

Article

The Role of Soil Moisture in the Infection of *Quercus suber* L. Roots by *Phytophthora cinnamomi* Rands and *Pythium spiculum* Paul

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Abstract

The survival of *Quercus* species in the Mediterranean region is challenged by root diseases caused by *Phytophthora cinnamomi* Rands and *Pythium spiculum* Paul, as well as by drought. This study aimed to examine the interaction between both pathogens under varying soil moisture levels. Seedlings were inoculated with *P. cinnamomi*, *Py. spiculum*, or both, and exposed to soil moisture conditions ranging from saturation to drought. Results showed that *P. cinnamomi* caused high levels of root necrosis in saturated-to-moderately dry soils, but it was unable to cause infection under drought conditions. Conversely, *Py. spiculum* infected roots under drought but not under saturation conditions and was less virulent in wet soils compared to *P. cinnamomi*. In seedlings inoculated with both pathogens, symptoms were similar to those induced by *P. cinnamomi* alone, without any synergistic effect. This study highlights that *P. cinnamomi* and *Py. spiculum* infect oak roots across a range of soil moistures, with *P. cinnamomi* being the predominant pathogen in wet-to-moderately dry soils, and *Py. spiculum* being the predominant pathogen in droughted soils. Under current and projected future water deficit conditions, oak woodlands infected by both pathogens face a significant threat to their survival.

Keywords: cork oak; drought; flooding; oak decline

1. Introduction

Cork oaks (*Quercus suber* L.) have high ecological, social, and economic value in the Mediterranean Basin [1], where they are considered keystone species [2]. In the Iberian Peninsula, evergreen oaks, including *Q. suber*, are the dominant species of dehesa agroforestry systems (montado in Portugal), which combine cork and acorn production with extensive livestock ranching [3], leading to a typical savannah-like landscape. The Mediterranean Basin is characterized by hot, dry summers and mild, wet winters, producing pronounced seasonal fluctuations in water availability [4]. *Quercus* species must withstand hot and dry summers for up to 4–5 months [5], but summer droughts will become a limiting factor for oak trees in dehesa under the increasing aridity predicted for the region in climate change projections [6,7]. In fact, drought-related mortality has recently emerged as a widespread issue with important implications for Mediterranean forest conservation [8,9]. However, climatic factors resulting from global climate change are not the only damaging agents acting on vegetation; other drivers with negative effects in regions with a Mediterranean climate, such as invasive microorganisms [10,11], seem to be increasing, and both climatic and biotic factors can be co-related [12]. Changes in the intensity, length,



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and frequency of dry periods will likely affect forest vulnerability to attacks by biotic agents [13], such as *Phytophthora cinnamomi* Rands, infecting highly susceptible hosts, such as oak species [14], or *Pythium spiculum* Paul, whose presence in the south of the Iberian Peninsula, infecting evergreen oaks, has increased in the last three decades, and they also threaten the survival of oak-based agroecosystems [15].

Phytophthora cinnamomi causes its most severe outbreaks on poorly drained or periodically waterlogged sites [16–18], which promote sporangial production and the zoospore release required for the spreading of disease [19]. On the other hand, species in the genus *Pythium* are important root pathogens of many agricultural crops, including forest nursery seedlings, and their high soil moisture requirements are like those of *Phytophthora* spp. [20]. Nevertheless, *Py. spiculum*, together with a few other *Pythium* spp. [21,22], does not seem to produce flagellated zoospores [23], and root infections depend on direct germination of hyphal bodies (sporangium-like structures). For this reason, its putative inability to produce swimming zoospores has led to the hypothesis that it is better adapted to terrestrial habitats compared with other oomycetes [24,25].

Phytophthora cinnamomi and *Py. spiculum* are frequently found in Spanish and Portuguese oak woodlands, infecting the roots of adjacent oak trees in the same site or even infecting the roots from the same oak [26]. Nothing has been reported about the influence of soil moisture in the competition between the two pathogens for *Q. suber* infection and root rot development. In this context, the main objective of this work was to determine the level of competition between *P. cinnamomi* and *Py. spiculum* on *Q. suber*, and whether it is dependent on soil water content, in pot experiments. Understanding how soil moisture can determine the etiology of oak root disease should lead to a better risk assessment of root rot development in cork oak open woodlands suffering the impact of climate change in the Mediterranean Basin.

2. Materials and Methods

2.1. Oomycete Material

Two isolates were used in this study: PE90 of *P. cinnamomi*, obtained from roots of *Q. ilex* L. subsp. *ballota* (GenBank AY943301); and PA54 of *Py. spiculum*, obtained from the rhizosphere of *Q. suber* (GenBank DQ196131). Both isolates were originally collected from woodlands in southern Spain [25] and were maintained at the oomycete collection of the Agroforest Pathology Group at the University of Cordoba, Spain, stored under sterile mineral oil. Identification of the isolates was previously confirmed by ITS region sequencing and comparison with sequences in GenBank [23,25].

2.2. Plant Material

Healthy 1-year-old cork oak seedlings potted in free-draining plastic containers with 40 cells of 0.3 L were obtained from San Jerónimo Forest Nursery, belonging to the Nursery Network of the Andalusian Government, Spain.

2.3. Soil Infestation

For pot experiments, fertilized peat (Turbar y Coco Mar Menor, Sucina, pH = 5.5, $\rho = 170 \text{ g L}^{-1}$), a standardized substrate for the growth of Mediterranean oak seedlings, was used. The substrate was infested with three different spore suspensions: (1) chlamydospores of *P. cinnamomi* PE90; (2) oospores of *Py. spiculum* PA54; and (3) a mix of resting spores (chlamydospores and oospores) from both pathogens. For inocula preparation, each isolate was grown separately in Petri dishes containing 20 mL of 20% carrot broth and incubated at 22 °C in the dark. After 4 weeks of incubation, the mycelium produced was aseptically filtered and washed with sterile water. The mycelium mats were shaken for

3 min with sterile water in an electric mixer at the highest speed (Oster™ Pulse-matic 16, London, UK), at a rate of three Petri dishes per 100 mL water. Spore concentration was estimated by counting in a Neubauer chamber and adjusted to 8×10^3 spores (chlamydospores or oospores) per mL. For *P. cinnamomi* soil infestation, the chlamydospore water suspension was added to the substrate in a ratio of 33 mL L⁻¹ of substrate, resulting in 1.5×10^3 chlamydospores of *P. cinnamomi* per gram of dry substrate (corresponding to 640 CFU g⁻¹ [27]). Similarly, the water suspension containing $8 \cdot 10^3$ oospores of *Py. spiculum* per mL⁻¹ was added to the substrate at the same ratio, resulting in a density of 1.5×10^3 oospores per gram of dry substrate. A third infested substrate was equally prepared by adding the same quantity of both inocula together, resulting in a density of 1.5×10^3 *P. cinnamomi* chlamydospores plus 1.5×10^3 *Py. spiculum* oospores per gram of dry substrate. Uninfested substrate with only water added was used as the control. Once the soils were infested, the oak saplings were removed from their original containers and re-potted in free-draining plastic pots, each containing 3 L of infested or control substrate. A total of 40 pots containing one oak seedling per inoculum plus 40 control pots were prepared, making a total of 160 pots (including replicates).

2.4. Watering Experiments

Eight pots per inoculum type and eight control pots were submitted to five different watering treatments corresponding to five experiments according to their soil water content (θ_s):

1. Saturation ($\theta_s = 100\%$): The pots were maintained in trays filled with tap water for 4 weeks, which was described as the most favourable condition for *P. cinnamomi* infections [28].
2. High moisture ($\theta_s \approx 90\%$): Maintaining the pots inside trays filled with tap water for 2 days per week, while allowing them to freely drain for the remaining 5 days. This water treatment was maintained for 12 weeks, as previously was described [28].
3. Moderate moisture ($\theta_s \approx 60\%$): 500 mL of tap water was added to each pot every 3 days for 12 weeks [28–30].
4. Low moisture ($\theta_s \approx 30\%$): Similar to the typical spring and summer conditions in dry Mediterranean years, obtained by adding 200 mL of tap water to each pot once a week for 24 weeks [17].
5. Drought ($\theta_s \approx 10\%$): Obtained by adding 50 mL of tap water per pot once a week for 20 weeks, maintaining a minimum volumetric soil water content for the survival of cork oaks [31].

All the pots were maintained in an acclimatized greenhouse (25 ± 2 °C day and 10 ± 2 °C night). To avoid cross-contamination, pots containing seedlings with different inocula were placed in separate trays. The duration of each watering regime differed because each soil moisture level reflects a distinct seasonal condition in Mediterranean forests, and symptom development occurs at different rates depending on water availability. Following previous studies on *P. cinnamomi* infection dynamics in *Quercus* spp., the duration of each experiment was adjusted to ensure that symptoms could fully develop under each specific moisture regime [17,28–31]. Therefore, disease severity was compared only within each watering treatment at its final assessment point.

2.5. Determination of Soil Water Content

To determine the exact content of water from each experiment, 8 extra pots holding 3 L (510 g) of dry substrate and submitted to each watering treatment, as described above (40 pots in total), were weighed daily for 6 weeks. The water content of the substrate (θ_s) for each watering treatment was calculated as the average difference in weight between the

time of watering (maximum value) and the weight just before the next watering (minimum value) for each pot, expressed as a percentage.

2.6. Symptom Assessment and Data Analysis

The severity of foliar symptoms was assessed weekly for each seedling according to the percentage of yellow, wilted leaves and defoliation on a 0–4 scale: 0 = 0%–10%; 1 = 11%–33%; 2 = 34%–66%; 3 = more than 67%; and 4 = dead foliage [28]. At the end of each experiment, root symptoms (Figure 1) were also assessed according to a similar 0–4 scale referring to the percentage of root necrosis or rootlet absence [28]. Segments from inoculated or control roots were plated on selective NARPH medium (17 g L⁻¹ corn meal agar; nystatin, 27 mg; ampicillin, 272 mg; rifampicin, 10 mg; PCNB, 92 mg; and hymexazol, 50 mg) for the re-isolation of the pathogens [32].

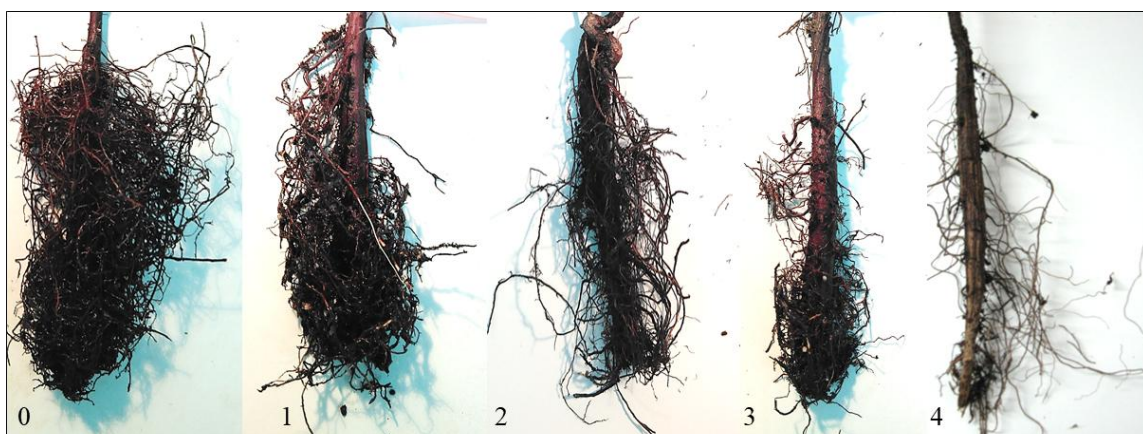


Figure 1. Scale (0–4) of root symptoms of *Quercus suber* L. seedlings inoculated with *Phytophthora cinnamomi* Rands and/or *Pythium spiculum* Paul submitted to different soil moisture conditions.

Data of foliar and root symptoms at the end of the different experiments were tested for homoscedasticity via Levene’s test; then, a one-way ANOVA test was performed, considering inocula as factor. For each analysis, when significance was achieved ($p < 0.05$), mean values were compared among them via Tukey’s HSD test at $\alpha = 0.05$ (Statistix software 10.0, Tallahassee, FL, USA).

3. Results

3.1. Soil Water Content

The average maximum and minimum soil water content (θ_s) for each watering treatment were as follows: 100% for saturation; 73%–100% for high moisture; 50%–77% for moderate moisture; 25%–36% for low moisture; and 9%–12% for drought.

3.2. Inoculation Experiments

Symptoms observed in cork oak seedlings were similar to those previously described in the field or in pot experiments for oaks infected with *P. cinnamomi* or *Py. spiculum* [17,26]: leaf yellowing, wilting, and defoliation; and necrosis and death of feeder roots.

At the end of each experiment, significant differences in final foliar symptoms between inocula (Figure 2) were observed in seedlings submitted to high moisture ($F = 9.70$, $p = 0.0001$), moderate moisture ($F = 6.45$, $p = 0.0019$), and drought ($F = 9.56$, $p = 0.0002$). Under these watering conditions, all inoculated cork oaks showed higher final foliar symptoms compared to the controls, except for those inoculated with *Py. spiculum* under saturation, where foliar symptoms did not differ from those of the control group. In general, seedlings

inoculated with *P. cinnamomi* showed more foliar symptoms than the controls in moisture conditions, where significant differences were detected.

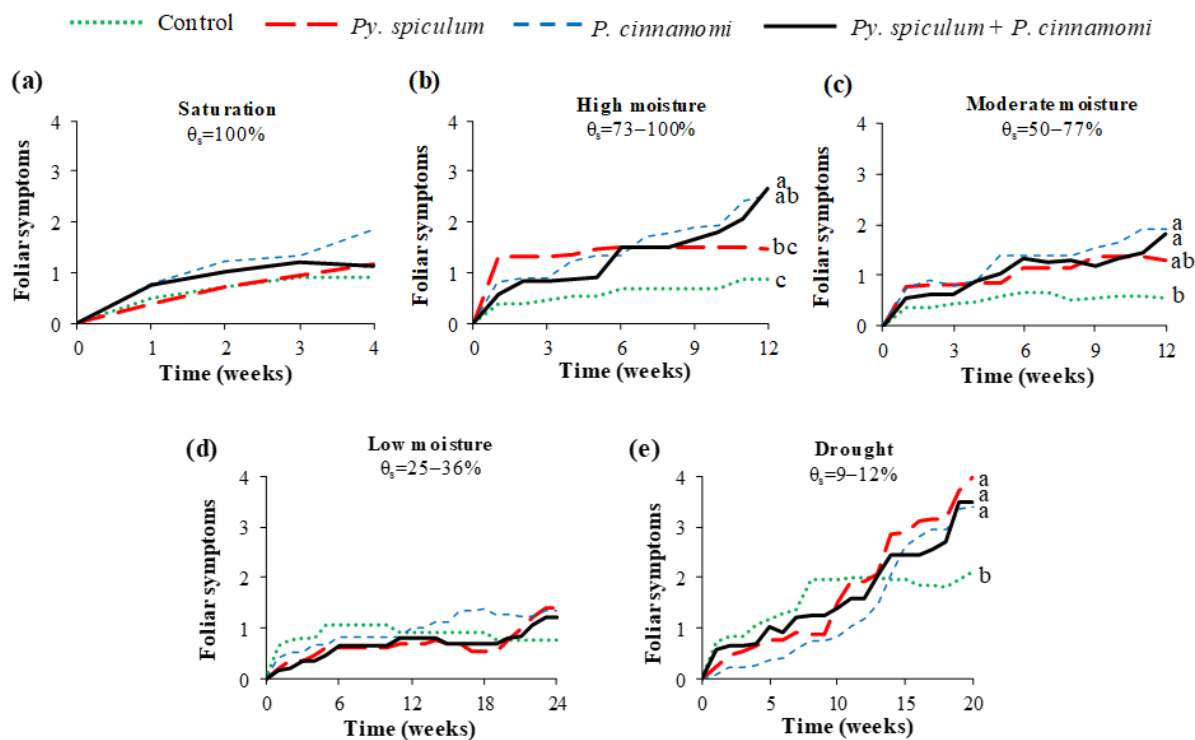


Figure 2. Evolution of foliar symptoms (0–4) of *Quercus suber* L. seedlings growing in uninoculated (control) soil and soils inoculated with *Pythium spiculum* Paul, *Phytophthora cinnamomi* Rands, or *Py. spiculum + P. cinnamomi* and submitted to five moisture conditions: (a) saturation; (b) high moisture; (c) moderate moisture; (d) low moisture; (e) drought. At the end of each experiment, lines with different letters differ significantly ($p < 0.05$) according to Tukey's HSD test.

In terms of root symptoms (Figure 3), there were significant differences depending on inocula in all experiments. Under saturation (Figure 3a), only seedlings exposed to *P. cinnamomi* or *P. cinnamomi* and *Py. spiculum* combined showed significantly higher root necrosis compared with controls ($F = 20.69$, $p < 0.0001$). For high moisture (Figure 3b), all inoculated plants presented root symptoms significantly higher than those of controls ($F = 102.07$, $p < 0.0001$), and root symptoms caused by *P. cinnamomi* or *P. cinnamomi + Py. spiculum* were significantly higher than those induced by *Py. spiculum* alone. Similar results were obtained for moderate moisture (Figure 3c): all the inoculated seedlings showed root symptoms significantly higher than those controls ($F = 31.82$, $p < 0.0001$), with *P. cinnamomi* and the mix of pathogens causing significantly higher root necrosis values than *Py. spiculum* alone. However, when seedlings grew under low moisture conditions (Figure 3d), no significant differences were found among the different inocula ($F = 3.69$, $p = 0.0234$). Finally, when seedlings were droughted (Figure 3e), the control plants already exhibited severe root necrosis, with average scores above 3, and only *Py. spiculum* induced necrosis levels significantly higher than those observed in the controls ($F = 3.17$, $p = 0.0396$).

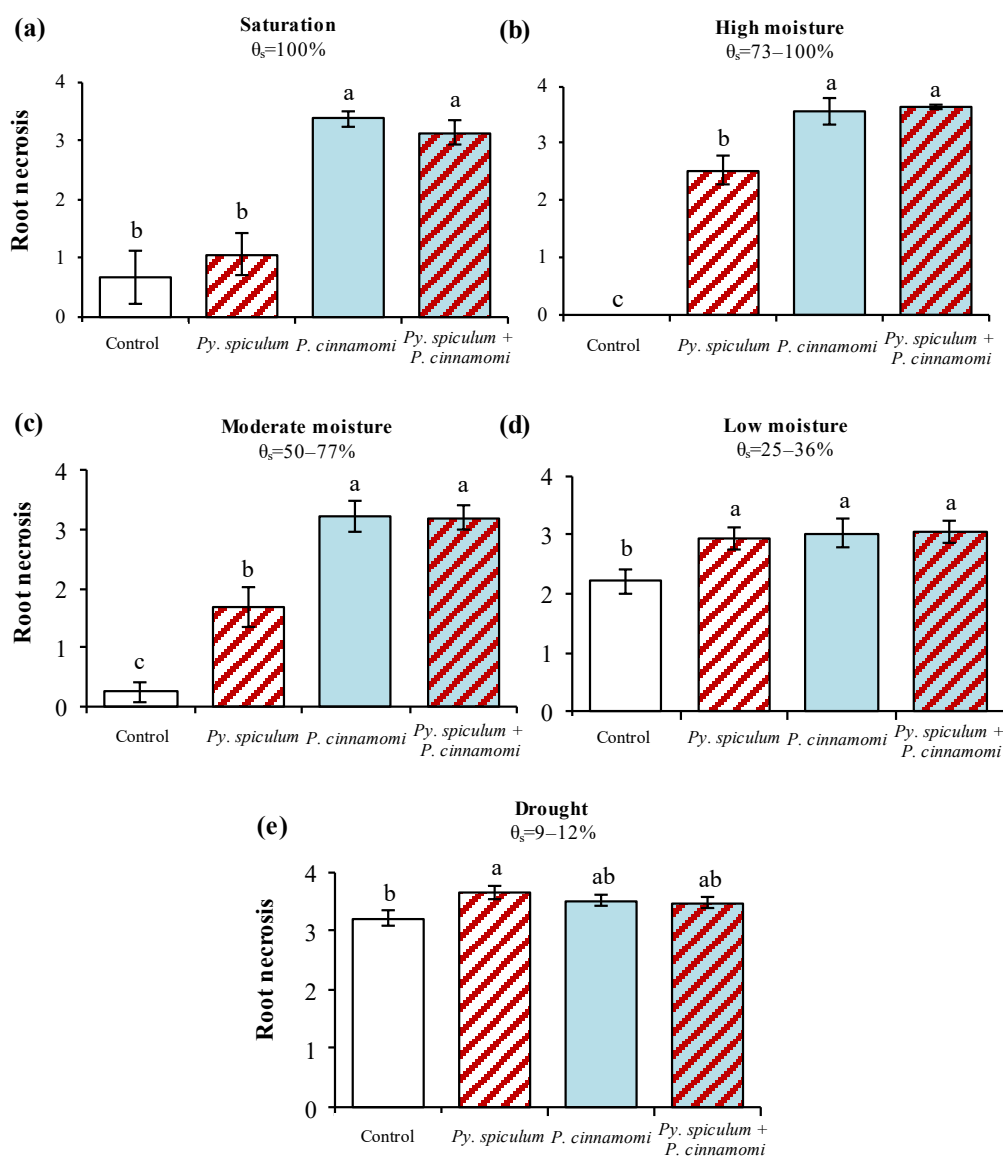


Figure 3. Average values of root symptoms (0–4) ± standard error recorded for cork oak seedlings growing in uninoculated soil (control) and soils inoculated with *Pythium spiculum* Paul, *Phytophthora cinnamomi* Rands, or *Py. spiculum* + *P. cinnamomi* and submitted to saturation (a), high moisture (b), moderate moisture (c), low moisture (d), and drought (e). For each graph, bars with different letters differ significantly ($p < 0.05$) according to Tukey’s HSD test.

3.3. Re-Isolation of Inoculated Oomycetes

In general, *P. cinnamomi* and *Py. spiculum* were re-isolated from symptomatic roots from seedlings inoculated with these pathogens, either separately or mixed. Re-isolation frequencies varied from 3 to 36% of positive isolations. Nevertheless, there were a few remarkable exceptions: (i) under saturation, *Py. spiculum* was always absent from roots coming from seedlings inoculated with only *Py. spiculum*, while it was re-isolated when seedlings were inoculated with both pathogens together; and (ii) *P. cinnamomi* was neither re-isolated from seedlings inoculated with *P. cinnamomi* nor from seedlings inoculated with both pathogens in droughted soils. Neither *P. cinnamomi* nor *Py. spiculum* were isolated from uninoculated control seedlings.

4. Discussion

The present study confirms that soil moisture strongly influences the pathogenic behaviour of *P. cinnamomi* and *Py. spiculum* on cork oak, with each species responding differently across the moisture gradient tested. These patterns align with previous observations regarding the contrasting ecological requirements and pathogenicity of these oomycetes in Mediterranean oak ecosystems. Many *Phytophthora* and some *Pythium* species have been associated with Mediterranean *Quercus* decline [33–41], but field outbreaks of *Q. ilex* or *Q. suber* root rot in southern Europe—and even in northern Africa—have been reported to be mainly associated with *P. cinnamomi* root infections [12,16,26,42–45]. In southern Spain and Portugal, *Py. spiculum* has also been consistently isolated from necrotic roots in declining oak woodlands [26,46], although its virulence has been described as lower than that of *P. cinnamomi* under controlled conditions [25,47]. The contrasting behaviour observed in our experiments under different moisture regimes is consistent with these previous findings.

Oomycete pathogens, both *Phytophthora* and *Pythium* spp., require wet soils for zoospore release and spread to the roots of host plants [20,48], whereas seasonal fluctuations between flooded soil and drought were especially favourable for *P. cinnamomi* epidemics [17,46]. Soil flooding is a common phenomenon in southern oak woodlands (dehesa) in Spain during rainy autumn–winter seasons, but the dry summer character of dehesa soils, in addition to their lack of nutrients and shallowness, is their most remarkable feature [49].

Comparative virulence between *P. cinnamomi* and *Py. spiculum* were previously checked in potted *Q. ilex* and *Q. suber* seedlings submitted to periodic soil flooding, showing *Py. spiculum* to be less pathogenic than *P. cinnamomi* [47], as confirmed in the present work. However, *Py. spiculum* seemed able to compete with the highly virulent pathogen *P. cinnamomi* in the field, sharing *Quercus* hosts and being the main species isolated from symptomatic oak roots in some woodlands [46]. In this work, we observed how different soil water contents determined the preferential oak root infection by *P. cinnamomi* or *Py. spiculum*. *Phytophthora cinnamomi* acted like a virulent pathogen in wet soils ($54\% \leq \theta_s \leq 100\%$) and even at medium water content ($25\% \leq \theta_s \leq 36\%$), causing a high level of necrosis of the oak root system. As expected, this is in good agreement with previous field reports of *P. cinnamomi* infecting *Q. ilex* and *Q. suber*, inducing severe root damage both in waterlogged soils and when soil flooding seasonally occurs for short periods [17,30]. However, *P. cinnamomi* virulence was drastically reduced in drought conditions ($9\% \leq \theta_s \leq 12\%$), becoming unable even to infect oak roots, as ascertained from the lack of reisolation from inoculated seedlings. Recent studies have observed that *P. cinnamomi* cause less infections on *Q. suber* and *Q. ilex* plants under soil moisture conditions near the wilting point [30]. This fact must be directly related to the requirement of soil moisture for sporangia development and zoospore release and spread in *Phytophthora* species [19,50].

In contrast with *P. cinnamomi*, *Py. spiculum* can infect cork oak roots under drought conditions, causing significant root necrosis when compared with roots from uninoculated control saplings, highly damaged by drought alone. However, *Py. spiculum* infections were not detected in flooded soil ($\theta_s = 100\%$) and were less virulent than *P. cinnamomi* in wet soils ($\theta_s \geq 50\%$), as previously reported [25], and they were equally found for holm oaks [47]. This better adaptation of *Py. spiculum* to terrestrial habitats has previously been suggested, considering its inability to release infective zoospores [24], and this has been demonstrated in the current work.

When both pathogens were inoculated together, no synergistic effect was observed under any of the soil moisture conditions considered, and the mixed inoculum consistently induced the same level of root necrosis as *P. cinnamomi* alone. These results do not suggest

direct competition or interaction between the two species; rather, they indicate that their capacity to infect roots is primarily governed by soil moisture. The capacity of *P. cinnamomi* to infect oak roots under a wide range of soil water contents makes it the main root pathogen for Mediterranean oaks, possibly demoting *Py. spiculum* to the role of a secondary root invader. In fact, *Py. spiculum* was reisolated, together with *P. cinnamomi*, from roots inoculated with both pathogens under flooding, even when *Py. spiculum* alone was not able to infect roots under high-water soil conditions. Nevertheless, during the dry summer season in the Mediterranean region, when soil moisture can drop to 5% [49], *P. cinnamomi* would be unable to infect roots, whereas *Py. spiculum* would be able to, adding necrosis symptoms to oak roots already highly affected by drought.

The Mediterranean Basin is considered a global climate change hotspot due to the forecasted rainfall reduction and warming and the expected increase in the occurrence of extreme climate events [6,51]. Trees growing under the increasingly long summer season in this region have evolved a wide range of morphological, physiological, and anatomical adaptations to survive the drought [8,52]. However, the present work indicates a high vulnerability to drought in cork oaks in the absence of pathogens, as previously reported for *Q. ilex* [53]. In contrast, cork oaks showed a low vulnerability to soil flooding, as previously reported in the field [26]. Accordingly, control seedlings maintained under saturated soil for only 4 weeks developed minimal root necrosis, whereas those subjected to low moisture were exposed to 24 weeks of drought and showed severe root damage, reflecting the cumulative effect of prolonged water deficit under pot conditions.

Overall, our results demonstrated how *P. cinnamomi* and *Py. spiculum*, common in Mediterranean oak woodland soils, can infect cork oak roots, causing decline in a wide range of soil moisture, with *P. cinnamomi* infecting roots in wet-to-moderately dry soils, and *Py. spiculum* infecting roots in droughted soils. However, although reflective of root symptomatology (primary symptoms), secondary foliar symptoms were, in general, of lower magnitude than those detected at the root level due to a delay between root infection and aboveground symptom development, as frequently reported for trees with coriaceous leaves, such as evergreen oaks [54]. Despite its intentionally simple experimental design, this study provides relevant information on the interaction between *P. cinnamomi* and *Py. spiculum* in cork oak ecosystems and on how soil moisture influences disease development. Therefore, understanding the effects of global climate change drivers on the health status of trees necessitates a close look belowground, as canopy deterioration does not seem to be a good tool with which to evaluate decline driven by root pathogens.

5. Conclusions

Phytophthora cinnamomi and *Py. spiculum* infect oak roots across a wide range of soil moisture conditions, with *P. cinnamomi* infecting roots in wet-to-moderately dry soils, and *Py. spiculum* infecting roots in droughted soils. At present, and also under the future soil water deficit projected for the Mediterranean region, oaks growing in woodland soils infested by both pathogens are at high risk of root disease outbreaks, which seriously endanger their future.

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