirmed the hypothesis of specific mechanisms of response against *P. cinnamomi* root rot [90] (Fig. 3). Compared with non-inoculated plants, both well-irrigated and drought treatments, inoculated plants presented higher water use efficiency and lower gas exchange and net photosynthetic assimilation, without a significant reduction in fluorescence parameters (Fv/Fm) [86•, 91].

The association of root rot with water stress originates from the assumption of generalized damage to the root absorbent system, but the whole system of fine absorbent roots may not be affected homogeneously by root rot in the early stages of infection. In laboratory and greenhouse experiments, the rate of fine root damage was found to depend on the inoculum concentration in the substrate and the root diameter distribution [63, 78], evidencing the influence of experimental design on the results. Also, in the field, the distribution of the pathogen depends on soil chemical and physical differences (microsite influence) (Rafael Sánchez-Cuesta, unpublished

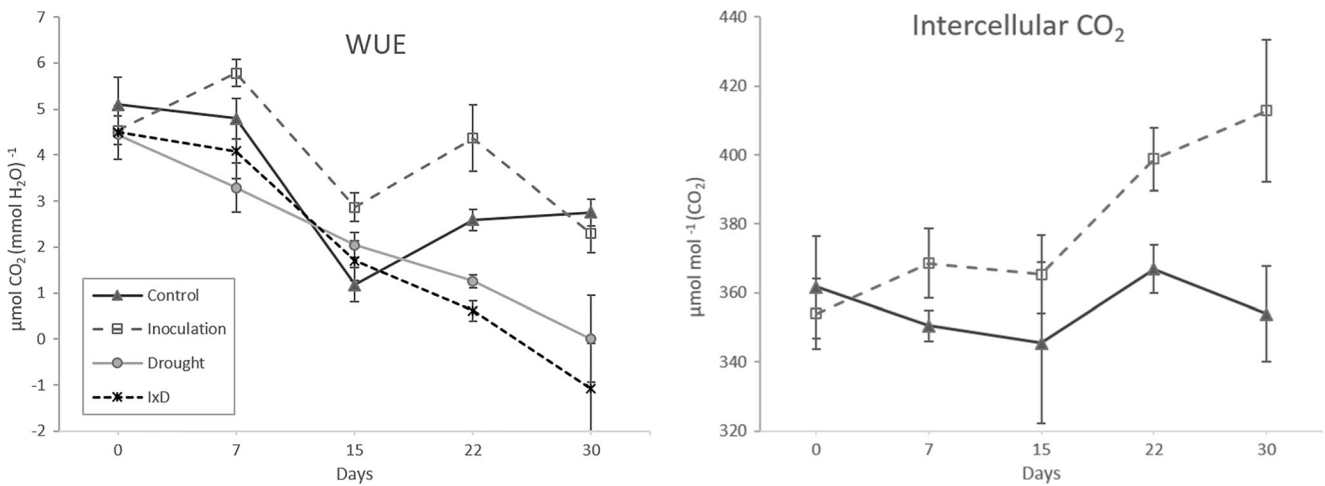
data). Thus, as the proportion of the fine roots which still remain undamaged at the different stages of the decline is unknown, there is the possibility that a tree already infected and showing symptoms does not suffer water stress, and without additional drought stress, stomatal closure may not be induced only by water deficit but by high CO<sub>2</sub> concentration in the leaves too.

Some secondary metabolic pathways that can be triggered by the presence of pathogens or endophytes divert carbon skeletons from primary to secondary metabolism, like the shikimate dehydrogenase and chalcone pathways, related with the production of phenolic compounds and phytoalexins in plants under biotic or abiotic stress [92]. These metabolic pathways catalyse the NADP<sup>+</sup> reversible reaction and lead to the increasing of the intracellular CO<sub>2</sub> concentration in leaves diverted from the pentose phosphate pathway. This alteration of the metabolic pathways and the carbon balance in leaves may favour stomatal closure and reduce the photosynthetic assimilation rate (which is usually calculated based on the CO<sub>2</sub> exchange rates) (Fig. 4), without lowering the quantum yield of PSII. These changes could be linked to the reverse osmosis mechanism through the relative increment of hydraulic potential in leaves and the osmosis balance produced by the accumulation of metabolites [93, 94]. Reverse osmosis has been described as a mechanism to restore the hydraulic conductivity in plants that have undergone vessel cavitation or are embolized, involving water transference from upper to lower plant parts. The effectiveness of this mechanism is related with the osmotic pressure [94].

Additionally, all the possible alterations in seedling physiology should lead to a sensible change in growth patterns, which may be a useful tool to characterize plant responses to different stressors; in particular, biomass allocation is a key factor [86•, 87•]. In inoculated holm oak seedlings, a decrease in total biomass and the root mass fraction (RMF), in comparison with control plants, was consistently identified [59, 86•, 87•]. However, drought stress in holm oak seedlings causes an increment in the root length and biomass, which are more significant for RMF [86•, 87•]. This response, considered an adaptation of drought-tolerant plants to drier conditions, does not seem to be influenced by the effects of inoculation.

## Environmental Factors Influencing Holm Oak Decline: the Soil Microbiota as a Key Element

Although the vulnerability of holm oak to climate change is not considered to be significant under moderate climate change scenarios [41], and niche habitat projections evidenced the future expansion of the species at the global level [42], even replacing less stress-tolerant species in some areas [95], the influence of climate should be considered together with other environmental factors. Land

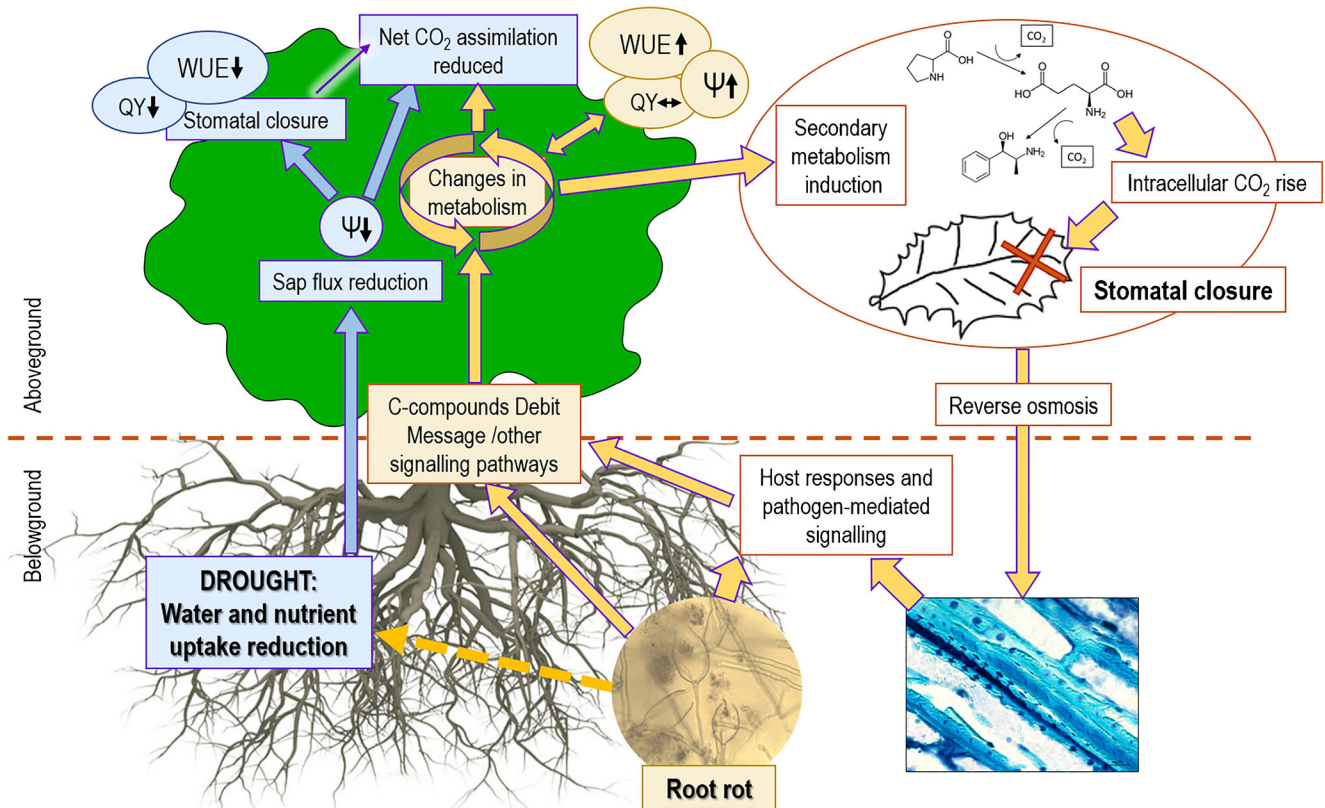


**Fig. 3** Comparison of the water use efficiency (WUE) for different treatments on *Quercus ilex* subsp. *ballota* plantlets: control non-inoculated watered plants (triangles), watered inoculated plants

(squares), drought non-inoculated plants (circles), and drought inoculated plants (stars). Source: Authors unpublished data

use changes, pathogen outbreaks, and incorrect management practices are key factors concerning forest health in Mediterranean oak woodlands. It has been demonstrated that repeated drought events, heat waves, intense freezing, and prolonged waterlogging are related to subsequent important forest decline episodes, also affecting holm oak [83]. Moreover, the influence of site conditions on the

plant physiological status and growth patterns is demonstrated by the evidence of local adaptations found in cross-planting and common garden experiments for several oak species, including *Q. ilex* subsp. *ballota*. Several cross-planting experiments with seven different *Quercus* species have shown that freezing tolerance of trees varies depending on the climate of origin, being this tolerance



**Fig. 4** Conceptual model of differential responses and interactions between biotic and abiotic stress factors in the holm oak decline involving *Phytophthora* root rot. Ψ, water potential; WUE, water use efficiency; QY, quantum yield of photosystem II

negatively associated with growth rate [96]. Also, ecotypes of *Q. ilex* coming from the driest locations presented lower growth rates and higher water potential on leaves under the same conditions than ecotypes coming from more mesic locations [97].

Plant-soil relationships are important ecological drivers of ecosystem dynamics influencing forest health [98]. Despite the lack of studies about the influence of soil properties on soil-borne pathogens and plant diseases in forest systems, soil must be considered a key element. The chemical composition and physical structure of soil have a significant influence on both the root density and the pathogen proliferation [99]. Additionally, the plant community diversity and specific composition are linked with the probability of *Phytophthora* root rot occurrence [99, 100]. The soil structure and composition, the local topography, mainly influencing the hydrology and thus the water availability and regime, and the diversity and composition of the ecosystem biota—including the aboveground and belowground biota—might be considered as the main factors configuring the microenvironmental conditions that affect the tree health status at the individual scale. The evidence of specific responses of the holm oak to soil-borne pathogens, including physiological alterations [19•, 86•, 91], makes it necessary to consider the influence of microsite conditions on tree decline. Several approaches can be used to evaluate the impact of environmental variables and microsite conditions at different scales. For spatially distributed climatic, edaphic, and topographic variables, spatial distribution models and habitat prediction models are powerful tools to evaluate the probability of disease and to implement appropriate management policies [16, 46]. For local conditions, the most common approach is to relate the characteristics of each environmental factor with observable or quantifiable factors linked to tree health [68•, 98, 101].

It is recognized that the soil microbiota influences the health status of the plant community in several ways, interacting as commensal, pathogenic, or mutualistic organisms. Plants, the soil community, and soil-borne plant pathogens create a tripartite relationship between the host, pathogens, and soil biota, which leads to complex interaction networks. Saprobies, ectomycorrhizas (EcM) and arbuscular mycorrhizal (AM) species influence plants, enhancing water and nutrient uptake of roots, improving soil fertility and nutrient availability, and triggering systemic defences; parasites of fungi, insects, and nematodes control plant pests, and others can act as antagonists of plant pathogens in several different ways [102, 103]. Particularly, the presence and abundance of EcM and AM species are important belowground characteristics related to fine root abundance or the establishment of seedlings in deciduous and semi-deciduous oak forests [104, 105]. In the case of holm oak, it has been demonstrated that EcM fungi are linked with changes in the health status of trees in declining stands [69•, 88•, 106•].

Two principal effects of the soil microbiota on *Phytophthora* spp. have been identified, concerning firstly niche competence and secondly the presence of antagonistic or parasitic species. Despite the ability of *P. cinnamomi* to adapt to changing conditions, it is known to be a poor competitor under saprophytic conditions [107]. Root rot symptoms were found to be less severe in trees located in soils with higher oomycete biodiversity rates [69•]. Regarding antagonism or parasitism between microbiota components, the influence of *Trichoderma* spp. on the root rot oomycetes has been identified as a key factor in future strategies of root rot control [69•, 108•, 109]. *Trichoderma* spp. are opportunistic, avirulent plant symbionts with recognized parasitic or antagonistic functions against phytopathogens, being one of the genera of fungi isolated most frequently from soils. Several *Trichoderma* spp. have been identified as plant endophytes, inducing plant phytoalexin accumulation or cell wall lignification [110] and other species of the genus have been found to have a proven role as an antagonist of several *Phytophthora* spp. and numerous other fungal pathogenic species [111–116]. In a study carried out in Italian nurseries, up to three different *Trichoderma* spp. were isolated from holm oak (*Q. ilex* subsp. *ilex*) rhizosphere, reducing root rot caused by *Phytophthora nicotianae* Breda de Haan and *P. cinnamomi* in different combinations [108•]. Recently, a significant correlation was found between the abundance of a single *Trichoderma* species—which remains unidentified at the species level—and the scarcity or absence of oomycete root rot pathogens in soils of holm oak *dehesas* affected by the oak decline [69•]. The management of the soil conditions and the soil microbiota to promote the presence of these *Trichoderma* spp. could be an advantageous strategy to improve the health status of declined trees [69•, 107–110]. Poorly drained soils favouring waterlogging and *Phytophthora* proliferation, organic matter, and nutrient scarcity on soil, chemical composition, or pH related with low suitability for fungal beneficial species, and specific management practices such as overgrazing or tillage, are factors which would be modified through soil amendments, incorporation of bioagents, or changing of silvicultural practices, which may have influence in the improvement of tree health status.

## Concluding Remarks

Global change has entailed the alteration of several environmental factors which directly influence the sustainability of Mediterranean oak woodlands. The combination of the expected climate changes and the occurrence of pathogen outbreaks—also linked to the global change—may be considered as the main driver of future holm oak decline in the Mediterranean basin [16, 25, 46]. Root rot caused by the presence of alien invasive *Phytophthora*



spp. is considered the triggering factor in tree decline and death, but most authors have linked the massive episodes of holm oak decline to the occurrence of both environmental and biotic stress, sequentially or together. This causality of tree death due to the synergistic effects of both factors is supported by the latest findings showing the different physiological response of *Q. ilex* seedlings to drought, waterlogging, and root rot, with important differences in growth patterns and the evidence of changes in the hydric and photosynthetic mechanisms facing drought and biotic stress [19••, 86•, 87•, 91]. Although holm oak is one of the most drought-tolerant species of the genus *Quercus*, its behaviour in the face of biotic stressors, which can involve changes in the metabolism and biomass allocation, may be a disadvantage if it concurs with a hydric stress episode. Chronic-to-moderate stress episodes progressively weaken the plant and lead to its death due to biotic or abiotic stress whose effects would not be as severe on their own [83].

Also, the presence of trees in affected stands which remain healthy even after intense decline episodes could correspond to the existence of local favourable microsite conditions. Among these, we highlight the influence of soil microbiota on the tree health status, based on the latest findings about the influence of EcM, AM, and *Trichoderma* spp. on the severity of the root rot symptoms and on the community interactions between the soil microbiota and the plant [69•, 106••, 108•].

After the review of the latest findings on the pathogen-plant interaction and the tree physiological responses, we consider that the adaptive silviculture of Mediterranean oak woodlands and the management of the soil microbiome status must be included in the integrated strategies to control holm oak decline in Mediterranean ecosystems. The modification of soil characteristics favouring well-drained soils, with an adequate organic matter content, controlling pH through mineral amendments, and the addition of key biocontrol agents, are strategies which may be included in the Integrated Pest Management (IPM) protocols looking for the improvement of the soil microbiota equilibrium.

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## Compliance with Ethical Standards

**Conflict of Interest** The authors declare that there are no conflicts of interests.

**Human and Animal Rights** This article does not contain any studies with human or animal subjects performed by any of the authors.

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