ScienceDirect

Forest Ecology and Management
Volume 518, 15 August 2022, 120281

Response of two riparian woody plants to *Phytophthora* species and drought

I. Gomes Marques [a, b], A. Solla [c], T.S. David [a, d], P.M. Rodríguez-González [a], M. Garbelotto [b]

Show more

Outline | Share | Cite

https://doi.org/10.1016/j.foreco.2022.120281

Get rights and content

Highlights

- Drought was the main stress in *Alnus rhombifolia,* pathogen infection was secondary.
- Alders infected by *Phytophthora* spp. increased their survival in drought conditions.
- Water availability favored infection of *Frangula californica* by *P. cactorum.*
- Combination of pathogen and drought induced changes in biomass allocation in alders.
- Minimizing disease spread will ensure greater success of habitat restorations.

Abstract

Disease combined with drought poses an important threat to plant survival, often compromising success in the restoration of riparian forests. Thus, understanding how biotic and abiotic stressors may affect plant survival and growth performance can greatly increase the success of ecosystem management strategies. The purpose of this study was to understand how two plant species, often used together in restoration of riparian ecosystems but with different ecological preferences, would respond to infection by each of two *Phytophthora* species in Mediterranean-climate regions, in the absence or presence of a simulated drought. Saplings of the drought resistant species *Frangula californica*, and of the riparian species *Alnus rhombifolia* were each inoculated in a greenhouse experiment with one of two *Phytophthora* species and exposed to two watering regimes. Saplings were allocated to six treatments, combining three levels of pathogen inoculation (no inoculation, inoculation with *Phytophthora cactorum* and inoculation with *Phytophthora crassamura*), and two watering regimes (well-watered and drought). The response of *A. rhombifolia* and *F. californica* saplings was assessed through the observation of health metrics and morphological parameters. Results showed that both *P. cactorum* and *P. crassamura* are important pathogens of *A. rhombifolia* and *F. californica*. As expected, drought conditions were the main cause of decline and mortality in *A. rhombifolia* saplings, while water availability was a facilitator of *P. cactorum* infection in *F. californica* saplings. We observed two seemingly contrasting results in *A. rhombifolia* saplings: infection by *Phytophthora* spp. decreased survival in well-watered plants, while the opposite was recorded for saplings under drought conditions whose survival increased in *Phytophthora*-inoculated treatments. Saplings of *F. californica* were able to cope with drought conditions, even when infected by *Phytophthora* species and water availability increased root infection and decreased sapling survival. We conclude that the continued use of *F. californica* and *A. rhombifolia* in sites infested by *Phytophthora* species can be beneficial in restoration, if appropriate management actions are adopted. Such actions include avoiding the planting of *F. californica* saplings in areas subjected to water accumulation, and ensuring that *A. rhombifolia* is planted in areas where drought stress is minimal and where *Phytophthora* species are possibly absent. We also emphasize the importance of ensuring that plant stock used in revegetation projects is not infected by *Phytophthora* species, and that biotic and abiotic risks are assessed prior to restoration actions.

< Previous

Next >

Keywords

Restoration; Planting; Host water relations; Drought; White alder; California coffeeberry; Riparian forest; *Alnus rhombifolia*; *Frangula californica*; *Phytophthora crassamura*; *Phytophthora cactorum*

1. Introduction

The protection of riparian forests from stressors, such as extreme climatic events (Rodríguez-González et al., 2021) and pathogen invasions (Garbelotto and Pautasso, 2012), is particularly important in regions with Mediterranean-climate. In these regions, riparian forests play an essential role in the functioning of riparian ecosystems while providing unique ecosystem services (Naiman et al., 2010, Riis et al., 2020, Ferreira et al., 2022). Management actions can contribute to enhance the resilience of forests to stressors when decision-making integrates evidence on abiotic and biotic drivers of such resilience (Buma and Wessman, 2013, Roberts et al., 2020), and is based on scientific knowledge about the ecological preferences of plant species (Lindner et al., 2020).

Plant species in riparian ecosystems of Mediterranean-climate regions show ecological adaptations to the particular climatic and to the hydromorphological conditions they are exposed to (Gasith and Resh, 1999, Dufour et al., 2019). These ecosystems present high seasonality in water flow, with a typical cycle of high discharge in late autumn or early spring, followed by a drought period in summer and early fall (Gasith and Resh, 1999). The predicted increase in the frequency of extreme weather events, such as droughts and floods (Spinoni et al., 2020), and the uncertainty about plants resilience to these changes, has fueled research on riparian vegetation management and conservation under climatic changes (Stella et al., 2013). Moreover, emerging biotic threats such as those posed by biological invasions, including those by pathogens, have added new constraints to the sustainability of riparian corridors (Grady et al., 2015). The effects of the combination of environmental stresses and plant pathogens on riparian ecosystems can be varied and multiple, depending on the driving factors and interactions at play (Stella and Bendix, 2018). Research often points to the existence of negative interactive effects, e.g. increasing temperatures and high frequency of drought events predisposing plants to pathogen infection (Corcobado et al., 2014, Colangelo et al., 2018). These effects are likely to occur much more often and with higher impacts due to projected future climatic conditions (La Porta et al., 2008, Delgado-Baquerizo et al., 2020), and to the continuous emergence of plant pathogens, including those belonging to the genus *Phytophthora* (Scott et al., 2019).

The combination in late spring of relatively high water availability and mild temperatures in riparian corridors and floodplains of Mediterranean-climate sites matches the conditions under which the release of zoospores - the main infection propagules of many *Phytophthora* spp. - typically occurs (Pfender, 1977, Rahimian and Mitchell, 1988, Morgan and Shearer, 2013, Garbelotto et al., 2018). Therefore, plant species in these ecosystems are particularly vulnerable to infection due to spring annual floods and to the spread of infested water in the rhizosphere (Browne et al., 2021). Infection is typically followed by drought periods which may hasten disease progression. In addition, projected future climatic conditions show that Mediterranean-climate regions will increase their status of drought hotspots, with longer and harsher drought events (Spinoni et al., 2020) likely to induce large scale plant mortality in riparian ecosystems. Finally, the unintended planting of infected plants in revegetation projects has resulted in the introduction of emergent *Phytophthora* spp. to novel geographic host ranges (Jung et al., 2016, Garbelotto et al., 2018, Frankel et al., 2020, Sims and Garbelotto, 2021).

Alnus rhombifolia Nutt. and *Frangula californica* (Eschsch) A. Gray are California endemic plant species that can co-occur in riverine ecosystems of interior chaparral and coastal scrub sites (Bendix and Cowell, 2010, Cash, 2013). These species are often jointly used in local riparian revegetation projects (Opperman and Merenlender, 2000, Ting and Pope-Daum, 2004, Trinh and Percelay, 2008, Fessler, 2015, Mucina et al., 2017) due to their complementary ecological preferences. *Frangula californica* is a perennial shrub adapted to a wide range of soil and shade conditions (McMurray, 1990). It tolerates well, semi-dry conditions, and it is commonly found either on riverbanks or in floodplain positions (Griggs, 2009). *Alnus rhombifolia,* instead, is a deciduous riparian tree species that occurs along streams (Griggs, 2009): it requires constant water availability, prefers direct light (Uchytil, 1989) and is flood-tolerant due to its capacity to thrive in poorly drained soils (Uchytil, 1989). The water availability requirements for *A. rhombifolia* suggest that this species should be more susceptible to drought than *F. californica*, given that the latter shows a wider range of tolerance to dry environments.

Recent studies in California have found *F. californica* to be one of the species with the highest *Phytophthora* disease incidence in native plant nurseries that produce plant stock for restoration projects (Sims et al., 2018, Rooney-Latham et al., 2019). Furthermore, the soilborne *Phytophthora cactorum* (Lebert & Cohn) J. Schröt and *Phytophthora crassamura* Scanu, Deidda & Jung were the most common pathogens found in California restoration sites, and their presence has been associated to the onset of recent disease outbreaks (Sims et al., 2019). *Phytophthora cactorum* was the most prevalent *Phytophthora* species in both field and nursery surveys (Sims et al., 2018, Rooney-Latham et al., 2019) and has been isolated from a wide range of plant hosts (Erwin and Ribeiro, 1996) in several ecosystems, including riparian habitats (https://blogs.cdfa.ca.gov/Section3162/?tag=phytophthora-cactorum, last access: 24 December 2021). This pathogen has also been reported on *Alnus glutinosa*, *A. incana* and *F. californica* both in Europe and North America (Hantula et al., 1997, Sims et al., 2018). In contrast, *P. crassamura* has only been recently first described in wildlands of Sardinia, Italy (Scanu et al., 2015), and, subsequently, it has been detected in Californian nurseries and restoration sites (Sims et al., 2018, Sims and Garbelotto, 2021). Given its overall recent discovery, it has only been reported on a narrow host range. Its virulence and spread to other hosts and ecosystems points to *P. crassamura* as a possible new emergent pathogen in Mediterranean-climate regions (Sims et al., 2018, Ahrens et al., 2019). However, no study has focused on riparian tree species infected by *P. cactorum* or *P. crassamura*, leaving a gap of knowledge concerning possible management options in infested river catchments. Finally, even if the combination of drought conditions and plant-pathogens combinations has been frequently studied in upland species (Gómez et al., 2018), drought-pathogen interactions are still understudied for riparian woody species.

In this study, we examined the individual and combined effects of drought and infection by *P. cactorum* or by *P. crassamura* on *A. rhombifolia* and *F. californica* plants in a common garden experiment. We simulated environmental conditions like those that could be experienced in the wild by riparian plants after revegetation efforts, such as plant infection occurring during late winter and spring floods followed by a summer drought. Specifically, we compared the morphological and physiological responses of plants subjected to (1) drought conditions, (2) infection by either a widespread (*P. cactorum*) or by an emerging *Phytophthora* species (*P. crassamura*) and (3) the combination of *Phytophthora* infection and drought conditions.

We hypothesized that cumulative negative effects would occur in the combination of *Phytophthora* infection and drought on both *A. rhombifolia* and *F. californica*. In addition, given the higher water requirements of *A. rhombifolia,* we hypothesized that this plant species would be affected by the combination of infection and drought more severely than *F. californica*. This study may help support forest management decisions based on plant responses to the interaction among stressors, while providing data useful to enhance the success of riparian restoration projects in areas previously infested by *Phytophthora* spp. or when *Phytophthora*-infected plant stock is involuntarily used in restoration efforts.

2. Material and methods

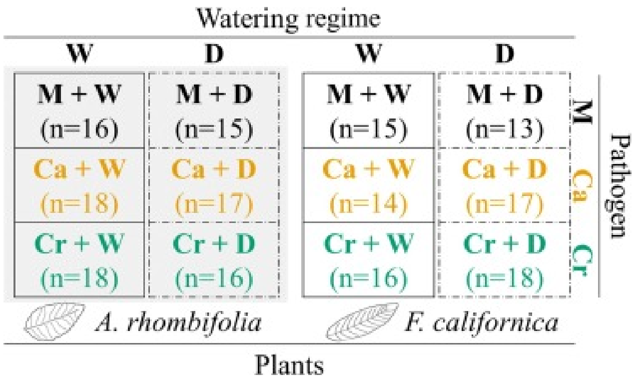
2.1. Plant species

A total of 118 *Frangula californica,* 16.6 cm (±2.6) in mean height and 5.4 mm (±0.9) in mean diameter, and 111 *Alnus rhombifolia* saplings, 56.9 (±13.8) in mean height and 7.4 mm (±1.4) in mean diameter, were obtained from two native plant nurseries in California (USA) and tested for the presence of *Phytophthora* spp. as follows. Before the experiment, 10–20 g of soil samples were taken from all pots and set to dry in plastic bags for 7 days at room temperature. Soil samples were then hydrated in the same plastic bags, left for two days at 5 °C and were flooded by adding water until 1 cm above the soil level. Three types of baiting were used: whole pears of the D'Anjou variety were placed on the soil half submerged by water and leaves of *Oreganum vulgare* and *Rhododendron macrophyllum* "Cunningham's White" were floated on the water surface. All baits were washed prior to baiting and baiting was performed at room temperature for 10 days. Visual screening of new lesions developing on the baits was done every 2–3 days and all brownish water-soaked spots were plated on V8-PARPH selective medium. Plates were incubated in the dark for 3 to 5 days before any and visibly growing colonies were transferred to V8-juice agar (V8A) medium. Initial identification of colonies was done morphologically and then confirmed molecularly as described in Sims et al. (2018).

After confirmation that *Phytophthora* spp. were absent, saplings were transferred to 2100 cm^3 individual plastic free-draining pots 23.5 cm in height and 9.5 cm in diameter, filled with a mixture of sand and peat (1:3) and left for one month in an outdoor lathehouse at U.C. Berkeley, California. In April 2021, all saplings were transferred to a room with 18 h photoperiod, 20–25 °C temperature and 40–50% relative humidity conditions, where they remained another month for acclimation before being inoculated with the pathogens. The environmental room conditions described above were maintained constant throughout the entire experiment.

2.2. Experimental design

Saplings from each species were randomly allocated to six treatments at the beginning of the experiment (Fig. 1). The experimental design combined three treatments of pathogen inoculation (Mock or M, *Phytophthora cactorum* or Ca and *Phytophthora crassamura* or Cr) with two watering regimes (Well-watered or W and Drought or D). As a result, the experiment included the following treatments: mock (no pathogen) inoculation followed by the well-watered regime (M + W), mock inoculation followed by the drought regime (M + D), *P. cactorum* inoculation followed by the well-watered regime (Ca + W), *P. cactorum* inoculation followed by the drought regime (Ca + D), *P. crassamura* inoculation followed by the well-watered regime (Cr + W) and *P. crassamura* inoculation followed by the drought regime (Cr + D).



	W	D	W	D	
	M + W (n=16)	M + D (n=15)	M + W (n=15)	M + D (n=13)	M
	Ca + W (n=18)	Ca + D (n=17)	Ca + W (n=14)	Ca + D (n=17)	Ca
	Cr + W (n=18)	Cr + D (n=16)	Cr + W (n=16)	Cr + D (n=18)	Cr
	A. rhombifolia		*F. californica*		

Fig. 1. Experimental design, combining three treatments of pathogen inoculation that include mock inoculation (M), Phytophthora cactorum inoculation (Ca) and *Phytophthora crassamura* inoculation (Cr), with two watering regimes - well-watered (W) and drought (D), applied to two plant species (*Alnus rhombifolia* and *Frangula californica).*

2.3. Inoculation

The isolates of *P. cactorum* (8HET.RH.1, GenBank accession no. MH171630) and *P. crassamura* (MP-7B-DIAU.1, GenBank accession no. MH171641) used in this study had been originally isolated from restoration sites in California and were morphologically and molecularly identified prior to this experiment (Sims et al., 2019). The isolates are preserved in the Fungal and oomycete collection of the University of California Berkeley Forest Pathology and Mycology Laboratory, under permission by USDA APHIS and CDFA. To increase infection success, two artificial inoculation procedures were used on all saplings and included the addition of both soil inoculum and a zoospore suspension to the soil mix of each plant.

Soil inoculum was produced for each strain according to Jung et al. (1996), by incubating 4 V8A plugs of 5-mm-diameter colonized by the *Phytophthora* species for 2 months at 24–25 °C in a mix of double-autoclaved V8, vermiculite and whole grain oats. Soil inoculum for the mock treatments consisted of the same mixture but without the pathogen-colonized V8A plugs. Approximately 80 mL of soil inoculum was added to the soil of each plant by opening 3 holes 2–3 cm deep in the margin of the pot. All saplings were well watered immediately after inoculation.

Zoospore suspensions were produced for each strain according to a method adapted from Sims and Garbelotto (2018) and were applied 24 h after application of the soil inoculum. A total of 9 plugs of 5-mm-diameter taken from the margin of 5 to 7 day-old cultures were put in 110-mm-diameter Petri plates and covered with a mix of 1 V8:4 soil solution. The plugs were left for 24 h at room temperature, rinsed with distilled water and left in soil solution for the next 48 h. Plates were then placed on a mix of water and ice for 1 h and left at room temperature while monitoring for zoospore release. Zoospore concentrations were calculated using a hemocytometer. A 40 mL zoospore suspension containing an estimated amount of 40×10^5 and 19×10^5 zoospores, for *P. crassamura* and *P. cactorum* respectively, was poured near the root collar of the plant over a 2–3 mm deep slit previously cut close to the soil line. Mock inoculations consisted of the same procedure but using soil solution with no zoospores. Saplings were kept under waterlogging conditions for 48 h after inoculation and in well-watered conditions for twenty-two days, until the two experimental water regimes were applied.

By the end of the experiment, root segments and stem pieces from the slit cut area of all saplings were plated on V8-PARPH selective media and resulting cultures were incubated and transferred to V8A agar medium. Confirmation of the pathogen was done through morphological comparison between the cultures reisolated from the inoculated plants and the cultures of the original strains used for inoculation and through molecular identification following the protocol used in Sims et al. (2018).

2.4. Watering regimes

The two experimental watering regimes started twenty-two days post inoculation, after infection by *P. cactorum* and *P. crassamura* was confirmed on at least five randomly selected *F. californica* and *A. rhombifolia* saplings. Before applying the different watering regimes, the weight of each pot at container capacity was obtained by weighing each pot after waterlogging and after waiting that all excess water had been drained out. Afterwards, watering was withheld from all the saplings under the drought treatment. Once the first signs of wilting were visible in at least 30% of the non-inoculated drought-exposed saplings, the soil water content corresponding to the wilting point was calculated and applied to all saplings assigned to the drought treatment. All plants were weighted and watered every two days to maintain either (i) container capacity in well-watered treatments or (ii) 39% of container capacity, corresponding to the soil water content calculated from the 30% of the non-inoculated drought-exposed saplings showing wilting symptoms.

2.5. Plant health and performance assessment

Health metrics of every sapling in response to the three pathogen inoculation treatments, the two watering regimes or the combination of both types of stressors were assessed by noting the time to death of saplings, the percentage of necrotic and wilted leaves, plant transpiration and leaf relative water content. Morphological parameters measured in all saplings included the number of leaves, specific leaf area, stem dry matter content, root dry matter content, leaf dry matter content, leaf area ratio, leaf mass ratio and stem mass ratio (Table S1).

The percentage of necrotic and wilted leaves and time to death of saplings were visually assessed every four days starting from the beginning of the drought regime. Percentage of necrotic and wilted leaves followed a classification score ranking between 0 (all leaves appear healthy) and 13 (dead plant).

All saplings were weighted every two days and the equivalent transpiration was calculated as the amount of water loss between consecutive days (Costa e Silva et al., 2004). To avoid water loss through evaporation, the top of the pot was covered with aluminum foil. Transpiration curves per treatment and species were built using the mean values of water loss from all plants per species and treatment.

The leaf relative water content, stem diameter, height and number of leaves of saplings were evaluated three times during the experiment: before inoculation (4th of May 2021), twenty-two days after inoculation (9th of June 2021) and 59 days post inoculation (16th of July 2021, at the end of the experiment). The leaf relative water content was calculated following a protocol modified from Cornelissen et al. (2003) and using a total of six discs of 5-mm-diameter (two discs from three fully mature leaves) from each plant. The same leaves were used for this measurement whenever the previous sampling appeared to have no negative impact on their health. Discs were cut, stored in aluminum foil envelopes between 3 and 5 °C and weighted as soon as possible to get their fresh weight. Then discs were kept in distilled water for 24 h under 3–5 °C and weighted again (turgid weight), after which they were oven-dried at 75 °C for 48 h (dry weight). The leaf relative water content was calculated as shown in formula (1).

$$\text{(1)}\quad \text{LRWC (\%)} = (\text{fresh weight} - \text{dry weight}) / (\text{turgid weight} - \text{dry weight}) \times 100$$

At the end of the experiment, all saplings were harvested and the overall plant biomass was obtained by weighing separately the leaves, stems and roots. Fresh weight was assessed immediately after destruction and dry weight was assessed after oven-drying until constant weight. Leaves were photographed while fresh without petiole and the total leaf area was calculated using the digital images in Adobe Photoshop (CC 2014). Several aboveground and belowground biomass traits were calculated for each plant at the end of the experiment (Table S1). Root damage was evaluated by attributing scores between 1 (healthy roots) and 6 (complete root system rotten away), adapted from Sims and Garbelotto (2018).

2.6. Statistical analysis

Survival probabilities were calculated using the Kaplan–Meier estimate, and differences among treatments for each plant species were examined using the log-rank test in the *survival* package (Thearneau and Grambsch, 2000, Therneau, 2021). Pairwise differences were determined using the *survminer* package (Kassambara et al., 2021).

Differences in number of leaves, root damage, leaf relative water content and biomass traits among treatments for the same plant species were tested using ANOVA. Tukey's test with a confidence interval of 95% was used to test for differences in mean values. Normality and homoscedasticity of the dependent variables were tested, and the biomass traits 'stem mass ratio' and 'root to shoot ratio' of *A. rhombifolia* and *F. californica* saplings (respectively) were square-root transformed. If normality and homoscedasticity were not met after transformation, a Mann-Whitney test was applied instead.

Linear regressions were fitted for each plant species between the total biomass of saplings and their biomass fractions (aboveground and belowground) to assess biomass allocation strategies between watering regimes and infection status. Regression fitting to our data was evaluated using the R^2 value and interaction between levels of variation was tested using analysis of covariance (ANCOVA) with the total biomass as a covariate. All statistical analyses were performed in R (v. 3.5.1; R Core Team 2018).

3. Results

3.1. Infection success and mortality

Pathogen infection of *Alnus rhombifolia* and *Frangula californica* saplings was successful by both *Phytophthora* species. Pathogens were only re-isolated from inoculated treatments and never from the controls; however, re-isolation success was variable among treatments and plant species. The highest re-isolation success for both plant species occurred for *Phytophthora crassamura* (56%) and the lowest for *P. cactorum* (12%). Re-isolation success for *P. crassamura* was highest in *F. californica* saplings under well-watered regime (78%), followed by *F. californica* and *A. rhombifolia* saplings under drought regime (61% and 50%, respectively). Saplings of *A. rhombifolia* under the well-watered regime had the lowest re-isolation success for *P. crassamura* (33%). Similarly, re-isolation success for *P. cactorum* was highest in well-watered *F. californica* saplings (32%), followed by *A. rhombifolia* under the well-watered or drought regimes (6% and 5%, respectively). There was no re-isolation of *P. cactorum* from saplings of *F. californica* under drought conditions.

The drought regime was the most significant effect in the survival probability of *A. rhombifolia* saplings, independent of infection levels (Fig. 2a). The survival probability was significantly higher in plants under the well-watered regime when compared to plants under the drought regime: 83% *vs* 16% in mock inoculated, 84% *vs* 44% in *P. cactorum* inoculated and 89% *vs* 56% in *P. crassamura* inoculated ($p < 0.05$, Fig. 2a). When looking at the survival probability in *A. rhombifolia* in the well-watered treatments, the survival probability was affected by pathogen infection and was highest in saplings inoculated with *P. crassamura* ($p < 0.05$, Fig. 2a). When looking at the survival probability in *A. rhombifolia* in the drought treatments, it was affected by pathogen infection and was higher in saplings inoculated with either *P. cactorum* or *P. crassamura* than in mock inoculated saplings ($p < 0.05$, Fig. 2a). In *F. californica*, the lowest survival probability among all treatments was identified in saplings under the well-watered regimes and inoculated with *P. cactorum* (52%, $p < 0.05$, Fig. 2b). Conversely, *F. californica* saplings inoculated with *P. cactorum* under the drought regime showed the highest survival probability (95%, $p < 0.05$, Fig. 2b).

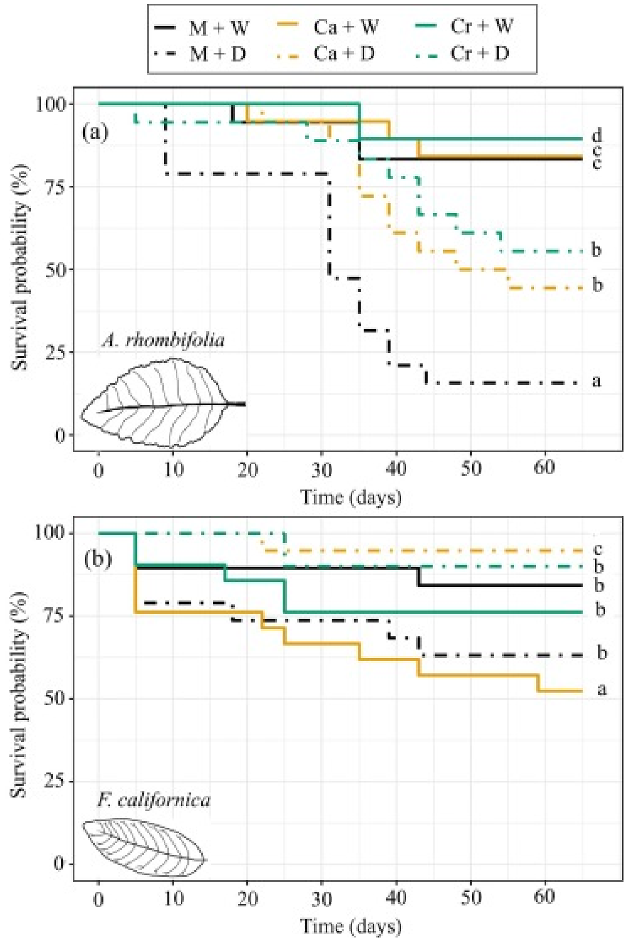


Fig. 2. Survival probability for *Alnus rhombifolia* (a) and *Frangula californica* (b) saplings in all treatments since the beginning of the experiment. M + W represents the mock-inoculated saplings under the well-watered regime, M + D represents the mock-inoculated saplings under the drought regime, Ca + W represents saplings inoculated with *Phytophthora cactorum* under the well-watered regime, Ca + D represents saplings inoculated with *P. cactorum* under the drought regime, Cr + W represents saplings inoculated with *P. crassamura* under the well-watered regime and Cr + D represents saplings inoculated with *P. crassamura* under the drought regime. Different letter combinations (a to d) indicate significant differences between treatments ($p < 0.05$).

The three *A. rhombifolia* drought treatments had higher necrotic leaves and wilting scores than the three well-watered treatments, irrespective of inoculation status or of *Phytophthora* species used ($p < 0.05$, Fig. 3a). Higher leaf damage was observed in *A. rhombifolia* than in *F. californica* saplings when drought and *Phytophthora* infection were combined ($p < 0.05$, Fig. 3). Between day 31 and day 39 post inoculation, *F. californica* saplings inoculated with *P. cactorum* and under well-watered conditions showed higher leaf necrosis than well-watered mock-inoculated plants ($p < 0.05$, Fig. 3b). However, there was no significant difference in leaf necrosis among *F. californica* treatments by the end of the experiment (Fig. 3b).

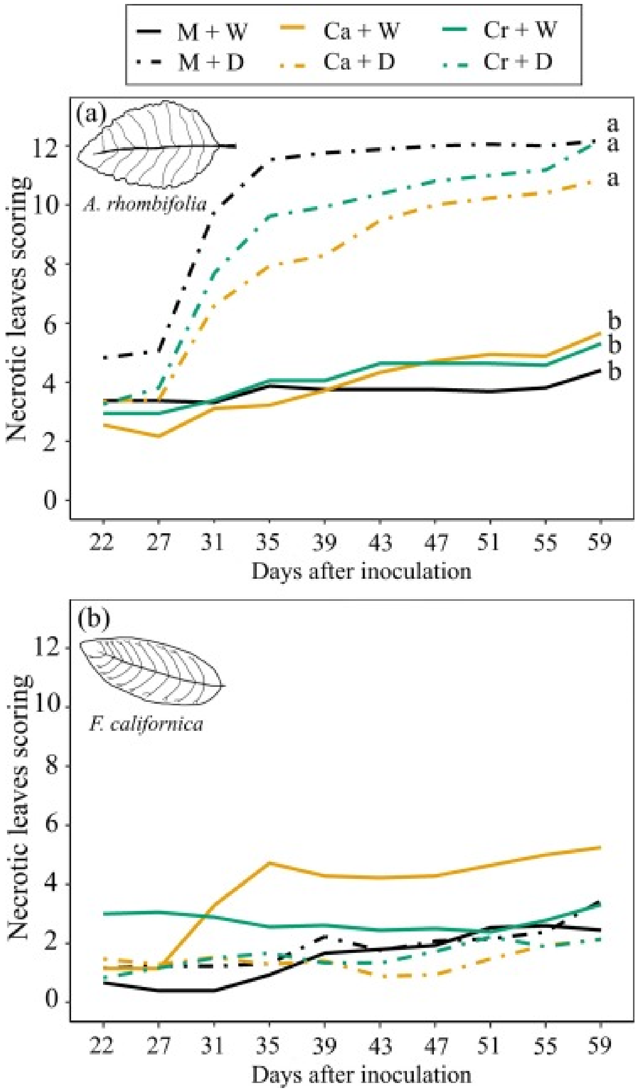


Fig. 3. Necrotic leaves scoring for *Alnus rhombifolia* (a) and *Frangula californica* (b) saplings in all treatments since the beginning of the experimental watering regimes. M + W represents the mock-inoculated saplings under the well-watered regime, M + D represents the mock-inoculated saplings under the drought regime, Ca + W represents saplings inoculated with *Phytophthora cactorum* under the well-watered regime, Ca + D represents saplings inoculated with *P. cactorum* under the drought regime, Cr + W represents saplings inoculated with *P. crassamura* under the well-watered regime and Cr + D represents saplings inoculated with *P. crassamura* under the drought regime. Different letters indicate significant differences between treatments ($p < 0.05$).

Root damage was significantly higher in both plant species inoculated with either *Phytophthora* spp., except for *F. californica* saplings inoculated with *P. crassamura* and under drought regime for which damage was indistinguishable from that of controls ($p < 0.05$, Fig. 4b). The highest root damage occurred in *F. californica* saplings inoculated with *P. cactorum* and under well-watered regime, although that damage level was only statistically different from that of drought saplings inoculated with *P. crassamura* (Fig. 4b). In *A. rhombifolia*, roots were equally and significantly damaged by both pathogens, irrespective of the watering regime (Fig. 4a).

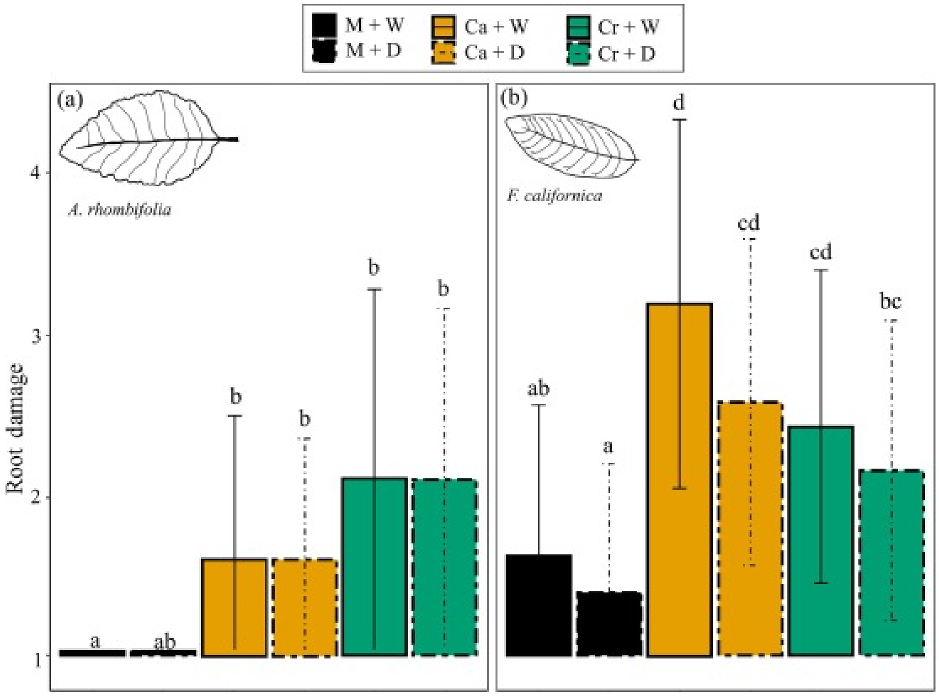


Fig. 4. Root damage at final harvest in *Alnus rhombifolia* (a) and *Frangula californica* (b) saplings of all treatments. M + W represents the mock-inoculated saplings under the well-watered regime, M + D represents the mock-inoculated saplings under the drought regime, Ca + W represents saplings inoculated with *Phytophthora cactorum* under the well-watered regime, Ca + D represents saplings inoculated with *P. cactorum* under the drought regime, Cr + W represents saplings inoculated with *P. crassamura* under the well-watered regime and Cr + D represents saplings inoculated with *P. crassamura* under the drought regime. Vertical lines are standard deviations, and different combination of letters (a–d) indicate significant differences within species ($p < 0.05$). Root damage was assessed according to the following visual observations (Sims and Garbelotto, 2018): 1, roots appeared healthy; 2, small lesions observed; 3, moderate root lesions observed; 4, moderate root lesions and roots that starting to degrade; 5, most of the main root rotten; 6, dead plant and its root system completely rotten.

3.2. Plant-water relations

Starting on day 24 post inoculation, two days after the beginning of the drought regime, water loss in well-watered *A. rhombifolia* saplings was significantly higher than water loss in saplings under the drought regime ($p < 0.05$, Fig. 5a), irrespective of inoculation status. In *F. californica* saplings, the differences in water loss between saplings under the well-watered and under drought regimes were only significant after day 42 (twenty days after the beginning of the drought regime, $p < 0.05$, Fig. 5b). Transpiration of *F. californica* saplings inoculated with *P. crassamura* under the well-watered regime was higher compared to transpiration of well-watered mock-inoculated saplings, between days 30 and 42 ($p < 0.05$, Fig. 5b). Overall, *A. rhombifolia* had higher transpiration values than *F. californica* for all the well-watered treatments, irrespective of inoculation level. Transpiration values were the lowest for both plant species under drought conditions ($p < 0.05$).

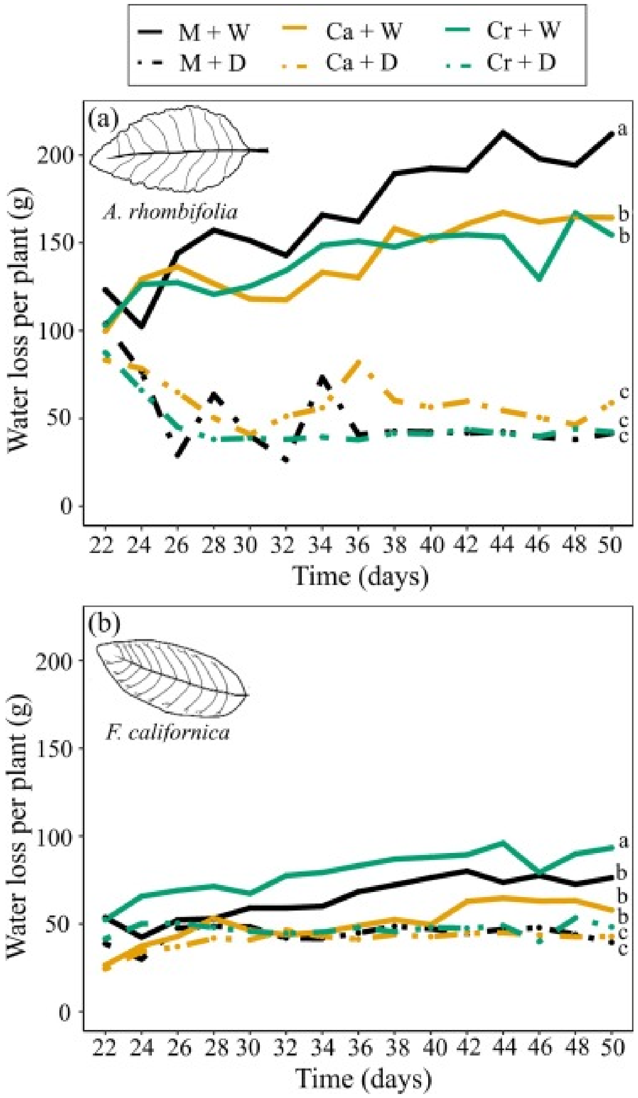


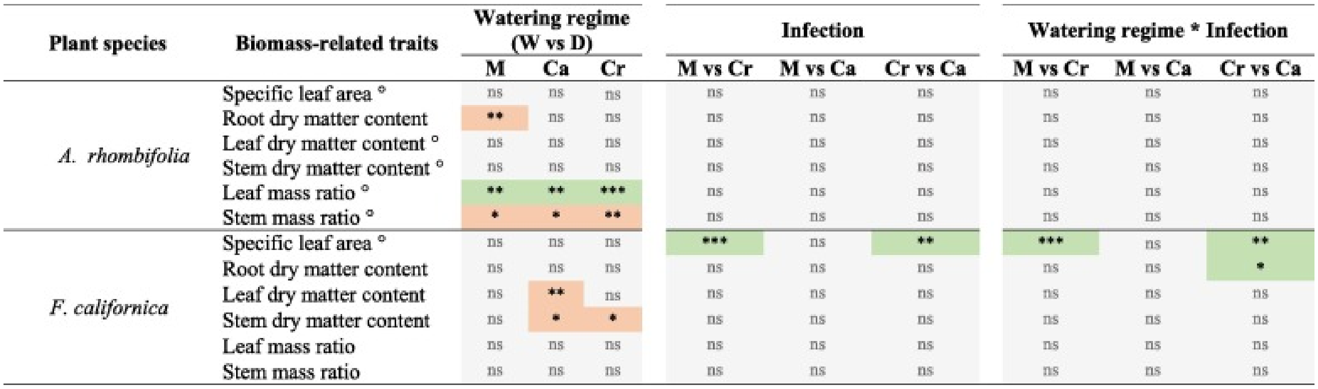
Fig. 5. Water loss (transpiration, in g) of *A. rhombifolia* (a) and *F. californica* (b) saplings once the water regimes treatments started. M + W represents the mock-inoculated saplings under the well-watered regime, M + D represents the mock-inoculated saplings under the drought regime, Ca + W represents saplings inoculated with *Phytophthora cactorum* under the well-watered regime, Ca + D represents saplings inoculated with *P. cactorum* under the drought regime, Cr + W represents saplings inoculated with *P. crassamura* under the well-watered regime and Cr + D represents saplings inoculated with *P. crassamura* under the drought regime. Treatments with distinct combination of lowercase letters (a–c) indicate distinct significant groups ($p < 0.05$).

Before applying the drought regime, the leaf relative water content was significantly higher in *F. californica* saplings inoculated with *P. crassamura* ($p < 0.01$), but by the end of the experiment, leaf relative water content of *F. californica* saplings inoculated with *P. crassamura* and under the drought regime were lower than those of all other treatments ($p < 0.05$).

3.3. Plant biomass traits

The observed differences of biomass traits in *A. rhombifolia* saplings occurred only when comparing well-watered saplings to saplings under the drought regime (Table 1). The well-watered regime allowed *A. rhombifolia* saplings to develop higher leaf mass ratio and lower stem mass ratio than saplings under the drought regime (Tables 1 and S2). The root dry matter content was also inhibited in mock inoculated *A. rhombifolia* saplings under the well-watered regime ($p < 0.01$, Tables 1 and S2). Saplings of *A. rhombifolia* inoculated with mock or *P. crassamura* and under the well-watered regime showed growth of new leaves, when compared to saplings inoculated with mock or *P. crassamura* and under the drought regime ($p < 0.01$). The well-watered regime caused a decrease in leaf dry matter content of *F. californica* saplings inoculated with *P. cactorum* ($p < 0.01$, Tables 1 and S2), and a decrease in stem dry matter content of saplings inoculated with *P. cactorum* and *P. crassamura* ($p < 0.05$, Tables 1 and S2). The inoculation of *F. californica* saplings with *P. crassamura* induced an increase in their specific leaf area, when compared with mocks and *P. cactorum*-inoculated, irrespective of watering regime ($p < 0.001$ and $p < 0.05$, respectively, Tables 1 and S2).

Table 1. Pair-wise ANOVA and post-hoc Tukey HSD test or Mann-Whitney test (marked with °) results for each plant species and experimental factor of variance. Colors represent the positive (green) or negative (red) relation between significantly different treatments and grey represents non-significant relationships. Asterisks indicate significant differences: 'ns' for not significant, '*' for $p < 0.05$, '**' p < for 0.01 and '***' for $p < 0.001$. M represents mock-inoculated saplings, Ca represents saplings inoculated with Phytophthora cactorum, Cr represents saplings inoculated with *Phytophthora crassamura*, W represents saplings under the well-watered regime and D represents saplings under the drought regime. Please see table S2 for additional information.



Plant species	Biomass-related traits	Watering regime (W vs D)			Infection			Watering regime * Infection		
		M	Ca	Cr	M vs Cr	M vs Ca	Cr vs Ca	M vs Cr	M vs Ca	Cr vs Ca
A. rhombifolia	Specific leaf area °	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Root dry matter content	🟥 **	ns	ns	ns	ns	ns	ns	ns	ns
	Leaf dry matter content °	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Stem dry matter content °	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Leaf mass ratio °	🟩 **	🟩 **	🟩 ***	ns	ns	ns	ns	ns	ns
	Stem mass ratio °	🟥 *	🟥 *	🟥 **	ns	ns	ns	ns	ns	ns
F. californica	Specific leaf area °	ns	ns	ns	🟩 ***	ns	🟩 **	🟩 ***	ns	🟩 **
	Root dry matter content	ns	ns	ns	ns	ns	ns	ns	ns	🟩 *
	Leaf dry matter content	ns	🟥 **	ns	ns	ns	ns	ns	ns	ns
	Stem dry matter content	ns	🟥 *	🟥 *	ns	ns	ns	ns	ns	ns
	Leaf mass ratio	ns	ns	ns	ns	ns	ns	ns	ns	ns
	Stem mass ratio	ns	ns	ns	ns	ns	ns	ns	ns	ns

The biomass allocation of *A. rhombifolia* saplings under drought, for all three inoculation treatments, showed a common response when compared to well-watered saplings, i.e., a decrease in aboveground biomass, mirrored by an increase in belowground biomass (*$p < 0.01$*, Fig. 6a).

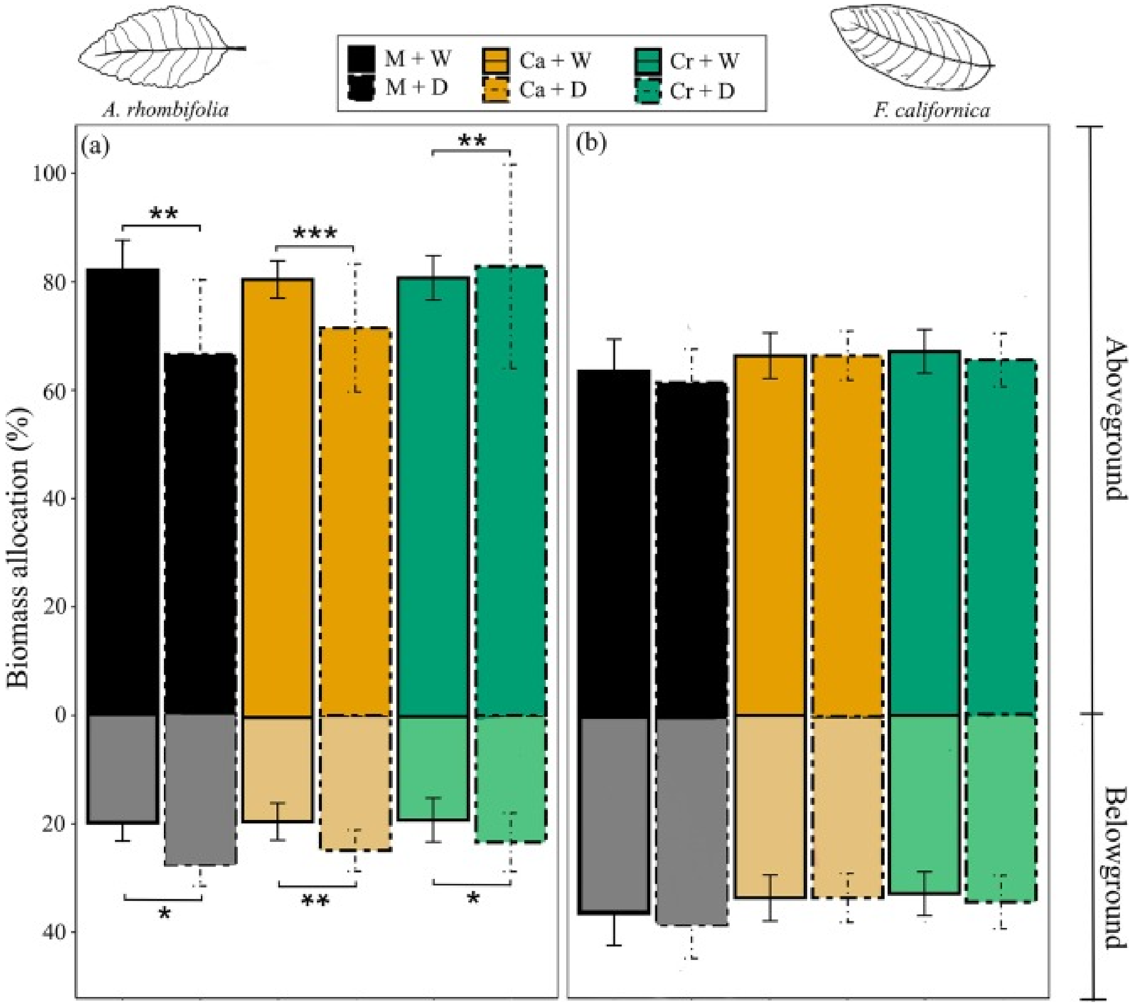


Fig. 6. Aboveground and belowground biomass allocation percentages of *Alnus rhombifolia* (a) and *Frangula californica* (b) saplings at the end of the experiment. M + W represents the mock-inoculated saplings under the well-watered regime, M + D represents the mock-inoculated saplings under the drought regime, Ca + W represents saplings inoculated with *Phytophthora cactorum* under the well-watered regime, Ca + D represents saplings inoculated with *P. cactorum* under the drought regime, Cr + W represents saplings inoculated with *P. crassamura* under the well-watered regime and Cr + D represents saplings inoculated with *P. crassamura* under the drought regime. Vertical lines are standard deviations and asterisks indicate significant differences within watering regime treatments in the same species at $p < 0.05$ (*), $p < 0.05$ (**), and $p < 0.01$ (***).

4. Discussion

4.1. Plant ecological preferences and the combination of stress

Plant species have evolved several mechanisms to respond to drought conditions, such as osmoregulation, changes in biomass allocation and regulation of gas exchanges (Garssen et al., 2014). In our experiment, *A. rhombifolia* saplings subjected to the drought regime experienced leaf shedding, a drought-avoiding strategy that decreases transpiration (Hawkins and McDonald, 1994, Eschenbach and Kappen, 1999), which in turn resulted in an increase of the percentage of belowground biomass and in a higher water uptake (Stella and Battles, 2010). Alders are very susceptible to drought conditions (Rodríguez-González et al., 2014, Gomes Marques et al., 2018) due to their reduced ability to efficiently regulate stomatal closure, a feature corroborated by the rapid water loss observed in this study since the first days of the drought regime. Assuming that transpiration was not effectively reduced during that time period, either by loss of leaf biomass or by osmoregulation, we suggest that hydraulic failure was the main causal factor of mortality for this species (Barigah et al., 2013), irrespective of infection levels.

When drought conditions were co-occurring with *Phytophthora* spp. inoculation of *A. rhombifolia* saplings, there was a two-fold unexpected effect in the decline and survival probability of this obligate riparian species. On one hand, we observed a negative effect on saplings' survival when infection and drought conditions were co-occurring, a result that has been previously documented mostly for upland species (Desprez-Loustau et al., 2006, Avila et al., 2019). On the other hand, and unexpectedly, we observed an increase in survival probability of *A. rhombifolia* saplings under drought treatments that had been inoculated with either *Phytophthora* species.

Plant decline associated with infection by *Phytophthora* spp. mostly occurs due to the necrosis of small and fine roots, ultimately causing tree mortality due to the shortage of water and nutrients (Jung and Blaschke, 1996). By reducing water uptake of roots, infection by the pathogen can also work as a further predisposing factor for plant decline, one that can be especially critical during extended droughts (Colangelo et al., 2018, Gómez et al., 2018). Moreover, drought conditions can also cause root necrosis because of dehydration of the root system, resulting from the drying of the surrounding soil (Galvez et al., 2013). Considering that water availability is a priority driver of plant health in alders (Rodríguez-González et al., 2014) it was expected that drought conditions would decrease plant health and survival on saplings already weakened by *Phytophthora* spp. infection.

We suggest instead that the unexpected increase in survival of *A. rhombifolia* saplings exposed to both pathogen inoculation and drought could be related to lower water loss of those saplings compared to that of non-inoculated saplings, compensating the effects of drought-imposed conditions. For example, in *Quercus ilex* forests, trees infected by *P. cinnamomi* had lower transpiration rates and less fine roots than non-infected trees, resulting in higher soil water content values within the rhizosphere of infected trees (Corcobado et al., 2013). Furthermore, infection by *Phytophthora* spp. can induce closure of stomata in *Alnus glutinosa* seedlings (Clemenz et al., 2008) or stimulate the accumulation of defense solutes, such as proline, in plant cells of *Castanea sativa* species (Camisón et al., 2019), a tree species known to be very susceptible to *Phytophthora cinnamomic*. Notably, proline and other defense solutes are known to increase cell water content through osmotic potential differences. It is likely that the above-mentioned mechanisms increased survival of *A. rhombifolia* saplings infected by *Phytophthora* species and in drought conditions because of the consequent decrease in water loss. Indeed, non-inoculated *A. rhombifolia* saplings under drought conditions maintained a higher water demand than that of inoculated saplings.

Consistent with the complementary ecological preferences of *F. californica vs. A. rhombifolia*, the combination of inoculation and drought conditions had an opposite effect on *F. californica* saplings than that observed on *A. rhombifolia*. In *F. californica*, dry conditions increased plant survival, while higher water availability conditions were prejudicial to plant survival. *Frangula californica* plants were able to cope with drought conditions thanks to specific physiological and morphological strategies. This species had the capacity to decrease transpiration, possibly through stomatal regulation and the mechanical reinforcement of tissues to avoid permanent damage caused by water deficit (De Micco and Aronne, 2012), thus avoiding the loss of leaves. Moreover, as commonly occurs in drought-adapted species (Bréda et al., 2006), saplings showed a high percentage of belowground biomass allocation, which allowed them to absorb higher water volumes and cope with drought. Besides the adaptive physiological and morphological response of this plant species to drought, dry soil conditions also resulted in a lower infection success of both *Phytophthora* species, contributing to the higher survival of *F. californica* saplings. On the contrary, the high-water content in the soil matrix that *F. californica* saplings were subjected to during inoculation is likely to have increased the plants' vulnerability to infection by the pathogen, because this species is not flood-tolerant and is more adapted to dry conditions (Griggs, 2009). Additionally, the water content in the soil matrix is particularly favorable for the movement and infection of woody plants by *Phytophthora* spp. zoospores (Davison, 2011, Corcobado et al., 2013), and, in fact, pathogen re-isolation success was higher in well-watered *F. californica* saplings than in drought exposed ones.

4.2. Susceptibility of plants to infection

Susceptibility to infection was also a determinant factor of plant health for both plant species in this experiment: the decline of *F. californica* saplings was mostly induced by *P. cactorum*, under well-watered conditions, while both pathogens were a secondary cause of decline in *A. rhombifolia*.

The long-lasting presence of *P. cactorum* in natural ecosystems with a Mediterranean-climate and its high number of North American plant hosts has led to the belief that this pathogen may be native to California (Erwin and Ribeiro, 1996, Sims and Garbelotto, 2018). High infection rates of *F. californica* by *P. cactorum* in natural ecosystems (Sims et al., 2018, Rooney-Latham et al., 2019), combined with low plant decline rates, further points to the possibility that *F. californica* may have a relatively low susceptibility to *P. cactorum*. However, most of these observations were done in chaparral ecosystems, under low water availability conditions, which do not correspond to the conditions used in this experiment for all treatments. We suggest that in our experiment, the higher water availability to which inoculated plants were subjected to (i) facilitated dissemination of *P. cactorum* zoospore and tissue colonization (Malajczuk and Theodorou, 1979, Hardham, 2001), resulting in higher *F. californica* root necrosis in well-watered conditions, and (ii) allowed increased infection success by *P. cactorum* in *F. californica*, which might have been impaired in the treatments where drought conditions were applied to the plants. The negative effect of the combined *P. cactorum* inoculation and water availability was specific to *F. californica*.

The mortality and resource allocation responses of *A. rhombifolia* saplings inoculated with *P. cactorum* also calls for attention, and its end effect may represent a threat to the long-term survival of this species in riparian corridors. Although infection temporarily increased the survival of drought-stressed plants, changes in stem and leaf biomass percentage, associated with the root rot caused by *P. cactorum*, anticipates long term negative effects in plant growth performance. A reduction in water and nutrients uptake, consequence of the decrease in belowground biomass allocation, is likely to decrease plant growth rates and thus reduce their competitive abilities during establishment phase in restoration sites. Moreover, the significant mortality of alders in a short-time period could be aggravated in the long-term under field conditions, especially in the absence of water availability (Gomes Marques et al., 2018). It is important for future studies to observe plant decline and survival for longer time periods when pathogen infection and drought conditions co-occur.

While the knowledge about the host range of *P. cactorum* is broad, our knowledge of the California host range of the emerging *P. crassamura* is limited (Sims et al., 2019, Sims and Garbelotto, 2021). This is inevitably due to the fact that its detection in natural ecosystems is recent not only in California, but worldwide, and due to the lack of formal pathogenicity studies. Our results deepen our knowledge on this pathogen by showing that in the presence of higher soil water content, this species can cause significant mortality in *F. californica* saplings. Likewise, even if drought had a priority effect on the decline of alder saplings, *P. crassamura* increased both the decline and mortality of *A. rhombifolia* saplings, and the magnitude of such increase was equivalent to that caused by *P. cactorum*.

5. Conclusions

To the best of our knowledge, this is one of the few studies that by focusing on the multiple interactions between several plants' ecological preferences, pathogens and the environment in riparian ecosystems provide evidence to support specific forest management decisions. The complementarity in ecological preferences of *A. rhombifolia* and *F. californica* played an important role in this experiment and corroborated the notion that different morphological and physiological responses are expressed by the two plant species when they are dealing with the combination of infection by *Phytophthora* spp. and drought.

This study provides evidence that *P. cactorum* and *P. crassamura* are significant pathogens to two plant species commonly used in Californian riparian restoration projects, namely, *A. rhombifolia* and *F. californica*. Both *Phytophthora* species have the potential to cause a significant impact on plant decline and mortality, directly contributing to the failure of restoration projects. This emphasizes the importance to ensure that plant stock used in revegetation projects is not infected by either one of these pathogens, through monitoring programs during plant production in nurseries and during/after planting (Sims et al., 2018). Assessing the occurrence of *P. crassamura* in riparian ecosystems may be particularly important because, as evidenced in this study, it is pathogenic to both plant species. Further research should focus on the pathogenicity of this newly described pathogen, to explore its full hots range and the risks it may pose to plant health in Mediterranean-climate riparian ecosystems.

Where planting is the preferential and adequate restoration approach, the continuing use of *F. californica* and *A. rhombifolia* in riparian sites previously infested by *Phytophthora* can be beneficial to revegetation actions if the planting is integrated in an appropriately designed restoration project. The planting of *Frangula* saplings in areas subjected to water retention should be avoided, to help minimize infection by *Phytophthora* species and the risk of plant decline and mortality, which can occur in the short term, as here documented, resulting in rapid failure of restoration efforts. Additionally, managers and practitioners must ensure planting sites meet the minimum water requirements for *A. rhombifolia*, which is critical in areas where infestation by *Phytophthora* is possible, given the negative effects reported here between *Phytophthora* infection and drought. Planting both plant species in the same riparian restoration sites, but ensuring their different ecological requirements, as stated above, may contribute to a decrease in disease expansion and plant decline in sites already or potentially infested by *Phytophthora* species.

Restoration of degraded riparian forests faces multiple challenges in the future, including those posed by climate change and by the increasing risk of globally invasive plant pathogens. We believe that there is an urgent need for more integrative projects in which the experience of practitioners is combined with the knowledge of researchers. These initiatives should comprehensively assess both biotic and abiotic risks prior to the planning of any restoration project, assign different restoration strategies within a catchment and include periodical and long-term monitoring programs to identify restoration failures and their specific causes.

CRediT authorship contribution statement

I. Gomes Marques: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **A. Solla:** Conceptualization, Methodology, Writing – review & editing. **T.S. David:** Conceptualization, Methodology, Writing – review & editing. **P.M. Rodríguez-González:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition. **M. Garbelotto:** Conceptualization, Methodology, Resources, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Tina Popenuck and Doug Schmidt for their help, support and insights throughout the experiment. Inês Gomes Marques was supported through a Fulbright/Portuguese Foundation for Science and Technology (FCT) Grant, Portugal, AY2021/2022 and through a PhD scholarship (SFRH/BD/133162/2017). Portuguese Foundation for Science and Technology funded Patricia M. Rodríguez González through the CEEC Individual Program (2020.03356.CEECIND) and Forest Research Centre through project UIDB/00239/2020. The authors would like to thank the two anonymous reviewers for their comments and suggestions on an earlier version of the manuscript. Support by U.C. Berkeley staff, greenhouse space rental, costs for supplies and plants and time spent by Matteo

Garbelotto on the project were possible thanks to funding by the San Francisco Public Utilities Commission through a grant managed by Ms. Susan Frankel at the USDA-Forest Service, Pacific Southwest Research Station (PSW) in Albany, CA.

Recommended articles

References

Ahrens et al., 2019 C.W. Ahrens, R.A. Mazanec, T. Paap, K.X. Ruthrof, A. Challis, G. Hardy, M. Byrne, D.T. Tissue, P.D. Rymer
Adaptive variation for growth and resistance to a novel pathogen along climatic gradients in a foundation tree
Evol. Appl., 12 (6) (2019), pp. 1178-1190, 10.1111/eva.12796
View Record in Scopus Google Scholar

Avila et al., 2019 J.M. Avila, A. Gallardo, L. Gómez-Aparicio
Pathogen-induced tree mortality interacts with predicted climate change to alter soil respiration and nutrient availability in Mediterranean systems
Biogeochemistry, 142 (1) (2019), pp. 53-71, 10.1007/s10533-018-0521-3
View Record in Scopus Google Scholar

Barigah et al., 2013 T.S. Barigah, O. Charrier, M. Douris, M. Bonhomme, S. Herbette, T. Améglio, R. Fichot, F. Brignolas, H. Cochard
Water stress-induced xylem hydraulic failure is a causal factor of tree mortality in beech and poplar
Ann. Bot., 112 (2013), pp. 1431-1437, 10.1093/aob/mct204
View Record in Scopus Google Scholar

Bendix and Cowell, 2010 J. Bendix, C.M. Cowell
Impacts of Wildfire on the Composition and Structure of Riparian Forests in Southern California
Ecosystems, 13 (1) (2010), pp. 99-107, 10.1007/s10021-009-9303-z
View Record in Scopus Google Scholar

Bréda et al., 2006 N. Bréda, R. Huc, A. Granier, E. Dreyer
Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences
Ann. For. Sci., 63 (6) (2006), pp. 625-644, 10.1051/forest:2006042
View Record in Scopus Google Scholar

Browne et al., 2021 G.T. Browne, J.K. Hasey, N.J. Ott, H. Forbes, K. Arnold, L. Milliron
Flooding by California rivers results in walnut scion infections by species of *Phytophthora*
Plant Heal. Prog., 22 (3) (2021), pp. 368-373, 10.1094/PHP-02-20-0011-RS
Google Scholar

Buma and Wessman, 2013 B. Buma, C.A. Wessman
Forest resilience, climate change, and opportunities for adaptation: A specific case of a general problem
For. Ecol. Manage., 306 (2013), pp. 216-225, 10.1016/j.foreco.2013.06.044
Article Download PDF View Record in Scopus Google Scholar

Camisón et al., 2019 Á. Camisón, M.Á. Martín, P. Sánchez-Bel, V. Flors, F. Alcaide, D. Morcuende, G. Pinto, A. Solla
Hormone and secondary metabolite profiling in chestnut during susceptible and resistant interactions with *Phytophthora cinnamomi*

J. Plant Physiol., 241 (2019), p. 153030, 10.1016/j.jplph.2019.153030
Article Download PDF View Record in Scopus Google Scholar

Cash, 2013 R.N. Cash
A Reference for Restoration: Applying the reference site model to riparian restoration sites in the California Coastal Sage Scrub, Chaparral, and Oak Woodlands Ecoregion
Riparian Restor., 25 (2013)
Google Scholar

Clemenz et al., 2008 C. Clemenz, F. Fleischmann, K.-H. Haberle, R. Matyssek, W. Osswald
Photosynthetic and leaf water potential responses of *Alnus glutinosa* saplings to stem-base inoculaton with *Phytophthora alni* subsp. *alni*
Tree Physiol., 28 (11) (2008), pp. 1703-1711, 10.1093/treephys/28.11.1703
View Record in Scopus Google Scholar

Colangelo et al., 2018 M. Colangelo, J.J. Camarero, M. Borghetti, T. Gentilesca, J. Oliva, M.A. Redondo, F. Ripullone
Drought and *Phytophthora* are associated with the decline of oak species in Southern Italy
Front. Plant Sci., 871 (2018), p. 1595, 10.3389/fpls.2018.01595
View Record in Scopus Google Scholar

Corcobado et al., 2013 T. Corcobado, E. Cubera, G. Moreno, A. Solla
Quercus ilex* forests are influenced by annual variations in water table, soil water deficit and fine root loss caused by *Phytophthora cinnamomi
Agr. For Meteorol., 169 (2013), pp. 92-99, 10.1016/j.agrformet.2012.09.017
Article Download PDF View Record in Scopus Google Scholar

Corcobado et al., 2014 T. Corcobado, E. Cubera, E. Juárez, G. Moreno, A. Solla
Drought events determine performance of *Quercus ilex* seedlings and increase their susceptibility to *Phytophthora cinnamomi*
Agric. For. Meteorol., 192–193 (2014), pp. 1-8, 10.1016/j.agrformet.2014.02.007
Article Download PDF View Record in Scopus Google Scholar

Cornelissen et al., 2003 J.H.C. Cornelissen, S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D.E. Gurvich, P.B. Reich, H. Ter Steege, H.D. Morgan, M.G.A. Van Der Heijden, J.G. Pausas, H. Poorter
A handbook of protocols for standardised and easy measurement of plant functional traits worldwide
Aust. J. Bot., 51 (2003), pp. 335-380, 10.1071/BT02124
Google Scholar

Costa e Silva et al., 2004 F. Costa e Silva, A. Shvaleva, J.P. Maroco, M.H. Almeida, M.M. Chaves, J.S. Pereira
Responses to water stress in two *Eucalyptus globulus* clones differing in drought tolerance
Tree Physiol., 24 (10) (2004), pp. 1165-1172, 10.1093/treephys/24.10.1165
View Record in Scopus Google Scholar

Davison, 2011 E.M. Davison
How do *Phytophthora* spp. de bary kill trees?
New Zeal. J. For. Sci., 41 (2011), pp. 26-37
View Record in Scopus Google Scholar

De Micco and Aronne, 2012 V. De Micco, G. Aronne
Anatomy and lignin characterisation of twigs in the chaparral shrub *Rhamnus Californica*
IAWA J., 33 (2) (2012), pp. 151-162, 10.1163/22941932-90000086

View Record in Scopus Google Scholar

Delgado-Baquerizo et al., 2020 M. Delgado-Baquerizo, C.A. Guerra, C. Cano-Díaz, E. Egidi, J.-T. Wang, N. Eisenhauer, B.K. Singh, F.T. Maestre
The proportion of soil-borne pathogens increases with warming at the global scale
Nat. Clim. Chang., 10 (6) (2020), pp. 550-554, 10.1038/s41558-020-0759-3
View Record in Scopus Google Scholar

Desprez-Loustau et al., 2006 M.-L. Desprez-Loustau, B. Marçais, L.-M. Nageleisen, D. Piou, A. Vannini
Interactive effects of drought and pathogens in forest trees
Ann. For. Sci., 63 (6) (2006), pp. 597-612, 10.1051/forest:2006040
Google Scholar

Dufour et al., 2019 S. Dufour, P.M. Rodríguez-González, M. Laslier
Tracing the scientific trajectory of riparian vegetation studies: Main topics, approaches and needs in a globally changing world
Sci. Total Environ., 653 (2019), pp. 1168-1185, 10.1016/j.scitotenv.2018.10.383
Article Download PDF View Record in Scopus Google Scholar

Erwin and Ribeiro, 1996 D.C. Erwin, O.K. Ribeiro
***Phytophthora* Diseases Worldwide**
Plant. Pathol., 47 (2) (1998), pp. 224-225, 10.1046/j.1365-3059.1998.0179a.x
Google Scholar

Eschenbach and Kappen, 1999 C. Eschenbach, L. Kappen
Leaf water relations of black alder [*Alnus glutinosa* (L.) Gaertn.] growing at neighbouring sites with different water regimes
Trees - Struct. Funct., 14 (1) (1999), pp. 28-38, 10.1007/s004680050004
View Record in Scopus Google Scholar

Ferreira et al., 2022 V. Ferreira, L.H.R. Pazianoto, A. Solla
Invasive forest pathogens affect the characteristics, microbial colonisation, and decomposition of leaf litter in streams
Freshw. Biol., 67 (2) (2022), pp. 416-429, 10.1111/fwb.13851
View Record in Scopus Google Scholar

Fessler, 2015 J.D. Fessler
Riparian Restoration, Success Criteria, and Application to the BART Sabrecat Creek Riparian Restoration Project in Fremont
University of San Francisco, California (2015)
Google Scholar

Frankel et al., 2020 S.J. Frankel, C. Conforti, J. Hillman, M. Ingolia, A. Shor, D. Benner, J.M. Alexander, E. Bernhardt, T.J. Swiecki
***Phytophthora* introductions in restoration areas: Responding to protect california native flora from human-assisted pathogen spread**
Forests, 11 (2020), pp. 1-21, 10.3390/f11121291
View Record in Scopus Google Scholar

Galvez et al., 2013 D.A. Galvez, S.M. Landhäusser, M.T. Tyree
Low root reserve accumulation during drought may lead to winter mortality in poplar seedlings

New Phytol., 198 (1) (2013), pp. 139-148, 10.1111/nph.12129
View Record in Scopus Google Scholar

Garbelotto and Pautasso, 2012 M. Garbelotto, M. Pautasso
Impacts of exotic forest pathogens on Mediterranean ecosystems: Four case studies
Eur. J. Plant Pathol., 133 (1) (2012), pp. 101-116, 10.1007/s10658-011-9928-6
View Record in Scopus Google Scholar

Garbelotto et al., 2018 M. Garbelotto, S.J. Frankel, B. Scanu
Soil- and waterborne *Phytophthora* species linked to recent outbreaks in Northern California restoration sites
Calif. Agric., 72 (4) (2018), pp. 208-216, 10.3733/ca.2018a0033
View Record in Scopus Google Scholar

Garssen et al., 2014 A.G. Garssen, J.T.A. Verhoeven, M.B. Soons
Effects of climate-induced increases in summer drought on riparian plant species: A meta-analysis
Freshw. Biol., 59 (5) (2014), pp. 1052-1063, 10.1111/fwb.12328
View Record in Scopus Google Scholar

Gasith and Resh, 1999 A. Gasith, V.H. Resh
Streams in Mediterranean Climate Regions: Abiotic Influences and Biotic Responses to Predictable Seasonal Events
Annu. Rev. Ecol. Syst., 30 (1) (1999), pp. 51-81
CrossRef View Record in Scopus Google Scholar

Gomes Marques et al., 2018 I. Gomes Marques, F. Campelo, R. Rivaes, A. Albuquerque, M.T. Ferreira, P.M. Rodríguez-González
Tree rings reveal long-term changes in growth resilience in Southern European riparian forests
Dendrochronologia, 52 (2018), pp. 167-176, 10.1016/j.dendro.2018.10.009
Article Download PDF View Record in Scopus Google Scholar

Gómez et al., 2018 F.J.R. Gómez, A. Pérez-de-Luque, R. Sánchez-Cuesta, J.L. Quero, R.M.N. Cerrillo
Differences in the response to acute drought and *Phytophthora cinnamomi* rands infection *in Quercus ilex* L. seedlings
Forests, 9 (2018), p. 634, 10.3390/f9100634
View Record in Scopus Google Scholar

Grady et al., 2015 K.C. Grady, T.E. Kolb, D.H. Ikeda, T.G. Whitham
A bridge too far: cold and pathogen constraints to assisted migration of riparian forests
Restor. Ecol., 23 (6) (2015), pp. 811-820, 10.1111/rec.12245
View Record in Scopus Google Scholar

Griggs, 2009 F.T. Griggs
California riparian habitat restoration handbook
(second ed.), Riparian Habitat Joint Venture (RHJV) (2009)
Google Scholar

Hantula et al., 1997 J. Hantula, A. Lilja, P. Parikka
Genetic variation and host specificity of *Phytophthora cactorum* isolated in Europe
Mycol. Res., 101 (5) (1997), pp. 565-572, 10.1017/S0953756296002900
Article Download PDF View Record in Scopus Google Scholar

Hardham, 2001 A.R. Hardham

The cell biology behind *Phytophthora* pathogenicity

Australas. Plant Pathol., 30 (2001), pp. 91-98, 10.1071/AP01006

View Record in Scopus Google Scholar

Hawkins and McDonald, 1994 B.J. Hawkins, S. McDonald

The influence of temperature and soil water on growth, photosynthesis, and nitrogen fixation of red alder (*Alnus rubra*) seedlings

Can. J. For. Res., 24 (1994), pp. 1029-1032, 10.1139/x94-134

View Record in Scopus Google Scholar

Jung and Blaschke, 1996 T. Jung, H. Blaschke

***Phytophthora* root rot in declining forest trees**

Phyt. – Ann. Rei. Bot., 36 (1996), pp. 95-102

View Record in Scopus Google Scholar

Jung et al., 1996 T. Jung, H. Blaschke, P. Neumann

Isolation, identification and pathogenicity of *Phytophthora* species from declining oak stands

Eur. J. For. Pathol., 26 (5) (1996), pp. 253-272, 10.1111/j.1439-0329.1996.tb00846.x

View Record in Scopus Google Scholar

Jung et al., 2016 T. Jung, L. Orlikowski, B. Henricot, P. Abad-Campos, A.G. Aday, O. Aguín Casal, J. Bakonyi, S.O. Cacciola, T. Cech, D. Chavarriaga, T. Corcobado, A. Cravador, T. Decourcelle, G. Denton, S. Diamandis, H.T. Doğmuş-Lehtijärvi, A. Franceschini, B. Ginetti, S. Green, M. Glavendekić, J. Hantula, G. Hartmann, M. Herrero, D. Ivic, M. Horta Jung, A. Lilja, N. Keca, V. Kramarets, A. Lyubenova, H. Machado, G. Magnano di San Lio, P.J. Mansilla Vázquez, B. Marçais, I. Matsiakh, I. Milenkovic, S. Moricca, Z.Á. Nagy, J. Nechwatal, C. Olsson, T. Oszako, A. Pane, E.J. Paplomatas, C. Pintos Varela, S. Prospero, C. Rial Martínez, D. Rigling, C. Robin, A. Rytkönen, M.E. Sánchez, A.V. Sanz Ros, B. Scanu, A. Schlenzig, J. Schumacher, S. Slavov, A. Solla, E. Sousa, J. Stenlid, V. Talgø, Z. Tomic, P. Tsopelas, A. Vannini, A.M. Vettraino, M. Wenneker, S. Woodward, A. Peréz-Sierra, M.-L. Deprez-Loustau

Widespread *Phytophthora* infestations in European nurseries put forest, semi-natural and horticultural ecosystems at high risk of *Phytophthora* diseases

For. Pathol., 46 (2) (2016), pp. 134-163, 10.1111/efp.12239

View Record in Scopus Google Scholar

Kassambara et al., 2021 Kassambara, A., Kosinki, M., Biecek, P., Fabian, S., 2021. Drawing Survival Curves using "ggplot2.".

Google Scholar

La Porta et al., 2008 N. La Porta, P. Capretti, I.M. Thomsen, R. Kasanen, A.M. Hietala, K. Von Weissenberg

Forest pathogens with higher damage potential due to climate change in Europe

Can. J. Plant Pathol., 30 (2) (2008), pp. 177-195, 10.1080/07060661.2008.10540534

View Record in Scopus Google Scholar

Lindner et al., 2020 Lindner, M., Nikinmaa, L., Brang, P., Cantarello, E., Seidl, R., 2020. Enhancing resilience to address challenges in forest management. In: Kruum, F., Schuck, A., Rigling, A. (Eds.), How to Balance Forestry and Biodiversity Conservation? A View across Europe. European Forest Institute (EFI), Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, pp. 147–155. doi: 10.16904/envidat.196.

Google Scholar

Malajczuk and Theodorou, 1979 N. Malajczuk, C. Theodorou

Influence of water potential on growth and cultural characteristics of *Phytophthora cinnamomi*
Trans. Br. Mycol. Soc., 72 (1) (1979), pp. 15-18, 10.1016/s0007-1536(79)80002-9
Article Download PDF View Record in Scopus Google Scholar

McMurray, 1990 McMurray, N.E., 1990. *Frangula californica*, in: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: https://www.fs.fed.us/database/feis/plants/shrub/fracal [2021, December 15].
Google Scholar

Morgan and Shearer, 2013 B.R. Morgan, B.L. Shearer
Soil type and season mediated *Phytophthora cinnamomi* sporangium formation and zoospore release
Australas. Plant Pathol., 42 (4) (2013), pp. 477-483, 10.1007/s13313-013-0201-7
View Record in Scopus Google Scholar

Mucina et al., 2017 Mucina, L., Bustamante-Sánchez, M.A., Pedra, B.D., Holmes, P., Keeler-Wolf, T., Armesto, J.J., Dobrowolski, M., Gaertner, M., Smith-Ramírez, C., Vilagrosa, A., 2017. Ecological restoration in mediterranean-type shrublands and woodlands, in: Routledge Handbook of Ecological and Environmental Restoration. pp. 173–196. doi: 10.4324/9781315685977.
Google Scholar

Naiman et al., 2010 R.J. Naiman, H. Decamps, M.E. McClain
Riparia: ecology, conservation, and management of streamside communities
Elsevier (2010)
Google Scholar

Opperman and Merenlender, 2000 J.J. Opperman, A.M. Merenlender
Deer herbivory as an ecological constraint to restoration of degraded riparian corridors
Restor. Ecol., 8 (1) (2000), pp. 41-47, 10.1046/j.1526-100x.2000.80006.x
View Record in Scopus Google Scholar

Pfender, 1977 W.F. Pfender
Production of sporangia and release of zoospores by *Phytophthora megasperma* in soil
Phytopathology, 77 (5) (1977), p. 657, 10.1094/Phyto-67-657
View Record in Scopus Google Scholar

R Core Team, 2018 R Core Team
R: A language and environment for statistical computing
R Foundation for Statistical Computing (2018)
Google Scholar

Rahimian and Mitchell, 1988 M.K. Rahimian, J.E. Mitchell
Detection and quantification of *Phytophthora cactorum* in naturally infested soils
Phytopathology, 78 (1988), pp. 949-952
CrossRef Google Scholar

Riis et al., 2020 T. Riis, M. Kelly-Quinn, F.C. Aguiar, P. Manolaki, D. Bruno, M.D. Bejarano, N. Clerici, M.R. Fernandes, J.C. Franco, N. Pettit, A.P. Portela, O. Tammeorg, P. Tammeorg, P.M. Rodríguez-González, S. Dufour
Global overview of ecosystem services provided by riparian vegetation
Bioscience, 70 (2020), pp. 501-514, 10.1093/BIOSCI/BIAA041
View Record in Scopus Google Scholar

Roberts et al., 2020 Roberts, M., Gilligan, C.A., Kleczkowski, A., Hanley, N., Whalley, A.E., Healey, J.R., 2020. The Effect of Forest Management Options on Forest Resilience to Pathogens. Front. For. Glob. Chang. doi: 10.3389/ffgc.2020.00007.
Google Scholar

Rodríguez-González et al., 2014 P.M. Rodríguez-González, F. Campelo, A. Albuquerque, R. Rivaes, T. Ferreira, J.S. Pereira
Sensitivity of black alder (*Alnus glutinosa* [L.] Gaertn.) growth to hydrological changes in wetland forests at the rear edge of the species distribution
Plant Ecol., 215 (2) (2014), pp. 233-245, 10.1007/s11258-013-0292-9
View Record in Scopus Google Scholar

Rodríguez-González et al., 2021 P.M. Rodríguez-González, M. Colangelo, Á. Sánchez-Miranda, R. Sánchez-Salguero, F. Campelo, A. Rita, I. Gomes Marques, A. Albuquerque, F. Ripullone, J.J. Camarero
Climate, drought and hydrology drive narrow-leaved ash growth dynamics in southern European riparian forests
For. Ecol. Manage., 490 (2021), p. 119128, 10.1016/j.foreco.2021.119128
Article Download PDF View Record in Scopus Google Scholar

Rooney-Latham et al., 2019 S. Rooney-Latham, C.L. Blomquist, K.L. Kosta, Y.Y. Gou, P.W. Woods
***Phytophthora* Species are common on nursery stock grown for restoration and revegetation purposes in California**
Plant Dis., 103 (3) (2019), pp. 448-455, 10.1094/PDIS-01-18-0167-RE
View Record in Scopus Google Scholar

Scanu et al., 2015 B. Scanu, B.T. Linaldeddu, A. Deidda, T. Jung, C. Armas
Diversity of *Phytophthora* Species from Declining Mediterranean Maquis Vegetation, including Two New Species, *Phytophthora crassamura* and *P. ornamentata* sp. nov
PLoS One, 10 (12) (2015), p. e0143234, 10.1371/journal.pone.0143234
View Record in Scopus Google Scholar

Scott et al., 2019 P. Scott, M.K.F. Bader, T. Burgess, G. Hardy, N. Williams
Global biogeography and invasion risk of the plant pathogen genus *Phytophthora*
Environ. Sci. Policy, 101 (2019), pp. 175-182, 10.1016/j.envsci.2019.08.020
Article Download PDF View Record in Scopus Google Scholar

Sims and Garbelotto, 2018 L.L. Sims, M. Garbelotto
Susceptibility to the rare *Phytophthora tentaculata* and to the widespread *Phytophthora cactorum* is consistent with host ecology and history
For. Pathol., 48 (5) (2018), p. e12446, 10.1111/efp.12446
View Record in Scopus Google Scholar

Sims et al., 2018 L. Sims, S. Tjosvold, D. Chambers, M. Garbelotto
Control of *Phytophthora* species in plant stock for habitat restoration through best management practices
Plant Pathol., 68 (1) (2019), pp. 196-204, 10.1111/ppa.12933
View Record in Scopus Google Scholar

Sims et al., 2019 L.L. Sims, C. Chee, T. Bourret, S. Hunter, M. Garbelotto
Genetic and phenotypic variation of *Phytophthora crassamura* isolates from California nurseries and restoration sites
Fungal Biol., 123 (2) (2019), pp. 159-169, 10.1016/j.funbio.2018.11.012

Article Download PDF View Record in Scopus Google Scholar

Sims and Garbelotto, 2021 L.L. Sims, M. Garbelotto
Phytophthora species repeatedly introduced in Northern California through restoration projects can spread into adjacent sites
Biol. Invasions, 23 (7) (2021), pp. 2173-2190, 10.1007/s10530-021-02496-6
View Record in Scopus Google Scholar

Spinoni et al., 2020 J. Spinoni, P. Barbosa, E. Bucchignani, J. Cassano, T. Cavazos, J.H. Christensen, O.B. Christensen, E. Coppola, J. Evans, B. Geyer, F. Giorgi, P. Hadjinicolaou, D. Jacob, J. Katzfey, T. Koenigk, R. Laprise, C.J. Lennard, M.L. Kurnaz, D. Li, M. Llopart, N. McCormick, G. Naumann, G. Nikulin, T. Ozturk, H.-J. Panitz, R.P. da Rocha, B. Rockel, S.A. Solman, J. Syktus, F. Tangang, C. Teichmann, R. Vautard, J.V. Vogt, K. Winger, G. Zittis, A. Dosio
Future Global Meteorological Drought Hot Spots: A Study Based on CORDEX Data
J. Clim., 33 (2020), pp. 3635-3661, 10.1175/JCLI-D-19-0084.1
Google Scholar

Stella and Battles, 2010 J.C. Stella, J.J. Battles
How do riparian woody seedlings survive seasonal drought?
Oecologia, 164 (3) (2010), pp. 579-590, 10.1007/s00442-010-1657-6
View Record in Scopus Google Scholar

Stella et al., 2013 J.C. Stella, J. Riddle, H. Piégay, M. Gagnage, M.-L. Trémélo
Climate and local geomorphic interactions drive patterns of riparian forest decline along a Mediterranean Basin river
Geomorphology, 202 (2013), pp. 101-114, 10.1016/j.geomorph.2013.01.013
Article Download PDF View Record in Scopus Google Scholar

Stella and Bendix, 2018 J.C. Stella, J. Bendix
Multiple Stressors in River Ecosystems
Multiple Stressors in River Ecosystems: Status, Impacts and Prospects for the Future, Elsevier (2018), pp. 81-110, 10.1016/B978-0-12-811713-2.00005-4
View Record in Scopus Google Scholar

Thearneau and Grambsch, 2000 T.M. Thearneau, P.M. Grambsch
Modeling Survival Data: Extending the Cox Model
Springer, New York (2000)
Google Scholar

Therneau, 2021 Therneau, T., 2021. A Package for Survival Analysis in R; Version 3.2-13.
Google Scholar

Ting and Pope-Daum, 2004 Ting, J., Pope-Daum, C., 2004. Post project evaluation of Miller Creek (Marin, CA) restoration: vegetation survival. Berkeley.
Google Scholar

Trinh and Percelay, 2008 Trinh, M., Percelay, J., 2008. Tassajara Creek restoration project: Continued riparian habitat monitoring. Berkeley.
Google Scholar

Uchytil, 1989

Uchytil, R., 1989. *Alnus rhombifolia*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.
Google Scholar

Cited by (0)

View Abstract
