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Response of Herbaceous and Woody Plant Species in Southern Portugal to Cope Oak Decline Associated to *Phytophthora cinnamomi*

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Abstract: The decline of oak canopies in Iberian woodlands is strongly influenced by abiotic and biotic stress factors, such as the oomycete *Phytophthora cinnamomi* which has the capacity to infect a wide range of plant species. Understory plant diversity plays an important role in the epidemiology of *P. cinnamomi* in these ecosystems. This study aimed to identify a set of woody and herbaceous plants that can impact oak decline. Twenty-two herbaceous plant species from three families, and nineteen woody plants (trees and shrubs) from seven families were assessed for their response to infection by *P. cinnamomi*. Most of the herbaceous species did not show evident susceptibility, only a few exhibited significant biomass root reduction and just seven were identified as hosts. Yellow lupin was the only herbaceous species showing high susceptibility. Among the woody plant species, only two shrub and two tree species exhibited disease symptoms. The other ones, mostly hosts, ranged between low susceptible and tolerant. These results highlight the possibility that many of these species can maintain the pathogen active in the soil or even increase its population. In this context, the findings of this study can contribute to effective management strategies to mitigate *Phytophthora* infection in woodland soils.

Keywords: susceptibility; Brassicaeae; Poaceae; Fabaceaea; Lamiaceae; Cistaceae montado

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Citation: Moreira, A.C.; Rodriguez-Romero, M.; Neno, J.; Rodrigues, A.; Calha, I. Response of Herbaceous and Woody Plant Species in Southern Portugal to Cope Oak Decline Associated to *Phytophthora cinnamomi*. *Ecologies* **2024**, *5*, 432–454. https://doi.org/10.3390/ecologies5030027

Academic Editor: Ram C. Sharma

Received: 3 July 2024
Revised: 19 August 2024
Accepted: 23 August 2024
Published: 28 August 2024

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1. Introduction

The conservation of Iberian evergreen oak woodland agrosylvopastoral ecosystems, is threatened by the progressive weakening of their main keystones which are cork oak (*Quercus suber* L.) and holm oak (*Quercus rotundifolia* Lam.) populations. Biotic and abiotic factors are associated to the ecosystem weakening, e.g., poor oak regeneration, one of the most outstanding threats and stressors under a context of climatic change. These ecosystems are commonly called as "montados" in Portugal and "dehesas" in Spain. Montado woodlands are very important to maintain a rich biodiversity and are classified among the habitats protected by the European Community Habitats Directive (Annex I of Council Directive 92/43/EEC on the Conservation of wild habitats and of wild fauna and flora) [1,2].

Portuguese 'montados' are open woodland anthropogenic canopies covering approximately one million hectares, primarily situated in the Alentejo province in the southern part of the country. Furthermore, both oak species exhibit socio-economic relevance in poor rural areas incomes from cork and acorn which is very relevant e.g., a very important income as food for wild species and, in particular, for feeding Iberian pigs during large part of the year.

These ecosystems feature gradients in tree density, age, and height, interspersed with zones of pasturelands or agriculture [3]. The understory canopy of cork and holm oak woodlands integrate grasslands, shrublands and croplands, where cattle, sheep and pigs are raised extensively and shaping the landscape. In general, it is possible to distinguish three sublayers: (i) dense shrubs canopies with strawberry trees (*Arbutus unedo*), (ii) dense shrubs canopies with rockrose and (iii) sparser canopies, including species such as gorse (*Ulex* spp.), sargassum (*Cistus* spp.), heather (*Erica* spp. and *Calluna* spp.), brambles (*Rubus* sp.), rockrose (*Cistus ladanifer* L.), prickly broom (*Pterospartum tridentatum* (L.) Willk.) and brooms (*Cytisus*, *Spartium*, *Retama* and *Adenocarpum*). These species, together with kermes oak (*Q. coccifera* L.), junipers (*Juniperus* spp.) and rosemary (*Rosmarinus* spp.) may also appear associated with (i) and (ii) sublayers [4].

Nowadays, changes in land use, combined with inadequate management practices, pose significant implications in soil fertility and in the presence of the herbaceous and shrubby species of undercover vegetation, reflected in weakened oak trees. Overall, tree death in 'montados' is thus strongly influenced by environmental factors that have an effect on pathogens, insects, hosts and in interactions between these factors. Particularly, the increase in temperature and the reduction and change in the annual distribution of precipitation can increase water stress (by deficit or excess of water) and the vulnerability of trees to the infection of biotic agents [5,6].

The soilborne pathogen *Phytophthora cinnamomi* Rands is an oomycete, that completes its entire life cycle in the soil and plant tissues. Under favorable conditions of soil moisture and temperature, it infects plant roots, causing damage that limits or completely prevents the absorption of water and nutrients, gradually weakening the plants, which, in most cases, ultimately die. This pathogen primarily infects the fine roots of trees and shrubs, invading the vascular tissues responsible for capturing and transporting water and nutrients. When these tissues become inoperative, the roots compromise the supply of water and nutrients to the aerial parts of the plants, leading to their progressive or sudden death. In herbaceous plants the root system is also affected, causing root death, followed by the death of the plant.

In this context, several studies linked decline and death of several *Quercus* species with different oomycetes species, and *P. cinnamomi* is the most frequently isolated species from soil in affected areas [5,7]. Nowadays, montado decline, associated to this pathogen, affects particularly the *Q. suber* and *Q. rotundifolia* trees which are susceptible hosts, what represents one of the biggest threats to the conservation of Iberian forests, putting their environmental, economic and cultural value at risk. The pathogen affects a large number of species worldwide, more than 5000, mostly woody species (trees and shrubs) and also herbs [8].

In cork and holm oak woodlands a representative biodiverse mosaic was identified, integrating plants belonging to as much as 29 families in the shrub and herbaceous sub-canopies [9]. Within these families, include 122 herbaceous species, from which 92% are annual. The presence of *P. cinnamomi* in these ecosystems could be thus critical for the survival of most of these species.

Control of *P. cinnamomi*, in 'montado' ecosystems must include a holistic approach, based on biological control measures, which for effects of forest management are still poorly developed. These should include procedures to limit new infections, improve soil fertility and drainage and reduce livestock. However, the implementation of these management measures, requires knowledge of the susceptibility of the different shrub and herbaceous species, either introduced as pastures as also as co-inhabitants in these ecosystems [10,11].

Susceptibility refers the concept of the predisposition of a host to develop a certain disease or infection, influenced by interaction of genetic and environmental factors [12,13]. A better scientific knowledge is needed about the susceptibility of shrub and herbaceous species to the *P cinnamomi* infection, and thereby about the uncertainties of whether these species can act as potential reservoirs to the epidemiology in cork and holm oak woodlands [10,12]. So, a better selection of shrub and herbaceous species to be used in reforestation or in uncovered land area, would turn more possible.

Tolerance, on other hand, represents a plant strategy for efficient defence against the pathogen, characterized by the plant's ability to limit the spread of the infection, regardless of the level of pathogen multiplication. Resistance is defined as host's ability to limit pathogen multiplication [14,15].

In plant-pathogen system, resistance and tolerance, both coexist [15]. Despite the abundant literature related to plant resistance to pathogens, mechanisms of plant tolerance are in generally poorly understood. This subject has not been extensively studied due to its difficulty on quantification of its levels and intensities [16]. Studies suggested that plants often compensate for damage caused by pathogen infection through the action of several mechanisms, such as increasing chlorophyll concentrations, nutrient uptake, size or number of tissues such as leaves, and delaying senescence and flowering. Plants can also change resource allocation patterns between roots and shoots or between growth and reproduction, for response to the infection [15].

In the whole above context, the main objective of this study was to assess the susceptibility and tolerance to the different trees, shrubs and herbaceous plants to *P. cinnamomi* infection, mainly cohabiting in "montados" or present in neighboring areas.

For that purpose, 22 herbaceous species belonging to Fabaceae, Poaceae and Brassicaceae families many of them used in pastures and 19 woody species (trees and shrubs) within the Cistaceae, Myrtaceae, Lamiaceae, Fagaceae and Pinaceae families common in the oak woodlands were tested under controlled conditions. Most of the selected plant species were previously considered as hosts through empirical or scientific information. In this way, the results of the study should contribute to a better understanding the role played by these species in the epidemiology of oak woodland decline.

2. Material and Methods

Plant native Portuguese species, woody (trees and shrubs) and herbaceous, were selected as potential hosts for evaluation of the level of susceptibility and tolerance to *P. cinnamomi* infection in greenhouse pot trials. Selected shrubs were all native and most of the chosen tree species are commonly found on cork oak woodlands or in neighbour areas. About 77% of the herbaceous species are commonly used as pastures, e.g., *Lolium* spp. and *Trifolium* spp., in extensive agriculture and the remaining e.g., *Diplotaxis* spp. and *Eruca* spp., are native ones.

These trials were carried out in three plant Batches (Table 1) corresponding to distinct times of seedlings supply. The greenhouse physical conditions reflected the seasonality of external environment.

Table 1. List of different species tested for susceptibility to *Phytophthora cinnamomi* infection.

Species	Common Name	Family	EPPO Code
Batch 1-Inoculated in Spring **Woody plants: shrubs**			
Cistus ladanifer L.	Rockrose	Cistaceae	CSTLA
Cistus albidus L.	Big rosete	Cistaceae	CSTAL
Cistus monspeliensis L.	Montpellier rockrose	Cistaceae	CSTMO
Myrtus communis L.	Myrtle	Myrtaceae	MYVCO
Lavandula dentata L.	Lavender	Lamiaceae	LAUDE
Woody plants: trees			
Quercus coccifera L.	Kermes oak	Fagaceae	QUECC
Quercus petrae (Mattuschka) Liebl.	Sessile oak	Fagaceae	QUEPE
Quercus robur L.	Oak	Fagaceae	QUERO
Quercus faginea Lam.	Oak fence	Fagaceae	QUEFG

Table 1. *Cont.*

Species	Common Name	Family	EPPO Code
Cupressus sempervirens L.	Mediterranean cypress	Cupressaceae	CVBSE
Cupressus lusitânica Miller	Cedar of Goa	Cupressaceae	CVBLU
Eucalyptus globulus Labill.	Blue gum	Myrtaceae	EUCGL
Eucalyptus gunnii Hook. F.	Cider gum	Myrtaceae	EUCGU
Eucalyptus nitens Maiden	Shining gum	Myrtaceae	EUCNT
Pinus pinea L.	Stone pine	Pinaceae	PIUPI
Pinus pinaster Aiton	Maritime pine	Pinaceae	PIUPL
Pinus nigra Arnold	Black pine	Pinaceae	PIUNI
Pinus sylvestris L.	Scots pine	Pinaceae	PIUSI
Pinus halepensis Miller	Allepo pine	Pinaceae	PIUHA
Batch 2-Inoculated in Spring Herbaceous plants			
Lupinus luteus L.	Yellow lupin	Fabaceae	LUPLU
Lupinus angustifolius L.	Blue lupin	Fabaceae	LUPAN
Lupinus albus L.	White lupin	Fabaceae	LUPAL
Hordeum murinum L.	Hare barley	Poaceae	HORDMU
Brachypodium distachyon (L.) P.Beauv	Purple false brome	Poaceae	BRCDI
Secale cereal L.	Rye	Poaceae	SECCE
Brassica nigra L.	Black mustard	Brassicaceae	BRSNI
Sinapis alba L.	White mustard	Brassicaceae	SINAL
Diplotaxis tenuifolia (L.) D.C.	Wallrocket	Brassicaceae	DIPTE
Eruca vesicaria (L.) Cav.	Rocket	Brassicaceae	ERUVU
Ornithopus sativus Brot.	Serradella	Fabaceae	OROSA
Vicia sativa L.	Common vetch	Fabaceae	VICSA
Batch 3-Inoculated in Autumn			
Lolium multiflorum Lam.	Annual ryegrass	Poaceae	LOLMU
Lolium rigidum subsp. *rigidum* Gaudin.	Annual ryegrass	Poaceae	LOLRI
Lolium perenne L.	Perennial ryegrass	Poaceae	LOLPE
Dactylis glomerata L.	Cocksfoot	Poaceae	DACGL
Festuca arundinacea Schreb.	Tall fescue	Poaceae	FESAR
Trifolium incarnatum L.	Italian clover	Fabaceae	TRFIN
Trifolium repens L.	White clover	Fabaceae	TRFRE
Trifolium subterraneum L.	Subclover	Fabaceae	TRFSU
Trifolium michelianum Savi	Balansa	Fabaceae	TRFMI
Medicago sativa L.	Alfafa	Fabaceae	MEDSA

2.1. Inoculum and Preparation of Soil and Plants

Soil samples used in the Batch 1 plants (Tables 1 and 2) was a loamy-sand (A) mixed with 10% of a green compost. For Batches 2 and 3 plants (Table 1), another loamy-sand (B) soil sample was used.

Table 2. Physical and chemical properties of soils used in the susceptibility assays.

Texture (1)	Csand (%)	Fsand (%)	Lime (%)	Clay (%)	pH	N (gKg^{-1})	P_2O_5 ($mgKg^{-1}$)	K_2O ($mgKg^{-1}$)	OM (%)
Loamy-Sand (A)	79.8	8.2	3.4	8.6	6.4	1.12	113.6	294.0	5.3
Loamy-Sand (B)	68.2	16.6	5.7	5.5	5,9	0.3	25.0	41.0	27.8

(1)—According International Classification for soil texture; Csand—Coarse sand; Fsand—fine sand; OM—organic matter.

For assuring that soils were free of *P. cinnamomi*, before tests starting, soils samples were air-dried, and were treated for the detection and isolation of *Phytophthora* through trapping and plating on selective media.

Isolates used to inoculation were obtained from roots of diseased trees in field and were kept in a juice agar medium accordingly with the methodology described in Moreira-Marcelino [17]. Both soils were infested with millet seeds (*Panicum miliaceum* L.) colonized by the pathogen, strains mating type A2 (5833 and 1539 from the INIAV fungal collection) referred in Sampaio [18] over three weeks in the dark at 25 °C. In the greenhouse, temperatures ranged between 17 and 27 °C during both spring and autumn. Plants were watered according to their physiological needs, without additional fertilization, and allowed to freely drain excess water.

Physical and chemical properties of both soil mixtures are shown in Table 2.

The plants of shrub and tree woody plants of Batch 1, included 19 species from 7 families, (Table 1) aged between six and eleven months and provided by commercial nurseries. The intraspecies variability was kept as low as possible through continuous assessment of plant height.

Plants were maintained in greenhouse during two months for acclimatization and thereafter transplanted to 10 × 10 × 20 cm diameter pots filled with the loamy-sand (A) soil, prepared as aforementioned, in a ratio of 25 g of millet seeds colonized by both *P. cinnamomi* isolates per 2 L of soil (*w*:*v*). Fifteen pots per each tree species and eight pots per each shrub species were inoculated (infested soil). The same number of pots per species were kept free from inoculum (control).

Herbaceous species in Batches 2 and 3 (Table 1) were obtained through propagation from commercial seeds sown directly in plastic pots (14.5 × 15 × 20 cm) filled with loamy-sand (B) soil (Table 2). Seed weight in each species ranged between 200 and 300 mg per pot, with the exception of species of *Eruca* and *Diplotaxis* with 5 mg per pot and *Brassica nigra* with 18 mg per pot. In each species, five pots were infested and another five pots were free of the inoculum (control). All infested pots were placed in separate trays and randomly on different benches from the no-infested to avoid contamination.

2.2. Plant Response to P. cinnamomi

Woody and herbaceous plant damage, evaluated through root and shoot symptoms and mortality, were visually estimated by an empirical severity score, for classifying species as highly susceptible, moderately susceptible, slightly susceptible, tolerant and host, highly tolerant and no-host, accordingly with criteria adapted from [19] shown in Tables 3 and 4.

At the end of the trial for Batch 1 (16 weeks) and Batches 2 and 3 (8 weeks) the plants in inoculated pots were assessed for *P. cinnamomi* root infection. The difference of the trial periods between Batch 1 and Batches 2 and 3 is due to the respective prevalent perennial and annual cycle of the plants of the three batches.

In Batch 1 the survival woody plants were removed from pots, and roots washed with water, blotted and dried. For both (live and dead) shoot and root systems were examined for evidence of chlorosis, defoliation, dieback, wilt, leaf necrosis, crown reduction, root necrosis, fine root death and plant mortality (%) was also assessed. The inhibition percentage of the total biomass of the average of the replicates was also calculated for each species accordingly with the equation: $[1 - (TBinf/TBninf)] \times 100]$.

In herbaceous plants, Batches 2 and 3, after being harvested, the roots were detached from shoots and the same parameters of Batch 1 were evaluated to determine the level of susceptibility and to assess also the number of colonies formed in soil.

Next, the material from woody and herbaceous species was dried during four days in an oven at 60 °C and weighed for determination of dry biomass. The presence of *P. cinnamomi* was also assessed in the roots of woody and herbaceous plants in both treatments (inoculated and control) accordingly with Moreira and Martins [7]. Roots were washed and examined for necrosis or other signs of infection. Selected small root segments, were surface sterilized and plated onto the selective medium (PARBHy). All plates were

incubated at 24 °C in the dark, during 48–72 h [7]. Thereafter, grown *P. cinnamomi* hyphae were transferred to potato dextrose agar medium (PDA).

The number of *P. cinnamomi* propagules in soil of all herbaceous pots was determined using the method described by Sampaio [18]. The method uses a suspension of each infested soil pot, prepared using 10 g of dried soil in 100 mL of water agar (0.2%) stirred for 2 h and then left to stand overnight. Then, 1 mL of each suspension was pipetted into a Petri dish (90 mm Ø) with PARPHy medium and spread evenly with a hansa. Ten replications were prepared for each sample. The plates were incubated at 25 °C in the dark. After 24 h, the plates were washed in running water to eliminate excess agar and placed again at 25 °C. The number of colonies was counted over the next 48 h and expressed as colony forming units per g of dry soil (cfu/g).

Additionally, for each species, the average of the replicates' inhibition percentage (InR% and InS%) for weight dry biomass of root and shoot of inoculated plants, was calculated (RBinf and StBinf, respectively) by comparison to no-inoculated roots and shoots (RBninf and StBninf, respectively) accordingly with Equations (1) and (2):

$$\text{InR\%} = [1 - (\text{RBinf}/\text{RBninf})] \times 100 \quad (1)$$

$$\text{InS\%} = [1 - (\text{StBinf}/\text{StBninf})] \times 100 \quad (2)$$

Statistical analysis using dry total and root biomass production as dependent variable for woody and herbaceous species was carried out through a general linear model approach for ANOVA, LS means, contrasts between groups, and significance of difference between inoculated and control plants for all combinations. These analyses were carried out with packages Statistica 6.0. Statsoft. USA. 2001 and SPSS (8.0.4) predictive analytical software.

3. Results

3.1. Susceptibility of Woody Species

3.1.1. Trees

Quercus spp.

All oak species tested were infected by *P. cinnamomi*, with different symptoms within a range of susceptibility. *Quercus coccifera* seedlings showed to be the oak species most susceptible to the *P. cinnamomi* infection. Symptoms started just two weeks after inoculation, and four weeks later 80% of infected plants had died. Plants that remained alive, showed marked symptoms. Infected seedlings of *Q. faginea* and *Q. petrae* showed fewer symptoms in the crown, but roots evidenced necrosis with *Q. petrae*, showing a smaller root system. Finally, infected seedlings of *Q. robur*, despite not displaying crown symptoms, showed some root necrosis. Total dry biomass of all the oak species, was statistically different ($p < 0.001$) between infected and control plants (Figure 1) reflecting absolute losses of biomass weight with pathogen infection. These losses evaluated in relative terms by the percent inhibition, were shown as smaller in infected plants of *Q. faginea* (11%) and *Q. robur* (6.8%) by comparison with the other two *Quercus*, reflecting the fact that these species were less susceptible to *P. cinnamomi* infection.

Pinus spp.

The five *Pinus* species tested were infected by *P. cinnamomi*, demonstrating, however, different susceptibility, due to significant difference in the total biomass of these species ($p < 0.001$) alongside with significant interactions "infection × species" ($p < 0.05$). *Pinus halepensis* was the most sensitive to *P. cinnamomi* infection. Infected plants showed initial symptoms just two weeks after planting and 67% of plants died four weeks later. The total biomass produced by these plants differed significantly from no-infected plants ($p < 0.05$) (Figure 2) with an inhibition of 67% compared to the control (Table 3). On contrary, *P. nigra* seedlings exhibited significant tolerance to the infection, since the infected roots and shoots had no symptoms, with even an increase of 20% in total biomass. This result may reflect the plant tolerance to *Phytophthora* infection through production of new roots.

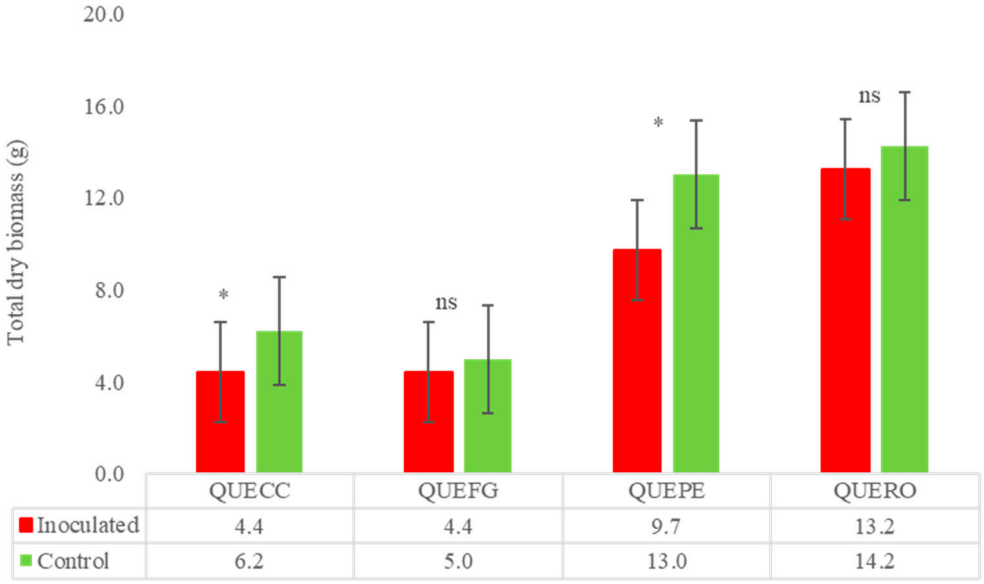


Figure 1. Total dry biomass of *Quercus* species tested for *P. cinnamomi* infection: mean of 15 plants per species inoculated and 15 plants control under controlled conditions, and standard error; * $p < 0.05$; ns—not significant. Species name is in accordance with the EPPO code listed in Table 1.

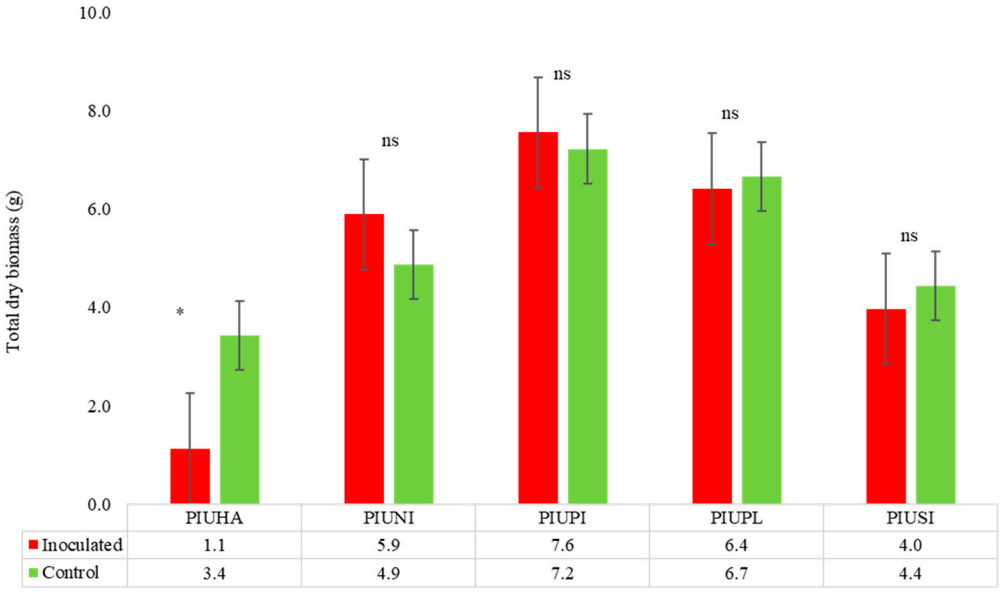


Figure 2. Total dry biomass of *Pinus* species tested for *P. cinnamomi* infection: mean of 15 plants per species inoculated and 15 plants control under controlled conditions, and standard error; * $p < 0.05$; ns—not significant. Species name is in accordance with the EPPO code listed in Table 1.

The symptoms of infected seedlings of *P. pinea* and *P. pinaster* were similar, with leaf chlorosis and wilting, defoliation, and necrosis in some roots. After 16 weeks of inoculation, they were classified as moderately susceptible, with 20% of dead seedlings of *P. pinaster* and 6.7% of *P. pinea*. The response of *P. sylvestris* plants, without mortality, were similar to *P. pinaster* plants, with only some chlorosis in the shoot and a less reduction on the root system, allowing for a classification as slight susceptible (Table 3). The total dry biomass for infected and no-infected plants of *P. pinea*, *P. pinaster*, and *P. sylvestris* species were not significantly distinct (Figure 2). However, in Table 3 it is quite noticeable the biomass reduction of infected plants in *P. halepensis*, by opposition with a biomass increase in *P. nigra* plants and a minor increase in *P. pinea*.

Table 3. Susceptibility categories in 19 woody species inoculated with *Phytophthora cinnamomi* under controlled conditions.

Species	[a] Mortality (%)	[b] Inoculated Plants Nº	Dead Nº	[c] Infection Reaction	Control Nº	[d] Total Biomass Reduction (%)	[e] Category of Susceptibility
Quercus coccifera	80.0	15	12	Symp-host	15	29.0	HS
Quercus faginea	0	15	0	Symp-host/Asymp host field	15	11.2	SS
Quercus petrae	0	15	0	Symp-host	15	25.2	MS
Quercus robur	0	15	0	Symp-host	15	6.8	SS
Pinus halepensis	67.0	15	10	Symp-host	15	67.1	HS
Pinus nigra	0	15	0	Asymp host	15	No-reduction	HT
Pinus pinea	6.7	15	1	Symp-host	15	No-reduction	MS
Pinus pinaster	20	15	3	Symp-host/Asymp host field	15	3.8	MS
Pinus sylvestris	0	15	0	Symp-host	15	10.6	SS
Cupressus lusitanica	0	15	0	Asymp-host	15	15.8	T
Cumpressus sempervirens	0	15	0	Asymp-host	15	No-reduction	HT
Eucalyptus globulus	0	15	0	Symp-host	15	16.1	T
Eucalyptus guinnii	0	15	0	Symp-host	15	8.7	SS
Eucalyptus nitens	0	15	0	Symp-host	15	17.0	SS
Cistus albidus	75.0	8	6	Symp-host	8	57.2	HS
Cistus ladanifer	87.5	8	7	Symp-host	8	36.4	HS
Cistus monspeliensis	12.5	8	1	Symp-host	8	12.9	MS
Lavandula dentata	0	8	0	Asymp-host	8	5.8	T
Myrtus communis	12.5	8	1	Symp-host	8	49.9	MS

[a] Mortality (%) calculated based on number of plants dead after inoculation and which yielded *P. cinnamomi*. [b] Inoculated plants: number of plants that have been in infested soil with or without symptoms. [c] Infection reaction: reaction of inoculated plants in each species, infected and no-infected: Symp-host-infected plants with symptoms in the greenhouse; Symp-host/Asymp-host field- infected plants with symptoms in greenhouse/infected plants without symptoms in field; Asympt-host- infected plants without symptoms in greenhouse. [d] Total biomass reduction %: relationship between total biomass production by inoculated plants compared to the biomass production by control plants. [e] Category of susceptibility: HS: highly susceptible; mortality due to *P. cinnamomi* was ≥60%; disease symptoms included wilt, leaf chlorosis, crown reduction, extensive root and collar rot, death; *P. cinnamomi* was reisolated from root tissue. MS: moderately susceptible; mortality due to *P. cinnamomi* was ≤20%; disease symptoms included slow dieback, wilt, leaf chlorosis, leaf and root area reduction, variable root and collar rot, death; *P. cinnamomi* reisolated from root tissue. SS: slightly susceptible; no mortality due to *P. cinnamomi*; disease symptoms included leaf defoliation and chlorosis, crown reduction, localized lesions on fine roots and smaller root system. T: tolerant; tolerant but host; inoculated plants highlighting slight symptoms as some reduction of leaf area and root system, although the roots are in good conditions; *P. cinnamomi* was reisolated from root tissue, no deaths. HT: tolerant; tolerant but host; inoculated plants remained without symptoms, root biomass could be increased; *P. cinnamomi* was reisolated from root tissue, no deaths (Adapted from [19]).

Cupressus spp.

Although both species of *Cupressus* were infected they showed to be very tolerant. *C sempervirens* seedlings showed no symptoms and *C. lusitanica* showed only a slight reduction in total dry biomass (15.8%) (Figure 3) between infected and no-infected plants. The difference of biomass produced, between the two species was significantly different ($p < 0.001$), as also was the interaction between "infection × species". Total dry biomass

produced by infected plants of *C. sempervirens* differed significantly from no-infected plants ($p < 0.05$) as shown in (Figure 3). This difference resulted from an increase in biomass (24%) compared to the control plants (Figure 3), as it is also observed in other species, such as, in cork oak seedlings [20]. According with the criteria presented in Table 3, both species were tolerant, with *C. sempervirens* considered as high tolerant (Table 3).

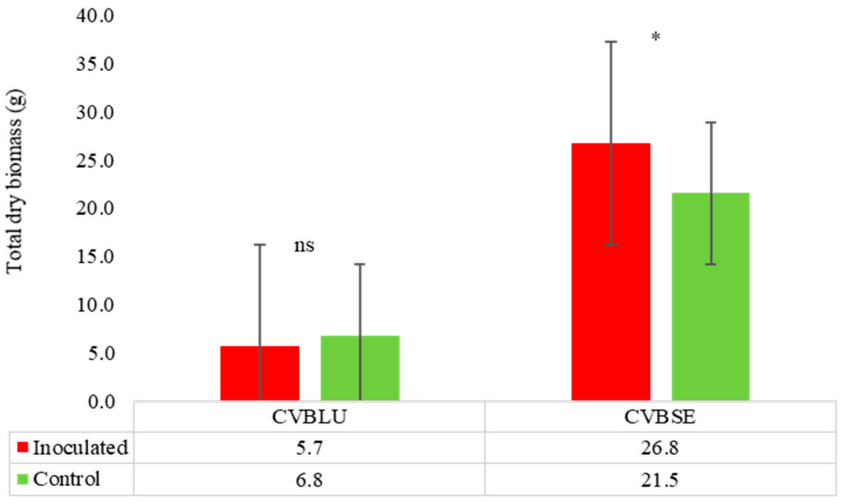


Figure 3. Total dry biomass of *Cupressus* species tested for *P. cinnamomi* infection: mean of 15 plants per species inoculated and 15 plants control under controlled conditions, and standard error; * $p < 0.05$; ns—not significant. Species name is in accordance with the EPPO code listed in Table 1.

Eucalyptus spp.

All the three *Eucalyptus* species tested were infected by *P. cinnamomi*. Infected seedlings of *E. nitens* and *E. guinnii* exhibited slight sensitivity to the pathogen, with leaf area reduction, smaller root system and few lesions on fine roots. On the other hand, few plants of *E. globulus* evidenced a smaller root system than the control without shoot symptoms and a minor total biomass reduction. No dead plants were recorded for these three species. No significant differences were observed between dry biomass produced by infected and no-infected *Eucalyptus* plants (Figure 4).

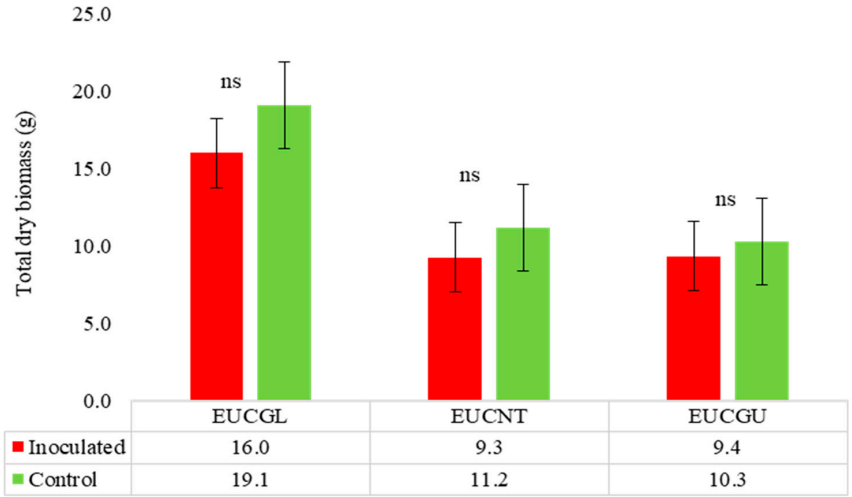


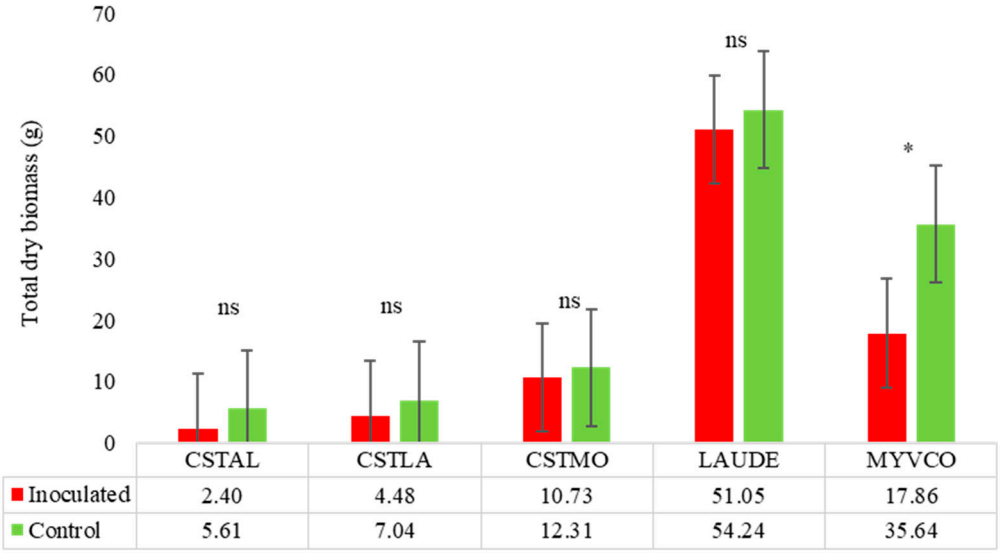
Figure 4. Total dry biomass of *Eucalyptus* species tested for *P. cinnamomi* infection: Mean of 15 plants per species inoculated and 15 plants of control under controlled conditions and standard error; ns—not significant. Species name is in accordance with the EPPO code listed in Table 1.

In *Eucalyptus gunnii* biomass reduction is lower (8.9%) (Table 3), about half the inhibition percent of plants of other two species, which indicates that this species has a less sensitive response to infection.

In summary among the woody tree species examined, plants of *Q. coccifera* and *P. halepensis* demonstrated the highest susceptibility to infection (HS). Symptoms included wilting, dry leaves in the crown, and a root system displaying necrosis, characterized by numerous dead roots, ultimately leading to significant mortality. On contrary, *P. nigra* and *C. sempervirens* species showed to be very tolerant (HT) tree species to the infection.

3.1.2. Shrub Species

All the five native shrub species inoculated were infected by the pathogen, highlighting, however, different susceptibility (Figure 5). Three weeks after soil infestation, infected plants of *C. ladanifer* and *C. albidus* started to show disease symptoms such as chlorotic and dry leaves, defoliation and wilt. The disease progressed and in the fourth week, plants began to die. Harvest occurred six weeks after soil infestation and all the plants of both species were infected with a mortality rate of 87.5% and 75%, respectively. These species thus showed to be highly susceptible to the pathogen under controlled conditions (Table 3).



	CSTAL	CSTLA	CSTMO	LAUDE	MYVCO
Inoculated	2.40	4.48	10.73	51.05	17.86
Control	5.61	7.04	12.31	54.24	35.64

Figure 5. Total dry biomass of shrub species tested for *P. cinnamomi* infection: mean of 8 plants per species inoculated and 8 control (no-inoculated) under controlled conditions and standard error. * $p < 0.05$; ns—not significant. Species name is in accordance with the EPPO code listed in Table 1.

The difference in absolute biomass produced by plants of the three *Cistus* sp. and *Lavandula* sp. was not statistically significant, by contrast with *Myrtus communis* plants (Figure 5) where the difference between the inoculated and the control plants was large. Infected plants of *M. communis* and *C. albidus* exhibited a biomass reduction of about 50% and 57.2%, respectively (Table 3), with evident infection symptoms, such as defoliation, reduction in leaf area, many dead roots and later flowering. Infected plants of *Cistus monspeliensis* showed a lower mortality of 12.5% (Table 3) and exhibit smaller root system than control, and a slower infection progress than the plants of other *Cistus* species.

By contrast to the other four-shrub species tested, infected plants of *Lavandula dentata* did not exhibit symptoms of the disease and showed a minor reduction in biomass of approximately 6% indicating a higher level of tolerance to infection (Table 3).

In short, *C. ladanifer* and *C. albidus* plants exhibited the higher susceptibility to infection, reflected by very high mortality rates and evident disease symptoms. In contrast *Lavandula dentata* plants showed the higher tolerance to the pathogen with nil mortality and no symptomatology. *P. cinnamomi* was recovered from all plants.

Table 3 presents a summary of the determinations carried out on the woody plants of the 19 species tested, classifying their susceptibility according to these parameters. The main results concern infection reaction, mortality (%), total biomass reduction (%) and category of susceptibility. Definitions of the variables assessed are shown in the legend of Table 3.

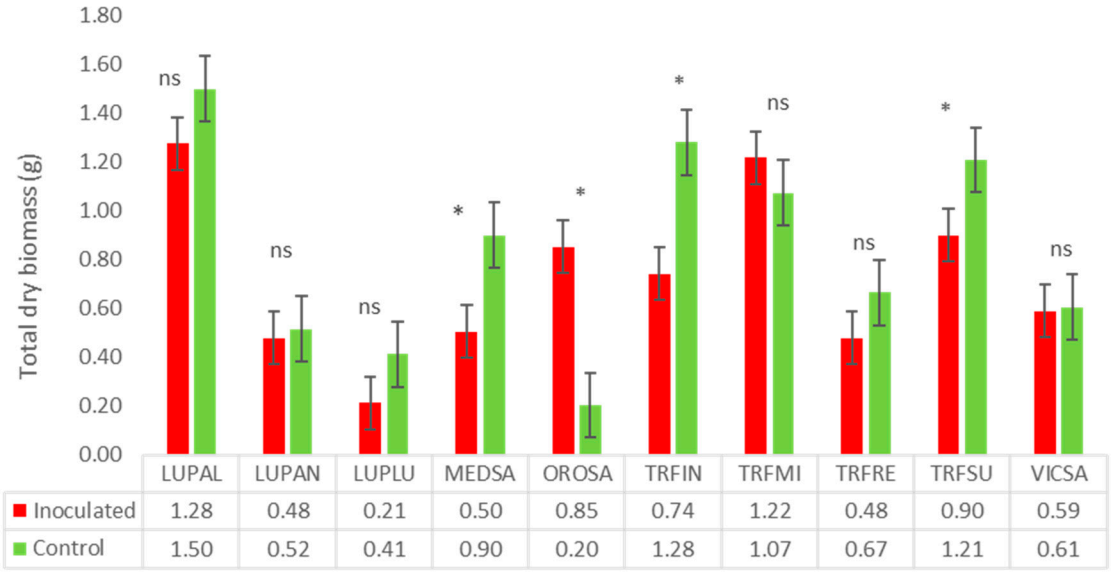
Pinus halepensis and *Quercus coccifera* showed to be high susceptible (HS) to the pathogen with mortality rates as high 67% and 80% respectively, with high biomass losses of 67% and 29%. The two high tolerant species *P. nigra* and *C. sempervirens* (HT) showed no biomass loss and nil mortality. The three tolerant species (T) *Eucalyptus globulus*, *Cupressus lusitanica* and *Lavandula dentata* had an average biomass loss of 12,6% and nil mortality.

3.2. Susceptibility of Herbaceous Species

3.2.1. Fabaceae Family

Within the Fabaceae family, a notable interaction "species × infection" was observed, highlighting significant variations among species in their susceptibility to the pathogen.

In this family, the species of *Lupinus* spp. and *Ornithopus sativus* stand out as hosts. In *Lupinus* spp., we observed the lowest, albeit no-significant difference in total dry biomass production between infected and no-infected plants in *L. angustifolius* and *L. albus*, which exhibited no relevant symptoms. Conversely, *L. luteus* demonstrated more pronounced external symptoms, including the 56% of dead plants specifically, emerged as highly susceptible to *P. cinnamomi* infection (Table 4). Although there were no significant differences in mean total dry biomass production among the three species (Figure 6).



	LUPAL	LUPAN	LUPLU	MEDSA	OROSA	TRFIN	TRFMI	TRFRE	TRFSU	VICSA
Inoculated	1.28	0.48	0.21	0.50	0.85	0.74	1.22	0.48	0.90	0.59
Control	1.50	0.52	0.41	0.90	0.20	1.28	1.07	0.67	1.21	0.61

Figure 6. Total dry biomass of Fabaceae species tested for *P. cinnamomi* infection: mean with standard error from 5 inoculated plants and 5 control plants under controlled condition; * $p < 0.05$; ns—not significant. Species name is in accordance with the EPPO code listed in Table 1.

The response of *O. sativus* was very interesting with 18% of dead plants (10 plants) (Table 4), four weeks after infestation. At the end, the infected survived plants showed a good development with a significant increase in biomass by comparison with no-infected ($p < 0.05$) (Figure 6).

Comparing the total biomass of the *Trifolium* spp. it was verified that the differences in treatment (infested vs. no-infested soil) between the four species proved to be statistically significant ($p< 0.05$). Plants of *T. michelianum* and *T. repens* stands out with inoculated plants showing a minor root biomass reduction (Table 4), however, not statistically significant (Figure 6). On contrary, *T. subterraneum* and *T. incarnatum* showed statistically significant

differences ($p < 0.05$), evident in particular at the root with a reduction of 43% and 76%, respectively (Table 4).

Vicia sativa plants were very tolerant with no deaths and no evidencing symptoms, with similar total biomass in inoculated and control plants. Lastly, *M. sativa* showed a high statistically significant difference in total biomass, ($p < 0.05$) between treatments (Figure 6), with a decrease by the inoculated plants, particularly at the root biomass, with a reduction of 61%.

In summary, some species exhibited only minor reductions, such as, *Trifolium repens*, *T. michelianum*, and *Lupinus albus*, while others demonstrated significant reductions, particularly in root biomass, such as, *Medicago sativa*, *Lupinus luteus*, *Trifolium incarnatum*, and *T. subterraneum.* On contrary, other species showed an increase in both root and shoot biomass, such as, *V. sativa* and *Ornithopus sativus*.

On this family some species increased *P. cinnamomi* inoculum in soil, such as, *Lupinus luteus*, *L. angustifolius* and *O. sativus* plants, showing a high number of *P. cinnamomi* propagules in soil, after two months of growth, which may cause some concern. This result indicates that these species could contribute, with favourable edaphic conditions, to maintain and increase the population of the pathogen in the soil. The other species inoculated, although not infected but showing some root reduction, may suggest some root impact with the presence of the pathogen although with a level of tolerance.

In inoculated Fabaceae plants, a comparison of the mean biomass produced by shoot with the mean total biomass, revealed a strong correlation between total biomass and mean shoot (96%) (Figure 7). However, the correlation between root biomass and total biomass was lower, (52%) (not shown). This relationship underscores the greater biomass produced by the shoot observed in Fabaceae species, indicating a higher susceptibility to infection in these species as evidenced by root reduction.

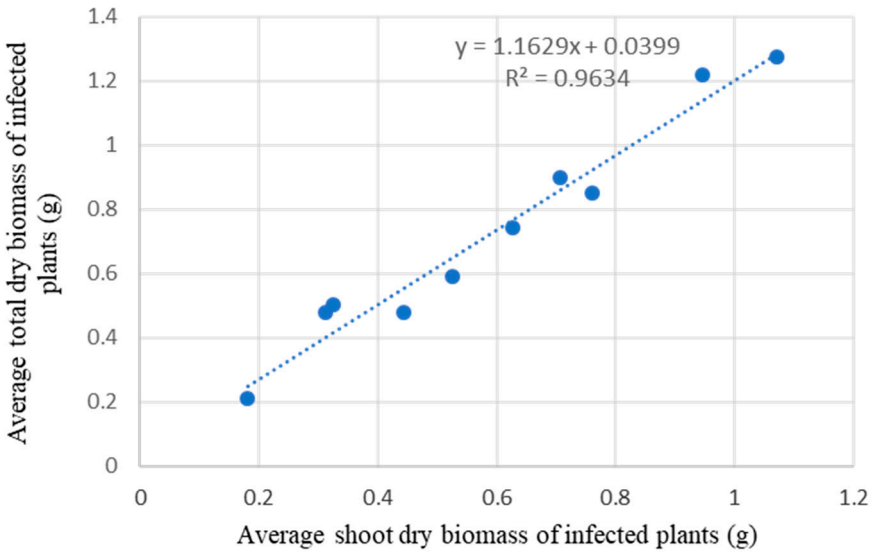


Figure 7. Linear relationship between average total dry biomass and average shoot dry biomass of tested Fabaceae plants.

3.2.2. Poaceae Family

In the species tested in Poaceae family, it was found that there were significant differences in total biomass produced between species and significant interaction effects "species × infection". Among the inoculated species only *Brachypodium distachyon* and *Hordeum murinum* plants have been shown to be hosts of *P. cinnamomi* (Table 4). Infected plants of *B. dystachyon* exhibited a minor reduction, in both root and shoot (Figure 8), while plants of *H. murinum* exhibited a slight disparity in biomass between shoot and root. This resulted in 12% reduction in root biomass and no reduction in shoot biomass with an increase in 40% (Table 4).

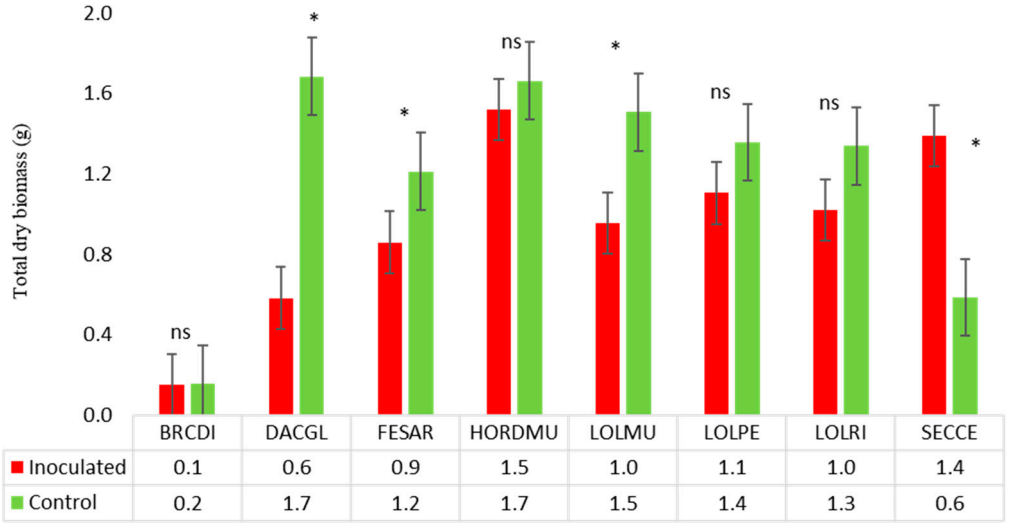


Figure 8. Total dry biomass of Poaceae species tested for *Phytophthora cinnamomi* infection: mean with standard error from 5 inoculated plants and 5 control plants, under controlled conditions; * $p < 0.05$; ns—not significant. Species name is in accordance with the EPPO code listed in Table 1.

It is possible to verify differences statistically significant ($p < 0.05$) between total biomass produced by inoculated and control plants of *Lolium multiflorum*, *Dactylis glomerata*, *Festuca arundinaceae* and *Secale cereal*, which indicates differences in response to *P. cinnamomi* presence (Figure 8). But while inoculated plants of *D. glomerata*, *F. arundinaceae* and *L. multiflorum* showed a high decrease (between 25% and 65%) in both root and shoot compared to the controls, plants of *S. cereale* showed an increase (no reduction-Table 4) in biomass of both root and shoot comparing to the controls. Inoculated plants of *Lolium perenne* and *L. rigidum* showed a very similar behaviour with no significative small differences of biomass produced in comparison to the control. At last *S. cereale* showed to be tolerant with an increase in biomass in both root and shoot (Figure 8).

Concerning pathogen inoculum density in the soil, our observations regarding the tested species within the Poaceae family suggest that these species may not have a significant impact on the pathogen multiplication in the soil as evidenced by the relatively low soil inoculum (Table 4). However, there was an exception noted with barley (*Secale cereale*), which, despite being asymptomatic, exhibited a notably higher colony count in the soil (>100 colonies per gram of dry soil). This finding is quite curious as this species has not been infected, however this result may suggest the potential contribution of a tolerant species as *S. cereale* to the maintenance, multiplication and dissemination of the pathogen.

A linear correlation between averages of total biomass and root biomass of inoculated Poaceae plants was expressed in Figure 9, and its adjustment indicates that 69% of the total biomass is produced by the roots which means that it contributes more to the total biomass than the shoot which explains only 22%. In fact, these species were more tolerant with less infected roots than the Fabaceae plants.

3.2.3. Brassicaceae Family

For the Brassicaceae tested, differences in total biomass between inoculated and control plants were statistically significant between all species ($p < 0.05$) as illustrated in Figure 10. Inoculated plants of *E. sativa* and *B. nigra* exhibited greater biomass production compared to the controls. Specifically, the shoot biomass of these species increased by 54% and 51%, respectively, while root biomass experienced only a slight reduction of 8.2% and zero (no reduction), respectively (Table 4). *Brassica nigra* and *E.sativa* were the species that exhibited behaviour more consistent with expectations for this family [20] that is, without reduction in biomass and no infection. However, in *D. tenuifolia* a significant reduction in

root biomass of approximately 64% was observed, while shoot showed a minor increase (Figure 10; Table 4).

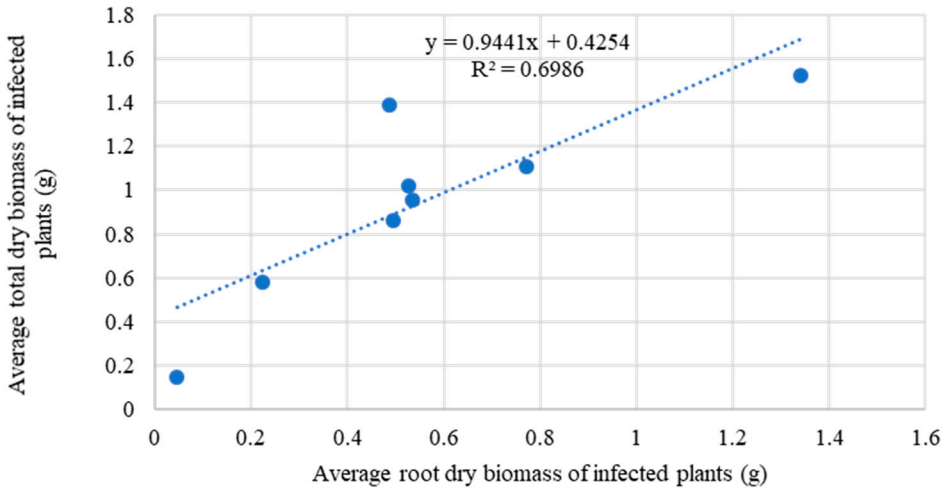
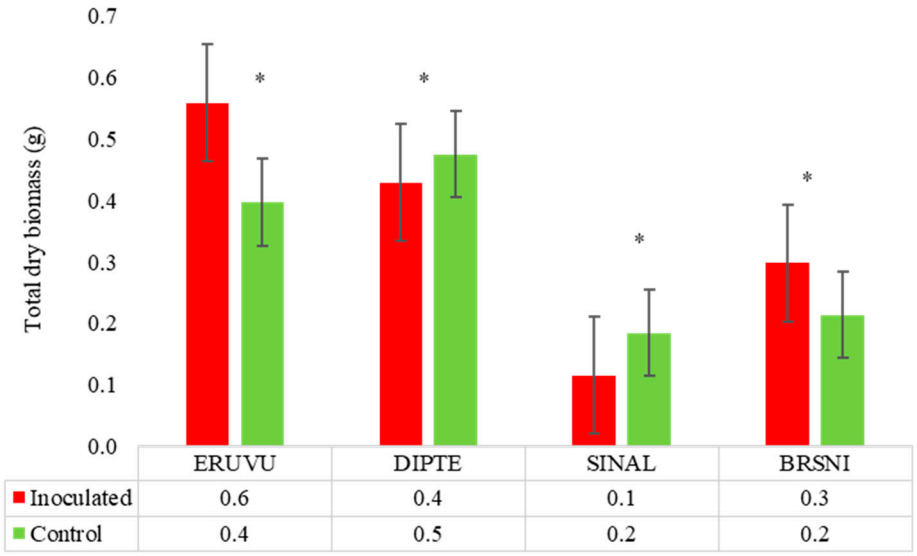


Figure 9. Linear relationship between average total dry biomass and average root dry biomass of tested Poaceae plants.



	ERUVU	DIPTE	SINAL	BRSNI
Inoculated	0.6	0.4	0.1	0.3
Control	0.4	0.5	0.2	0.2

Figure 10. Total dry biomass of Brassicaceae tested species for *Phytophthora cinnamomi* infection: mean with standard error from 5 replicates inoculated and 5 control (no-inoculated), under controlled conditions; * $p < 0.05$. Species name is in accordance with the EPPO code listed in Table 1.

An important aspect to consider is the effect of the interaction plant-pathogen. In Table 4, a notable observation is the high number of *P. cinnamomi* colonies detected in *B. nigra* soils (85 cfu per g dry soil). The observation of increased inoculum in the soil with *B. nigra* suggests that this species may contribute to the maintenance and increase the pathogen population in the soil what contrasts with the result of the other species within Brassicaceae family in this study where a low number of colonies was detected. Species from Brassicaceae family presented anti-*Phytophthora* effect. In fact, *B. nigra* has been use as a fumigated species in field to control *P. cinnamomi* population [21].

During this study, *D. tenuifolia* exhibited a markedly different development compared to previous studies of Sampaio [18] and Moreira et al. [20]. In earlier research, this species showed no susceptibility to the pathogen, displaying neither reductions in biomass nor symptoms, indicative of its tolerance. This was consequence of its inhibitory effect on *P. cinnamomi* activity. This distinct behaviour resulted in its data being excluded from the

regression calculation (Figure 11). A linear correlation of 98% (Figure 11) was observed between averages of root and shoot biomass produced by infected plants of three Brassicaceae species tested (*B. nigra*, *E. vesicaria* and *S. alba*) suggesting a balanced behaviour of the whole set in presence of *P. cinnamomi*. This was the best linear fit achieved between biomass produced by infected plants. However, if we add data of *D. tenuifolia* the adjustment decreases to 77% (not shown), which indicates less root biomass production.

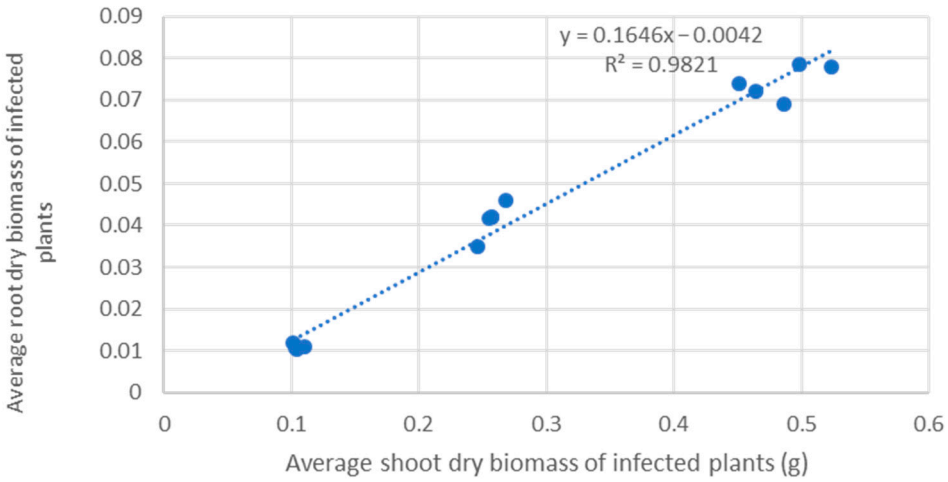


Figure 11. Linear relationship between averages root and shoot dry biomass of tested Brassicaceae plants.

Table 4 expresses the results of whether *P. cinnamomi* infection was present in the roots of 22 herbaceous plants in both treatments. The main variables cited in Table 4 are: infection reaction, mortality (%), shoot and root biomass reduction (%), category of susceptibility and colonies number (cfu/g soil). Definitions of the variables assessed are shown in the legend of the table. Table 4 provides a scale summary of the susceptibility of herbaceous species tested based on the characteristics indicated in reference [19]. It's important to note that this list serves as an indication rather than a definitive classification, given that the assessment was conducted under controlled conditions.

Host species as *Lupinus luteus*, and *L. angustifolius* presented high inoculum density of 49 and 162 cfu/g soil, with a significant impact on the epidemiology of the disease. Although the *Ornithopus sativus* host presented a high inoculum with 61 cfu/g soil, it did not show many symptoms and at the end did not show any reduction of root and shoot biomasses. The behaviour of this species raises some doubts regarding its impact on the epidemiology of the disease. It is also important to highlight the potential effect of the high inoculum of the pathogen detected in the soil of uninfected and tolerant species, such as *B. nigra* and *S. cereale*.

Another aspect to be highlighted, is the fact, that there are non-host plants, which nevertheless present high root reduction, such as *Dactylis glomerata*, *Lolium multiflorum*, *Trifolium incarnatum* and *Medicago sativa*. However, these species do not show a tendency to increase the pathogen inoculum in the soil.

Of the 22 herbaceous species tested, 15 were shown as slightly susceptible (SS) to the pathogen with nil mortality and averages root and shoot biomass reductions of 28.7% and 22.9%, respectively. The *L. luteus* species (HS) showed a mortality of 56% and root and shoot biomass reductions of 40.6% and 49.5%, respectively. The five tolerant species (T) were: *Vicia sativa*, *Secale cereale*, *Eruca vesicaria*, *Diplotaxis tenuifolia* and *Brassica nigra.* Their mortality and root and shoot biomass reductions were overall nil.

Table 4. Susceptibility categories in 22 herbaceous species inoculated with *Phytophthora cinnamomi* under controlled conditions.

Species	[a] Mortality (%)	[b] Inoculated Plants N°	[c] Infection Reaction	Control Plants N°	[d] Root Biomass Reduction (%)	[e] Shoot Biomass Reduction (%)	[f] Colonies Number cfu/g Soil	[g] Category of Susceptibility
Trifolium incarnatum	0	98	Symp-no-host	98	76.2	13.5	5	SS
T. repens	0	80	Asymp-no-host	99	2.8	32.4	17	SS
T. subterraneum	0	112	Asymp-no-host	112	43.1	8.9	12	SS
T. michelianum	0	90	Asymp-no-host	90	11.7	No reduction	20	SS
Lupinus angustifolius	0	36	Asymp-host	27	14.4	5.6	162	SS
L. luteus	56.0	18	Symp-host	22	40.6	49.5	49	HS
L. albus	0	18	Symp-host	24	2.7	9.52	2	SS
Ornithopus sativus	18.0	56	Symp-host	109	No reduction	No reduction	61	MS
Vicia sativa	0	72	Asymp-no-host	81	No reduction	2.9	21	T
Medicago sativa	0	72	Symp-no-host	72	61.1	19.6	23	SS
Lolium multiflorum	0	128	Asymp-no-host	92	31.0	31.0	13	SS
L. rigidum	0	93	Asymp-no-host	93	21.1	24.3	28	SS
L. perenne	0	86	Asymp-no-host	86	29.9	29.9	8	SS
Dactylis glomerata	0	73	Symp-no-host	73	59.3	59.3	22	SS
Festuca arundinacea	0	80	Asymp-no-host	80	24.1	24.1	5	SS
Brachypodium distachyon	0	67	Asymp-host	126	5.6	5.6	22	SS
Hordeum murinum	0	53	Asymp-host	102	12.4	No reduction	2	SS
Secale cereale *	0	17	Asymp-no-host	19	No reduction	No reduction	125	T
Eruca vesicaria	0	44	Asymp-no-host	47	8.2	No reduction	23	T
Diplotaxis tenuifolia	0	38	Asymp-no-host	38	64.0	No reduction	23	T
Sinapis alba	0	145	Symp-host	100	35.0	35.0	3	SS
Brassica nigra *	0	43	Asymp-no-host	53	No reduction	No reduction	85	T

[a] Mortality (%) calculated based on number of plants dead after inoculation and which yielded *Phytophthora cinnamomi;* [b] Inoculated plants: number of plants that have been in infested soil with or without symptoms; [c] Infection reaction: reaction of inoculated plants in each species, infected and no-infected; Symp-no-host: plants with biomass reduction >40%, but not infected; Asymp-no host: plants without symptoms (some with root reduction) and not infected (no yielded *Phytophthora cinnamomi*); Asymp-host: plants without symptoms, but infected; Symp-host: plants infected and with symptoms; [d] Root biomass reduction (%):relationship between root biomass production by inoculated plants compared to the root biomass control plants defined in Equation (1); [e] Shoot biomass reduction (%): relationship between shoot biomass production by inoculated plants compared to the shoot biomass control plants defined in Equation (2).; [f] Colonies Number cfu/g soil: colony-forming units per g dry infested soil; [g] Category of susceptibility: HS: highly susceptible; mortality due to *P. cinnamomi* was ≥50%; disease symptoms included wilt, defoliation, leaf chlorosis, shoot reduction, root rot and death; *P. cinnamomi* was reisolated from root tissue. MS: moderately susceptible; mortality due to *P. cinnamomi* was ≤20%; disease symptoms included wilt, leaf chlorosis, leaf area reduction, and death; *P. cinnamomi* reisolated from root tissue. SS: slightly susceptible; no mortality due to *P. cinnamomi*; slight disease symptoms included some leaf and root area reduction; *P. cinnamomi* was not reisolated from root tissue. T: tolerant: plants highlighting slight reduction or no reduction of leaf area and root system, although the roots are in good conditions; *P. cinnamomi* was not reisolated from root tissue. (Adapted from [19]); *—Species that were not hosts but showed a high number of colonies in soil.

4. Discussion

This study has determined the level of susceptibility of 19 woody and 22 herbaceous species to *P. cinnamomi* infection. The majority of these plants are annuals, with a few perennials among them, and many were previously not known to be susceptible to the pathogen. The 41 species tested under controlled conditions exhibited varying degrees of

susceptibility/tolerance to *Phytophthora* dieback, allowing for the isolation of the pathogen from both symptomatic and asymptomatic plants. The results regarding the susceptibility of the 41 species are categorized and presented in two lists (Tables 3 and 4). However, it's important to note that these lists are only indicative, not definitive. They provide insights into the potential impact of *P. cinnamomi* on vegetation, whether native or cultivated. Controlled conditions provided optimal circumstances for pathogen development. Nevertheless, it's crucial to recognize that the response to infection in the greenhouse may differ from that observed in the field. Indeed, environmental factors such as precipitation, temperature, and soil type, vary in the field and influence the manifestation of the disease differently compared to controlled conditions. Thus, the host response under controlled conditions may not accurately reflect the typical response observed in field conditions [22] but it is indicative. Additionally, hosts of *P. cinnamomi* may exhibit no apparent symptoms of infection in natural settings [23]. Nonetheless, in this study results remain comparable, as all species were evaluated under similar controlled conditions.

4.1. Response of Woody Species

In all 19 tested woody species, trees and shrubs, root samples yielded *P. cinnamomi*, which indicates that they were hosts of the pathogen. The majority of these have already been referred as hosts by other authors, whether in the field, nurseries or under controlled conditions [12,24,25]. Of the 19-woody species, four were highly susceptible, three moderately susceptible, six slightly susceptible and seven presented some tolerance. It was also clear from the results of this study, that there was considerable variation in the disease expression within the correspondent families and genera.

In the pine trees tested, a notable variation in behaviour within genera was observed. For instance, while *P. halepensis* exhibited high susceptibility, *P. nigra* displayed significant tolerance. Also, *P. pinea* (stone pine) showed moderate susceptibility under controlled conditions. *Pinus pinaster* plants, also included in the study, provided an interesting case study, highlighting the influence of environmental conditions on potential plant infection by the pathogen. Under controlled conditions, this species displayed moderate susceptibility with minor symptomatology and mortality. This contrasts with previous reports of asymptomatic behaviour in field conditions, indicating a high level of tolerance to the pathogen [16]. On the other hand, for *P. pinaster* in the Mediterranean basin, a study [26] indicated that maritime pine decline seemed driven by a combination of the predisposing and inciting abiotic factors (microenvironment and drought stress) and biotic factors such as the plant parasite *Viscum album*, however, without having found *P. cinnamomi* or other root pathogenic fungi.

Among the tested *Quercus* species, *Q. faginea* and *Q. petrae* exhibited slight susceptibility to infection, consistent with findings from other studies with the same species [25,27,28]. In fact, these authors found that the fine roots of these two Quercus species presented less damage than in other more susceptible, such as *Q. suber* and *Q. rotundifolia*. In the field, other studies [25,29] confirmed that *Q. faginea* was a species with tolerance to the disease caused by *P. cinnamomi*, showing no mortality and minor root symptoms. On the contrary, *Q. coccifera* proved to be very susceptible with a high number of dead plants.

Regarding the *Eucalyptus* species tested, all of them have previously been confirmed as hosts by other authors [12]. Under controlled conditions, *E. globulus*, *E. gunnii*, and *E. nitens* plants were infected by *P. cinnamomi*, but they did not exhibit very evident symptoms of the disease. In Australia, a high degree of tolerance was observed in *E. globulus* plants towards this pathogen considering it as a "field resistant" species [29] what means that this species has the ability to limit pathogen multiplication in the field [15]. In South of Portugal the pathogen has already been isolated from roots of *E. globulus* trees in the field (Moreira 2018, results not published) however, the trees showed only slight symptoms. Recently, in central of Portugal, other *Phytophthora* species, as *P. hibernalis*, *P. multivora* and *P. niederhauserii* were isolated from *E. globulus* plantations, whose trees exhibited evident decline symptoms [30]. The study was the first report of these three *Phytophthora* species

on *E. globulus* in Portugal. The rise in the detection of new organisms serves as an indicator of the introduction of exotic harmful organisms in Europe. These new pests are frequently introduced inadvertently through the extensive intercontinental trade of living plants. Many of them are only identified years after establishment, rendering their eradication nearly impossible, especially in the case of pathogens [31]. The involvement of multiple *Phytophthora* spp. on *E. globulus* plantations in Portugal is of particular concern due to the alien species detected and due to its potential dissemination into other natural ecosystems.

Some species, such as *Pinus nigra* and *Cupressus sempervirens*, demonstrated a notable level of tolerance, wherein the host effectively countered the effects of pathogen infection by increasing biomass root production. Other authors have observed similar responses in other species, considering this stimulation as a plant reaction to *Phytophthora* infection [32–35]. A similar reaction was described by other authors [36] in infected young *Quercus suber* seedlings. This involved an increase in net photosynthetic rates aimed at mitigating the loss of root functionality. These studies demonstrated that under certain conditions, plants may exhibit the ability to get mechanisms to compensate de damage caused by the infection.

Our results showed different levels of susceptibility among shrubs species tested. Infected plants of *Cistus ladanifer* and *C. albidus*, exhibited high symptomatology and susceptibility to the pathogen, while other shrubs such as *Lavandula dentata* when infected, became asymptomatic and exhibited an evident tolerance to the pathogen.

Thus, in a 'montado' it is possible to find infected plants of the natural flora such as *Calluna vulgaris* and *Cistus populifolius* presenting evident symptoms, while others remain asymptomatic, such as, *Arbutus unedo*, *Ulex* spp. and *L. dentata* and *L. dentata* [7]. All these species are native from southern Portugal, present in woodland areas, so that the mitigation of this pathogen can be compromised, since some of these species are asymptomatic hosts contributing to maintaining the pathogen population. Both tree and shrub community can have a strong impact on the amount of pathogen inoculum in the soil and on its microbial community [37,38].

4.2. Response of Herbaceous Species

Knowledge of the susceptibility to infection caused by *P. cinnamomi* in herbaceous plants has been neglected in relation to the larger plants, as trees species. Regarding herbaceous plants, our findings indicate significant differences in total dry biomass between inoculated and control plants (no-infested soil). During this study, many of the tested species belonging to the three families Fabaceae, Poaceae and Brassicaceae were not infected.

The infection of annual and perennial herbaceous plants by *P. cinnamomi* was referred by [39], despite the prevailing belief that the pathogen did not affect these plants. In the same way, previous studies [40] indicated that, under favourable field conditions herbaceous plants could contribute to increase the pathogen's inoculum density and contributing to the pathogen's persistence in soil, particularly in the areas of Mediterranean ecosystems. Accordingly, based on these findings, our study revealed that 32% of the 22 herbaceous species tested were found to yield *P. cinnamomi* and were considered hosts. By comparison, other studies already identified *L. luteus* and *L. angustifolius* as hosts showing disease symptoms [12,41,42]. Our results indicated that *L. luteus* is a very susceptible species that contributed to increase and maintain the pathogen in the soil, what is line with other studies [40,43]. The infection of this species leads to new production of chlamydospores in infected roots and zoospores in the soil [42], enhancing *P. cinnamomi* inoculum densities and causing thereby new infections [40]. *Lupinus* species, particularly *L. luteus* is still widely used in Portuguese "montado" woodlands as pastures for animal feed and soil improvement so, it would be prudent to avoid using them in areas infested with the pathogen.

It was observed that certain species, mostly no-hosts, exhibited reduction biomass, particularly in their roots. These species included *Trifolium incarnatum*, *T. subterraneum*, *Medicago sativa*, *Lolium multiflorum*, *L. rigidum*, *Dactylon glomerata* and *Sinapis alba* and

Diplotaxis tenuifolia. Many of these species are important annual plants as for example, ryegrasses, such as, *L. multiflorum* and the perennial lucerne *Medicago sativa* which are widely used as forage options in Mediterranean conditions. However, *P. cinnamomi* was not re-isolated from the roots of these plants, with the exception of *S. alba*, which is indeed a host. By the end of our experiment, the number of propagules detected in the potting infested soils of all these no-hosts species was low, suggesting that these plants may not significantly contribute to maintaining the pathogen's activity or facilitating its dissemination. Nevertheless, the biomass reduction observed in most of these species, despite not being infected, raises concerns. Our findings underscore the importance of understanding the role of different plant species in pathogen dynamics, contributing to more effective disease control strategies in agriculture.

On contrary, asymptomatic species, such as *Ornithopus sativus*, *Secale cereale*, and *Brassica nigra*, exhibited a high number of *P. cinnamomi* colonies in the infested potting soil where they grew up. These species, in particular, *S. cereale* and *B. nigra* although tolerant, they cause some concern, particularly with regard to ecosystem management. Some reports indicate that *P. cinnamomi* can persist within contained root lesions in resistant grass species up 10 days and the pathogen is also able to produce sporangia in the root surface of the resistant species providing a long-term continued inoculum of the pathogen, after the susceptible species have died [43]. In the line of this study, these tolerant herbaceous species may increase the inoculum of the pathogen in the soil. Therefore, it is suggested to avoid sowing these species in areas with characteristics conducive to the disease.

Additionally, *O. sativus*, *B distachyon*, *S. cereale*, *B. nigra* and *V. sativa* exhibited tolerance in the presence of the pathogen increasing their biomass, as it is observed with *Pinus nigra* and *Cupressus sempervirens*. This 'overcompensation', was attributed to the plants producing more roots to replace those that were lost, which led subsequently to an increase in shoot biomass as well. This adaptive response to the pathogen presence underscores the tolerance of these plant species., only *V. sativa* presents the potential for disease management in agricultural systems [44]. In similar tests, despite being infected, *Vicia sativa* exhibited tolerance to the infection, displaying mild symptoms [40]. Our study further supports this finding, indicating that *V. sativa* was not a host plant and this species, when in contact with the pathogen, react with a small increase in root biomass compared to the control. Based on these characteristics, *Vicia sativa* would be a good species to replace lupins (*L. luteus* and *L. angustifolius*).

Among the species of the Mediterranean flora there is a wide range of plants, shrub and herb, from different families that have an inhibitory effect on *P. cinnamomi* contributing to the reduction of its inoculum in the soil [45–47]. Evidences showed that species from the Brassicacae family are rich in glucosinolates (sulfur-containing compounds, found naturally in brassicas, such as broccoli, cabbage, etc.) that present antagonistic characteristics for the *Phytophthora*, thus being able to contribute to its mitigation. Release of plant root exudates in the aqueous phase of the soil by alone or interacting plants, counteracting the *Phytophthora* effect, can be determinant to the tolerance of *Eruca vesicaria*, as well as *Diplotaxis tenuifolia*, *Brassica nigra* and other Brassicaceae species to *P. cinnamomi* contact [18,20,47]. Studies in vivo also indicated that root exudates of these species reduce the inoculum levels of *P. cinnamomi*, having an effect on microorganisms in the rhizosphere [43]. In this study, the response of *D. tenuifolia* to the presence of *P. cinnamomi*, evidenced root biomass reduction by 64%, giving an idea of some susceptibility to the pathogen, in contrast with the expected tendency for tolerance and inhibition effect to *P. cinnamomi*, which has already been demonstrated in previous experiments [18,20]. These differences would certainly have been due to changes in development conditions, such as watering and temperature, which occurred during the experiment and which greatly affected the plants of this species. By contrast, the tolerant response of *E. vesicaria* and *B. nigra* was as expected from the cited literature [20,47].

The knowledge of the plant susceptibility (woody and herbs) is crucial for 'montado' management strategies in areas heavily affected by decline and with poor regeneration.

Associating known no hosts with anti-*Phytophthora* effect plant species in existing pastures is essential for reducing the pathogen's inoculum in these areas. Furthermore, understanding the susceptibility of not only typical 'montado' forest plants (trees and shrubs) but also of other cohabiting species in this ecosystem (herbs) is vital for effective management.

With predicted climate changes in the Mediterranean region, including reduced precipitation and increased temperatures, conditions are expected to negatively impact the dynamics of *P. cinnamomi* populations, limiting their abundance and dissemination. Indeed, a recent study [48] observed a significant decrease in the population abundance of the pathogen under low soil moisture conditions. However, *P. cinnamomi* is capable of surviving long periods, and extreme precipitation events can contribute to population increases and subsequent spread [49]. Forecasts also suggest the pathogen's adaptation to new areas previously cooler but now warming up, as it thrives in higher temperatures, indicating that this pathogen will pose a real threat to the conservation of forest ecosystems where water is not a limiting factor [50]. In light of these findings, forest management in the Mediterranean region will require increased attention to the selection of different plant species.

5. Conclusions

The results clearly demonstrate significant variation in disease expression within some of the genera studied, both in woody and herbaceous species. The susceptibility lists presented under controlled conditions are indicative rather than definitive. They offer insights into the potential impact of *P. cinnamomi* on vegetation, whether native or cultivated.

In agrosilvopastoral systems, annual and perennial herbaceous species represent a high percentage of the total vegetation. Therefore, this study underscores the importance of these herbaceous species, whether exhibiting symptoms or not, as hosts or no-hosts of *P. cinnamomi* in the host-pathogen system. Some of these plants, contribute to the persistence of the pathogen in the ecosystem, which may have implications for disease management, particularly, in natural environments. Incorporating no-host species with allelopathic effects into pastures should be considered an effective measure in oak woodland management to reduce the pathogen's population.

It is also important to avoid planting susceptible species (woody or herbaceous) in areas affected by *P. cinnamomi* or prone to the decline, such as, *Lupinus luteus*, or others species that cause concern, like *Lolium multiflorum*, *Medicago sativa*, *Dactylis glomerata*, *Trifolium incarnatum* and *T. subterraneum.* Although these species are no-hosts, they exhibit significant root reduction, and their role in the root-pathogen system is not yet well understood. In contrast, *Vicia sativa*, a legume that does not host the pathogen, would be a suitable alternative to *L. luteus* either sown alone or mixed with other plants not susceptible to *P. cinnamomi.* Our results, also indicate that all tree species tested were infected, but they exhibited different levels of susceptibility. This finding suggests the possibility of a novel approach to the composition of oak stands. This may entail integrating several more tolerant species into plantations. Additionally, using tolerant species as rootstock, such as *Quercus faginea*, or other tolerant species, could be feasible to mitigate root infection.

Although climate change predictions for the Mediterranean region indicate drought and warming, some studies suggest that the pathogen can adapt to new warming areas where water is not a limiting factor. Understanding the susceptibility of plants in ecosystems vulnerable to disease is crucial for mitigating the impact of pathogens and associated diseases under a scope of forest management of oak ecosystems.

Author Contributions: Conceptualization, writing—original draft preparation and reviewing, A.C.M. and I.C. Lab and greenhouse work was supported by A.C.M., I.C., J.N. and M.R.-R. Last review and statistical analysis were carried out A.R. and A.C.M. All authors have read and agreed to the published version of the manuscript.

Funding: The work was financially supported by the project intitled "Declínio do Montado no Alentejo", with the reference PDR2020 (101-031496). Additionally, the work was partially funded by FCT—Fundação para a Ciência e Tecnologia, I.P., by project references UIDB/50022/2020 and UIDB/04035/2020 for IDMEC and GeoBioTec, respectively.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The datasets generated and/or analysed during this study are available from the corresponding author. Data will be shared upon reasonable request.

Acknowledgments: The authors would like to thank to ACPA—Association of Pig Breeders of Alentejo—for their support in the field.

Conflicts of Interest: The authors declare no conflict of interest.

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