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ORIGINAL RESEARCH ARTICLE

Selecting plant species to rehabilitate *Phytophthora cinnamomi* infested forest

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Abstract

For most Western Australian plant species, no information is available on the effect of *Phytophthora cinnamomi* on seedling emergence, early survival, and early plant growth. Such information is required when selecting species for rehabilitating *Eucalyptus marginata* (jarrah) forest areas affected by Phytophthora dieback. This study evaluates the response of several native species to *P. cinnamomi* to identify those resistant to the pathogen at the early stages of plant development. Firstly, the effect of *P. cinnamomi* on seedling emergence and early survival was evaluated for 50 native species. Then, 24 species were selected and tested for their resistance to *P. cinnamomi* when more mature. They were infested at 5–7 months old and disease impact assessed after two months. Of 38 species that emerged in sufficient numbers for statistical analysis, *P. cinnamomi* did not affect either emergence or survival of 9 species, emergence or survival was decreased in 14 species, and both emergence and survival were significantly decreased in 15 species. Of the species tested at 5–7 months old, two were resistant, six were moderately resistant, ten were susceptible, three were highly susceptible, and three were tolerant hosts of *P. cinnamomi*. These results indicate that field resistance recorded from mature plants may be due to asymptomatic infection or resistance may not be present in seedlings. Therefore, data from mature plants may not be appropriate when selecting species for seed-based restoration.

Keywords Phytophthora · Susceptible · Resistance · Native species · Rehabilitation · Jarrah forest

Introduction

The soil-borne root pathogen *Phytophthora cinnamomi* has caused a significant reduction in biodiversity in many Australian natural ecosystems (Cahill et al. 2008). For example, in Western Australia, more than a million hectares of native flora have been extensively damaged (Department of Environment 2014) including the biodiverse ecosystems of the jarrah (*Eucalyptus marginata*) forest (Shearer and Tippett 1989) and the Swan Coastal Plain (Shearer and Dillon 1996). Even though the initial introduction of the pathogen to the jarrah forest occurred in the 1920s, species diversity in the infested areas has not recovered (Podger 1972; Shearer et al. 2007, 2009). The pathogen can persist in areas where susceptible woody plant species have been killed through its asymptomatic infections of annual and herbaceous perennial plants (Crone et al. 2013). Rehabilitation of infested areas through broadcasting seeds requires the use of species known to be resistant to the pathogen at the stage of seedling emergence and early seedling survival, as well as when plants are mature.

Many studies report the disease response of Australian species to *P. cinnamomi* (Shearer and Dillon 1995, 1996; Shearer et al. 2004; Kueh et al. 2012; Belhaj et al. 2018; Migliorini et al. 2019). These are mainly based on field observation of which species die as the disease front progresses and glasshouse studies of plants established in pots before inoculation. Species responses to *P. cinnamomi* have been compiled by McDougall (2005) and Groves et al. (2009). However, McDougall (2005), lists information on only approximately 8% of Western Australian species, and Groves et al. (2009) include only Western Australian species suitable for domestic or amenity horticulture in infested soil.

Thus, the disease response of most Western Australian species to *P. cinnamomi* is unknown, and the available

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records provide information on the species losses expected should the pathogen be introduced into a particular area. However, there is less information on the species' response to the pathogen at seedling emergence and early seedling survival. The effect of the pathogen on seedling emergence and early survival of five mallee eucalypt taxa and several plant species native to kwongan plant communities has been reported (Simamora et al. 2017; Shaw 2019). Information on responses at the stages of emergence and early survival is essential as it cannot be assumed that species showing resistance as mature plants will also be resistant at these early stages. Plants may become more resistant to *P. cinnamomi* as they mature due to changes in physiology and biochemistry between the juvenile and mature growth phases, the formation of protective sheaths of mycorrhizae or the acquisition of protective endophytes, all of which will alter the disease response (Simamora et al. 2017). It is more difficult to hypothesise why a species might become less resistant as an adult. This study aimed to identify the plant species resistant to *P. cinnamomi* at the early stages of plant development. Firstly, the effect of *P. cinnamomi* was evaluated on seedling emergence and early survival of fifty species native to Western Australia. These included species with desirable properties for rehabilitation programs but for which there was no information on their disease response at seedling emergence and early seedling survival, and some species for which reported disease ratings were variable. Then 24 species, ranging from susceptible to resistant, were selected from the first experiment and were evaluated for their resistance to *P. cinnamomi* when more mature at five to seven months old.

Materials and methods

Study location and overview

Two experiments were conducted in an evaporatively cooled glasshouse environment at Murdoch University, Perth, Western Australia. The first experiment was conducted between February to April 2021 to evaluate the effect of *P. cinnamomi* on seedling emergence and early survival of fifty native plant species. The glasshouse temperature during the experiment was between 17.6 ± 0.26°C and 27.7 ± 0.45°C. The second experiment was conducted between July 2021 to May 2022 to evaluate the effect of *P. cinnamomi* on 5–7-month-old plants of twenty-four species selected from experiment one. The glasshouse temperature was between 17.7 ± 0.23°C and 26.7 ± 0.29°C during the experiment.

Isolation of *Phytophthora cinnamomi*

A soil sample was collected from a dying *Xanthorrhoea gracilis* tree in a *Phytophthora*-infested area of the Black Cockatoo Reserve, Mundaring, Western Australia, in November 2020. The topsoil layer was removed around the lower trunk, and around 150 g of soil and fine roots were collected into a zip-lock bag. The soil sample was transported to the laboratory and baited to isolate the pathogen according to the methods described by Simamora et al. (2018). Plates were incubated at 25°C, and *P. cinnamomi* growing out of baits was identified based on morphological characteristics. The isolate was freed of contaminants by transferring mycelial tips to NARH (Simamora et al. 2018) and then to half-strength potato dextrose agar to maintain a pure culture. Per ml of deionised water, NARP contains, 17 g of oxiod cornmeal agar, 1 ml nystatin (Nilsat, Wywth-Ayerst Australia Pty Ltd, Baulkham Hills, NSW), 100 mg ampicillin sodium (Fisons Pty Ltd, Sydney, NSW), 10 mg rifampcin (Rifadin, Hoechst Marion Roussel Australia Pty Ltd, Lane Cove, NSW), and 50 mg hymexazol (Tachigaren, Sankyo Company, Tokyo, Japan). The antibiotics were dissolved in sterile water and added to cooled agar (about 50°C) prior to pouring into plates. The identification of the *P. cinnamomi* isolate (MUCC845—GenBank accession number OR244346) was further confirmed by amplifying the ITS gene region using ITS IF and ITS4 primers at the Centre of Phytophthora Science and Management, Murdoch University, Western Australia.

Inoculum preparation

About 150 ml of millet seeds (*Panicum miliaceum* L.) and 120 ml of distilled water were added to 1000 ml conical flasks and sealed with a non-absorbent cotton plug. The flasks were covered with aluminium foil and autoclaved at 121°C for 20 min for three consecutive days to ensure the sterilisation of the millet seeds. The flasks were allowed to cool for 24 h and then inoculated with the *P. cinnamomi* isolate (MUCC845) grown in two V8 (vegetable juice) agar plates incubated at 25°C for 7 days. The flasks were shaken to distribute the agar plugs evenly, and then flasks were placed into ziplock bags and incubated at 25°C in the dark. The flasks were shaken weekly for even colonisation. *Phytophthora cinnamomi* colonisation was confirmed by plating a sub-sample of the millet inoculum on NARH medium and incubating it in the dark at 25°C (Simamora et al. 2018). The plant growth medium (river sand or

potting mix) was inoculated with *P. cinnamomi* at 1% of the dry sand weight. Sterilised non-inoculated millet seeds were used for the controls.

Experiment 1 - Effect of *P. cinnamomi* on seedling emergence and early survival of fifty native species

Species selection

Seeds of 50 species from eight families, native to Western Australia, were sourced from Nindethana Seed Service (Albany, Western Australia) (Tables 1 and S1). The species were selected based on seed availability, plant height (to include a wide range of plant heights), distribution through the southwest of Western Australia, drought tolerance, provision of food and refuge to the wildlife and available records of *P. cinnamomi* susceptibility. Assessment of drought tolerance and value to wildlife through the provision of food and/or refuge was based on experimental evidence where available, species distributions and information from seed suppliers (Table S2). Hard seeds that required heat treatment for softening were soaked in hot water at 100°C for 2 min, and those that responded to smoke water were treated with smoke water (Grayson Australia, Bayswater, Victoria) diluted at 1:10 with deionised water for 24 h (Fryer 2006).

Experimental design

Washed river sand (Richgro, Canning Vale, Western Australia) steam pasteurised for two hours at 65°C was used as the growth medium. Propagation punnets (138 × 66 × 48 mm, Garden City Plastics, Forrestfield, Western Australia) with the base lined with cloth (Superwipes, Chux, Clorox Holdings Pty Limited, Australia) were filled with pasteurised river sand for controls and inoculated sand for treatments. Seeds of each species were sown at a depth of half the seed size for each species, approximately 30 mm apart. The number of seeds sown in each punnet varied based on the seed size of each species (Table 1). Multiple seeds (10–12) were sown in each indentation for the species that had tiny seeds. Five control and five treatment punnets were set up for each species to give 500 punnets. Ten punnets of randomly chosen species were placed on a tray (35 × 295 × 50 mm, Garden City Plastics, Forrestfield, Western Australia), each tray was positioned randomly within the glasshouse, and the position of the trays was randomised weekly. Separate trays were used for the control and infested punnets to avoid contamination. Punnets were hand-watered daily. The number of emerging seedlings was counted every third day. Plant species with tiny seeds had a cluster of seedlings per indentation. The number of seedlings in each indentation was also counted to determine the number of seedlings that had emerged per punnet. After three months, the final number of surviving seedlings was counted. Seedlings that died during the experiment before the final harvest were tested for *P. cinnamomi* in the roots by plating a root sample onto NARH.

Statistical analysis

One-way ANOVA was used to determine whether there was an impact of *P. cinnamomi* on seedling emergence and survival of seedlings during the first three months for each species. The seedling emergence or survival percentage was the response variable, and treatment was the predictor variable. The normality of residuals and homogeneity of variances were checked visually and statistically (Shapiro test and LeveneTest). For the species where normality and homogeneity of variances assumption were not met, the Kruskal–Wallis test and Welch ANOVA were used, respectively. Statistical analyses were performed in R version 4.1.2 (R Core Team 2021).

Experiment 2 – Screening selected plant species susceptibility from experiment 1 to *P. cinnamomi*

Species selection

Twenty-four plant species were selected from experiment 1 based on high seedling emergence and early survival in the presence of *P. cinnamomi.* Most had no information on their disease resistance as older plants. Five species in which *P. cinnamomi* affected both seedling emergence and early survival and were known to be susceptible as adult plants in the field were also included as controls (Table 1).

Experiment design

Native plant potting mix (Richgro, Canning Vale, Western Australia) steam pasteurised for two hours at 65°C was used as the growth medium. Three to five months old seedlings were taken from the seedlings germinating in propagation punnets and transferred to slimline pots (125 mm, 1.1 L, Garden City Plastics, Forrestfield, Western Australia) lined with Superwipes as described before. Two sterile plastic tubes (10 ml) were inserted on either side of the seedling. Seedlings were grown for two months and then inoculated with *P. cinnamomi* by removing the two plastic tubes and placing inoculum in each hole created by the tube. Sterilised non-inoculated millet seeds were used for the controls. At the time of inoculation, plant height was measured. There were 20 replicates for each species (10 for controls and 10 for inoculation), but deaths after transplantation reduced this number to 18 for four and 16 for seven species. The pots were placed randomly within the glasshouse, and the position of the pots was randomised weekly. The pots were

Table 1 Plant species used in this study; their height and natural distribution, response to *Phytophthora cinnamomi*, seed treatments required to optimise germination and the number of seeds placed in each punnet. The information collected from [a]Western Australian Herbarium (1998), [b]McDougall (2005) and Groves et al. (2009) and [c]Fryer (2006)

Family	Species	Plant height (m)[a]	Distribution[a]	Susceptibility to *P. cinnamomi*[b]	Seed treatment[c]	Number of seeds per punnet
Asteraceae	*Olearia muelleri*	1.5	Wheatbelt, Geraldton, Esperance	Unknown	None	15
Chenopodiaceae	*Rhagodia preissii*	4	Jarrah Forest, Wheatbelt, Geraldton	Unknown	Smoke Water	150 - 180[d]
Fabaceae	*Acacia acuminata*	7	Jarrah Forest, Wheatbelt, Esperance, Swan Coastal Plain	Unknown	Hot Water	15
Fabaceae	*Acacia dentifera*	3	Esperance, Jarrah Forest, Swan Coastal Plain	Unknown	Hot Water	15
Fabaceae	*Acacia drummondii*	1	Jarrah Forest, Esperance	Resistant[F]	Hot Water	15
Fabaceae	*Acacia neurophylla*	5	Wheatbelt, Geraldton	Unknown	Hot Water	15
Fabaceae	*Acacia saligna*	6	Jarrah Forest, Wheatbelt, Esperance, Geraldton	Resistant[F]	Hot Water	15
Fabaceae	*Acacia pycnantha**	8	Jarrah Forest, Wheatbelt, Esperance, Swan Coastal Plain	Unknown	Hot Water	15
Fabaceae	*Labichea lanceolata*	3	Jarrah Forest, Wheatbelt, Esperance, Swan Coastal Plain	Unknown	Hot Water	15
Fabaceae	*Templetonia retusa*	4	Jarrah Forest, Swan Coastal Plain, Geraldton	Unknown	Hot Water	15
Lamiaceae	*Hemiandra pungens*	1	Jarrah Forest, Wheatbelt, Swan Coastal Plain, Geraldton	Resistant[F]	Smoke Water	150 - 180[d]
Loranthaceae	*Nuytsia floribunda*	10	Jarrah Forest, Wheatbelt, Swan Coastal Plain, Geraldton	Resistant[F]	None	6
Myrtaceae	*Astartea scoparia*	1.8	Jarrah Forest, Wheatbelt, Swan Coastal Plain	Unknown	Smoke Water	150 - 180[d]
Myrtaceae	*Callistemon phoeniceus*	6	Jarrah Forest, Wheatbelt, Esperance, Geraldton	Unknown	None	150 - 180[d]
Myrtaceae	*Calothamnus gilesii*	3	Wheatbelt, Geraldton	Unknown	None	150 - 180[d]
Myrtaceae	*Calothamnus hirsutus*	1.5	Jarrah Forest, Wheatbelt, Swan Coastal Plain, Geraldton	Unknown	None	150 - 180[d]
Myrtaceae	*Calothamnus quadrifidus*	3	Jarrah Forest, Wheatbelt, Esperance, Swan Coastal Plain	Resistant[F]	None	150 - 180[d]
Myrtaceae	*Calothamnus sanguineus*	2	Jarrah Forest, Wheatbelt, Esperance, Swan Coastal Plain	Resistant[F]	None	150 - 180[d]
Myrtaceae	*Eremaea pauciflora*	4	Jarrah Forest, Wheatbelt, Esperance, Geraldton	Unknown	Smoke Water	150 - 180[d]
Myrtaceae	*Eucalyptus macrocarpa*	5	Wheatbelt, Geraldton	Unknown	None	15
Myrtaceae	*Hypocalymma angustifolium*	1.5	Jarrah Forest, Wheatbelt, Esperance	Resistant[F]	Smoke Water	150 - 180[d]
Myrtaceae	*Kunzea pulchella*	3	Jarrah Forest, Wheatbelt, Swan Coastal Plain	Unknown	None	150 - 180[d]
Myrtaceae	*Kunzea recurva*	2	Jarrah Forest, Wheatbelt, Esperance, Swan Coastal Plain	Susceptible[F]	None	150 - 180[d]
Myrtaceae	*Leptospermum erubescens*	3	Jarrah Forest, Wheatbelt, Esperance, Swan Coastal Plain	Resistant[F]	Smoke Water	150 - 180[d]

Table 1 (continued)

Family	Species	Plant height (m)[a]	Distribution[a]	Susceptibility to *P. cinnamomi*[b]	Seed treatment[c]	Number of seeds per punnet
Myrtaceae	*Melaleuca adnata*	5	Wheatbelt, Geraldton, Esperance	Unknown	None	150 - 180[d]
Myrtaceae	*Melaleuca conothamnoides*	1.5	Jarrah Forest, Wheatbelt, Geraldton	Unknown	None	150 - 180[d]
Myrtaceae	*Melaleuca preissiana*	9	Jarrah Forest, Wheatbelt, Swan Coastal Plain, Geraldton	Resistant[F]	None	150 - 180[d]
Myrtaceae	*Melaleuca seriata*	1	Jarrah Forest, Wheatbelt, Swan Coastal Plain	Resistant[F]	None	150 - 180[d]
Myrtaceae	*Regelia ciliata*	2	Jarrah Forest, Wheatbelt, Swan Coastal Plain, Geraldton	Unknown	Smoke Water	150 - 180[d]
Myrtaceae	*Regelia inops*	2.5	Jarrah Forest, Wheatbelt, Swan Coastal Plain	Susceptible[F]	Smoke Water	150 - 180[d]
Proteaceae	*Banksia caleyi*	2	Esperance	Susceptible[G]	None	10
Proteaceae	*Banksia elderiana*	4	Wheatbelt, Esperance	Susceptible[G]	None	10
Proteaceae	*Banksia lemanniana*	5	Esperance	Susceptible[G]	None	10
Proteaceae	*Banksia repens*	0.4	Jarrah Forest, Wheatbelt, Esperance	Susceptible[F]	None	10
Proteaceae	*Banksia sessilis*	8	Jarrah Forest, Wheatbelt, Esperance	Susceptible[F]	None	15
Proteaceae	*Grevillea endlicheriana*	3	Jarrah Forest, Wheatbelt, Swan Coastal Plain	Unknown	Smoke Water	15
Proteaceae	*Grevillea eriostachya*	5	Jarrah Forest, Wheatbelt, Swan Coastal Plain, Geraldton	Unknown	Smoke Water	15
Proteaceae	*Grevillea paniculata*	3	Jarrah Forest, Wheatbelt, Geraldton	Unknown	Smoke Water	15
Proteaceae	*Grevillea pterosperma*	4	Wheatbelt, Geraldton	Unknown	Smoke Water	15
Proteaceae	*Grevillea vestita*	3	Wheatbelt, Geraldton	Unknown	Smoke Water	15
Proteaceae	*Hakea anadenia*	2	Jarrah Forest, Swan Coastal Plain, Geraldton	Unknown	None	15
Proteaceae	*Hakea laurina*	6	Jarrah Forest, Wheatbelt, Esperance, Swan Coastal Plain	Susceptible[F]	None	8
Proteaceae	*Hakea petiolaris*	9	Wheatbelt, Jarrah Forest, Swan Coastal Plain	Resistant[F]	None	10
Proteaceae	*Hakea ruscifolia*	3	Jarrah Forest, Wheatbelt, Esperance, Swan Coastal Plain	Resistant[F]	None	10
Proteaceae	*Hakea trifurcata*	3	Jarrah Forest, Wheatbelt, Esperance, Geraldton	Susceptible[F]	None	10
Proteaceae	*Isopogon dubius*	1.5	Jarrah Forest, Wheatbelt, Esperance, Geraldton	Unknown	Smoke Water	15
Proteaceae	*Petrophile biloba*	2	Jarrah Forest, Swan Coastal Plain	Susceptible[G]	Smoke Water	15
Proteaceae	*Xylomelum angustifolium*	7	Jarrah Forest, Wheatbelt, Swan Coastal Plain	Susceptible[F]	None	4
Rhamnaceae	*Trymalium ledifolium*	5	Jarrah Forest, Wheatbelt, Geraldton	Susceptible[F]	Hot Water	15
Rhamnaceae	*Trymalium odoratissimum*	4	Jarrah Forest, Swan Coastal Plain	Unknown	Hot Water	15

Susceptibility and resistance determined by F – Field observation, G – Glasshouse experiment

d 10 to 12 tiny seeds placed in each of 15 holes in the planting medium

*A species endemic to southeast Australia

hand-watered daily. Quarter-strength Dynamic Lifter liquid fertilizer (Yates Gardening Products) was used fortnightly.

Two months after inoculation, the height of the plants was measured, then plants were harvested, and the roots were gently washed with running water and blotted dried using paper towels. The root system of each plant was visually assessed and scored for root damage (1 = healthy roots, 2 = 1–25% damaged roots, 3 = 26–50% damaged roots, 4 = 51–75% damaged roots and 5 = 76–100% damaged roots) (Farooq et al. 2023). A surface sterilised root sample of each plant was plated in NARH to confirm the presence of *P. cinnamomi*. Roots were then dried at 37°C for one week, and the dry weight was recorded. Plant deaths observed during the experiment were recorded, and root samples from the dead plants were also plated onto NARH to reisolate *P. cinnamomi.*

Statistical analysis

The mean and standard deviation of shoot growth, root weight and root score for each species were calculated using the *aggregate* function. To determine whether *P. cinnamomi* inoculation affected the shoot growth, root weight and root score, the *metafor* package (Viechtbauer 2010) was used. The effect size estimates (mean difference) and the variance of each parameter separately for each species were calculated using the *escalc* function. Effect size estimates, and variance were fitted into a random model to calculate the random meta-analysis using *rma* function. To visualise the results, forest plots were created for each parameter using the *forest* function. Statistical analyses were performed in R version 4.1.2 (R Core Team 2021).

Results

Experiment 1 - Effect of *P. cinnamomi* on seedling emergence and early survival of fifty native plant species

Of the 50 plant species used, 38 emerged in sufficient numbers in both the control and inoculated treatments to perform the statistical analysis. The effect of *P. cinnamomi* on seedling emergence and early survival varied between species. For nine species, the presence of *P. cinnamomi* caused no significant ($p > 0.05$) changes to seedling emergence or survival (Table 2). Seedling emergence but not survival was significantly ($p < 0.05$) reduced in nine species, and seedling survival was significantly ($p < 0.05$) reduced in five species in the presence of *P. cinnamomi* (Table 2). In fifteen species, both seedling emergence and early survival were significantly ($p < 0.05$) reduced by *P. cinnamomi* (Table 2).

P. cinnamomi was not isolated from non-inoculated controls that died during the experiment, and it was isolated from approximately 60% of the dead seedlings from inoculated pots across all the species.

Experiment 2 – Screening selected plant species susceptibility from experiment 1 to *P. cinnamomi*

Of twenty-four species inoculated at 5–7 months old, no deaths were observed in *P. cinnamomi* inoculated plants of six species, and no *P. cinnamomi* was reisolated from the roots of these species (Table 3). In three species, no deaths were observed even though *P. cinnamomi* was reisolated from the roots (Table 3). One or more of the ten plants died in inoculated soil of thirteen species, and *P. cinnamomi* was reisolated from their roots (Table 3). Some deaths of plants of nine species occurred in the control non-inoculated pots, but no *P. cinnamomi* was reisolated from any of the dead plants. Plant deaths were observed in all five species previously recorded to be susceptible.

Shoot growth

In 15 species, there was no effect of *P. cinnamomi* on shoot growth (Fig. 1). However, for eight species: *Acacia dentifera*, *Banksia sessilis*, *Eucalyptus macrocarpa*, *Grevillea pterosperma*, *Hakea laurina*, *Kunzea pulchella, K. recurva* and *Regelia ciliata,* shoot growth was significantly reduced by *P. cinnamomi* (Fig. 1). In contrast, significantly higher shoot growth was observed in *Rhagodia preissii* inoculated plants (Fig. 1).

Root weight and root score

The root weight of 18 species was not affected by the pathogen. *P. cinnamomi* significantly reduced the root weight of six species compared to the controls: *A. dentifera*, *E. macrocarpa*, *G. pterosperma*, *K. pulchella, K. recurva* and *R. ciliata* (Fig. 2).

Significantly different root damage scores compared to the controls were observed for *B. sessilis, G. pterosperma, K. pulchella, K. recurva, Templetnia retusa* and *Xylomelum angustifolium* (Fig. 3).

Screening 24 species (at 5–7 months old) susceptibility to *P. cinnamomi*

Twenty-four plant species tested in the second experiment were allocated into five different categories based on the results of experiments 1 and 2 (Table 3). Species that had no mortality in inoculated plants in which *P. cinnamomi* was not isolated from the roots and did not affect any of the measured parameters for seedlings or 7–9 months old

Table 2 Mean and standard error of percentage seedling emergence and early survival of native species inoculated with *Phytophthora cinnamomi*. Data are only shown for species giving sufficient germination for statistical analysis, and data for the additional species are given in Table S3. Highlighted values indicate resistant species in which *P. cinnamomi* causes no significant (P > 0.05) differences in emergence and survival compared to non-inoculated controls

	Emergence (Percentage ± SE)		Survival (Percentage ± SE)	
Plant Species	Control	Inoculated with *Phytophthora*	Control	Inoculated with *Phytophthora*
*Acacia acuminata**	72.0 ± 3.86	46.8 ± 12.82	97.8 ± 2.22	67.6 ± 18.28
*Acacia dentifera**	46.6 ± 7.10	21.2 ± 3.93	100 ± 0	65.3 ± 18.31
Acacia neurophylla	44.0 ± 5.73	9.4 ± 3.36	100 ± 0	80.0 ± 20.00
Acacia pycantha	57.4 ± 8.81	25.4 ± 4.79	98.0 ± 2.00	95.00 ± 5.00
*Acacia saligna**	46.8 ± 4.27	26.6 ± 4.74	100 ± 0	100 ± 0
Astartea scoparia	76.8 ± 9.33	15.0 ± 1.48	40.8 ± 13.88	47.6 ± 9.94
*Banksia caleyi***	74.0 ± 4.00	24.0 ± 12.08	100 ± 0	60.0 ± 18.71
*Banksia elderiana***	74.0 ± 6.78	18.0 ± 5.83	96.7 ± 3.33	40 ± 19.43
*Banksia lemanniana***	84.0 ± 6.78	16.0 ± 11.66	100 ± 0	30.0 ± 20.00
Banksia repens	50.0 ± 5.48	16.0 ± 2.45	92.14 ± 5.10	60.0 ± 18.71
*Banksia sessilis***	36.0 ± 7.80	7.8 ± 3.18	79.8 ± 6.27	20.0 ± 20.00
*Callistemon phoeniceus**	93.4 ± 2.28	39.6 ± 4.41	83.2 ± 5.40	80.9 ± 3.53
*Calothamnus gilesii**	12.6 ± 1.43	11.2 ± 2.54	38.7 ± 13.87	16.6 ± 7.89
*Calothamnus hirsutus**	78.6 ± 5.74	61.6 ± 7.81	83.8 ± 4.53	67.3 ± 8.15
Calothamnus quadrifidus	6.4 ± 0.68	3.0 ± 0.89	67.3 ± 8.15	41.5 ± 13.8
*Calothamnus sanguineus**	16.6 ± 4.13	7.0 ± 1.87	96.9 ± 3.07	75.5 ± 5.35
Eremaea pauciflora	15.0 ± 3.65	4.6 ± 2.25	86.3 ± 4.45	42.9 ± 17.96
*Eucalyptus macrocarpa**	49.4 ± 7.15	49.4 ± 4.51	93.6 ± 4.39	61.4 ± 8.91
Grevillea eriostachya	22.4 ± 4.51	0	67.3 ± 10.67	0
*Grevillea pterosperma**	8.0 ± 2.40	0	80.0 ± 20.00	0
*Hakea laurina**	75.4 ± 9.68	72.8 ± 4.65	100 ± 0	100 ± 0
*Hakea petiolaris**	48.0 ± 9.67	26.0 ± 10.77	100 ± 0	76.6 ± 19.44
Hakea ruscifolia	70.0 ± 8.94	24.0 ± 6.78	100 ± 0	73.3 ± 19.44
*Hakea trifurcata**	66.0 ± 16.0	50.0 ± 6.32	100 ± 0	77.3 ± 11.27
*Kunzea pulchella**	44.8 ± 8.67	23.2 ± 5.62	81.4 ± 3.64	31.8 ± 9.96
*Kunzea recurva**	47.6 ± 8.08	53.4 ± 5.64	100 ± 0	83.1 ± 3.72
*Labichea lanceolata**	77.4 ± 3.41	22.6 ± 10.28	98.3 ± 1.66	17.2 ± 9.39
Leptospermum erubescens	60.0 ± 7.33	9.8 ± 2.10	38.8 ± 7.52	2.43 ± 1.49
Melaleuca adnata	11.2 ± 3.30	5.2 ± 1.39	36.18 ± 13.65	30.3 ± 17.79
Melaleuca preissiana	57.2 ± 6.79	59.0 ± 10.12	42.8 ± 12.33	35.3 ± 9.60
*Melaleuca seriata**	60.2 ± 0.97	48.6 ± 4.63	53.4 ± 12.95	29.1 ± 11.10
Olearia muelleri	16.0 ± 3.44	4.2 ± 1.71	40.0 ± 18.71	0
Petrophile biloba	25.2 ± 3.88	2.8 ± 1.71	100 ± 0	40.0 ± 24.49
*Regelia ciliata**	14.2 ± 3.36	5.0 ± 1.73	99.2 ± 0.77	44.86 ± 15.10
Regelia inops	12.8 ± 3.80	2.4 ± 1.25	72.5 ± 12.75	13.3 ± 13.33
*Rhagodia preissii**	18.2 ± 3.25	12.6 ± 2.76	96.0 ± 4.00	69.8 ± 8.66
*Templetonia retusa**	82.8 ± 1.71	33.4 ± 4.74	98.5 ± 1.54	90.3 ± 6.10
*Xylomelum angustifolium***	75.0 ± 7.91	5.0 ± 5.00	100 ± 0	20.0 ± 20.00

*Represents 24 species selected for Experiment 2

**Represents the five species in which *P. cinnamomi* affected both seedling emergence and early survival and were known to be susceptible as adult plants

Table 3 Summary of species responses to *Phytophthora cinnamomi* as young (3 months old) seedlings, and when inoculated at 5–7 months of age and harvested 2 months later. Species are categorised from the significant effects on seedling emergence, survival within the first 3 months, shoot growth, root weight and root score. Previous information on species responses to the pathogen (McDougall (2005) and Groves et al. (2009)) is also shown

Species	Effect of *P. cinnamomi*							*P. cinnamomi* response category	
	Young seedlings		7–9 months old plants					Current Experiment	Previous Reports*
	Reduction in emergence	Reduction in survival at 3 months	Reduction in shoot growth	Reduction in root weight	Increase in root damage	Deaths of inoculated plants (%)	Re-isolation of *Phytophthora*		
Acacia acuminata	−	−	−	−	−	0	−	Resistant	Unknown
Calothamnus gilesii	−	−	−	−	−	0	−	Resistant	Unknown
Banksia elderiana	+	+	−	−	−	10.0	−	Moderately Resistant	Susceptible
Callistemon phoeniceus	+	−	−	−	−	0	−	Moderately Resistant	Unknown
Calothamnus sanguineus	−	+	−	−	−	0	−	Moderately Resistant	Resistant
Hakea laurina	−	−	+	−	−	0	−	Moderately Resistant	Susceptible
Melaleuca seriata	−	−	−	−	−	30.0	−	Moderately Resistant	Resistant
Rhagodia preissii	−	+	+	−	−	0	−	Moderately Resistant	Unknown
Acacia saligna	+	−	−	−	−	0	+	Tolerant Host	Resistant
Calothamnus hirsutus	−	−	−	−	−	0	+	Tolerant Host	Unknown
Templetonia retusa	+	−	−	−	+	0	+	Tolerant Host	Unknown
Acacia dentifera	+	−	+	+	−	40.0	+	Susceptible	Unknown
Banksia caleyi	+	−	−	−	−	20.0	+	Susceptible	Susceptible
Banksia lemanniana	+	+	−	−	−	50.0	+	Susceptible	Susceptible
Banksia sessilis	+	+	+	−	−	71.5	+	Susceptible	Susceptible
Eucalyptus macrocarpa	−	+	+	+	−	50.0	+	Susceptible	Unknown
Hakea petiolaris	−	−	−	−	−	37.5	+	Susceptible	Resistant
Hakea trifurcata	−	−	−	−	−	25.0	+	Susceptible	Susceptible
Labichea lanceolata	+	+	−	−	−	11.1	+	Susceptible	Unknown
Regelia ciliata	+	+	+	+	−	60.0	+	Susceptible	Unknown
Xylomelum angustifolium	+	+	−	−	+	20.0	+	Susceptible	Susceptible
Grevillea pterosperma	+	+	+	+	+	88.9	+	Highly Susceptible	Unknown

Table 3 (continued)

Species	Effect of *P. cinnamomi*							*P. cinnamomi* response category	
	Young seedlings		7–9 months old plants					Current Experiment	Previous Reports*
	Reduction in emergence	Reduction in survival at 3 months	Reduction in shoot growth	Reduction in root weight	Increase in root damage	Deaths of inoculated plants (%)	Re-isolation of *Phytophthora*		
Kunzea pulchella	−	+	+	+	+	90.0	+	Highly Susceptible	Unknown
Kunzea recurva	−	+	+	+	−	87.5	+	Highly Susceptible	Susceptible

Resistant – Mortality 0%, no *P. cinnamomi* was re-isolated from the roots and *P. cinnamomi* did not affect any of the measured parameters; Moderately Resistant—Mortality 0–30%, no *P. cinnamomi* re-isolated from roots and *P. cinnamomi* affected at most two measured parameters; Tolerant Host – Mortality 0%, *P. cinnamomi* re-isolated from roots and *P. cinnamomi* affected at most two measured parameters; Susceptible – Mortality < 80%, *P. cinnamomi* re-isolated from roots, *P. cinnamomi* affected up to three measured parameters; Highly susceptible – Mortality > 80%, *P. cinnamomi* re-isolated from roots and *P. cinnamomi* affected up to five measured parameters

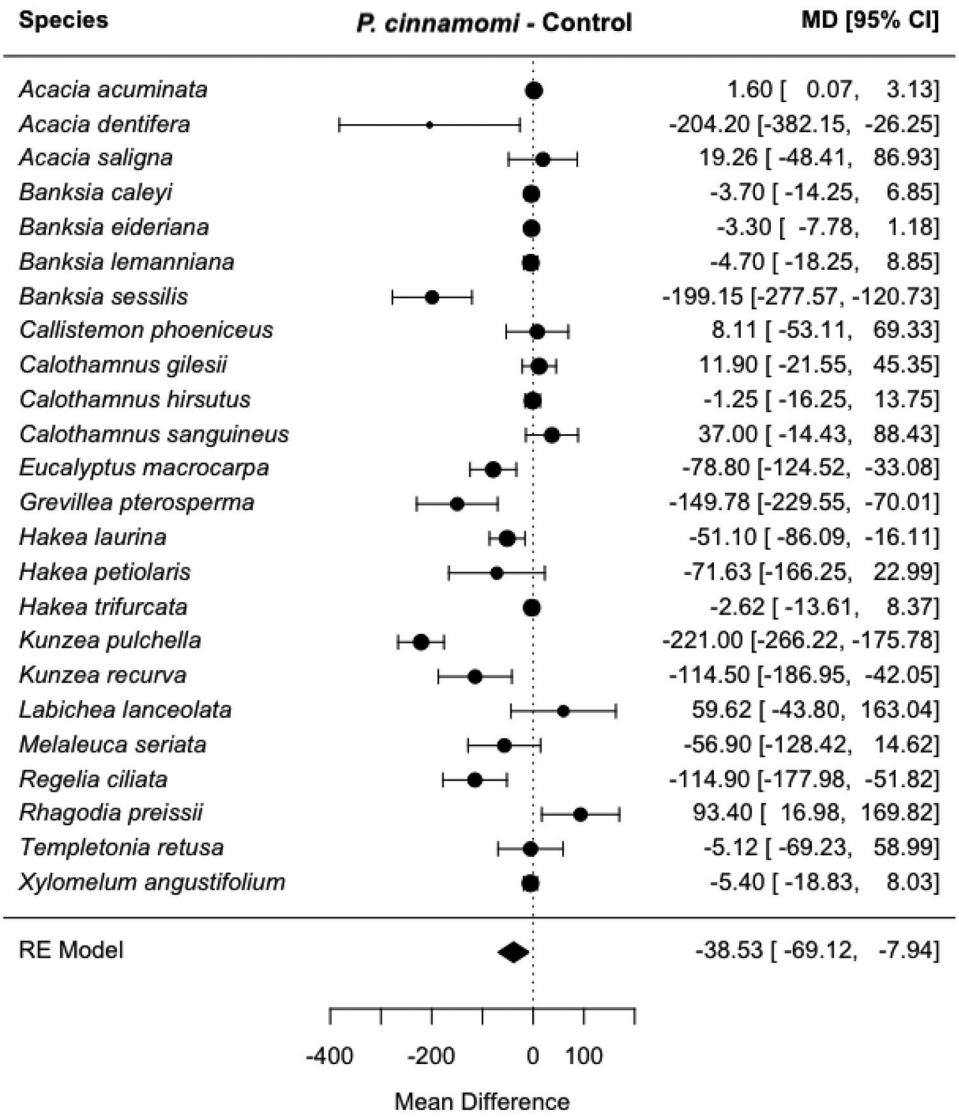


Fig. 1 Shoot growth of 24 species after inoculation with *Phytophthora cinnamomi* versus control Control and *P. cinnamomi* treatments are significantly ($p < 0.05$) different when the confidence interval for each species does not overlap with the line of no effect (Mean difference = 0). The size of the circle indicates the magnitude of the effect

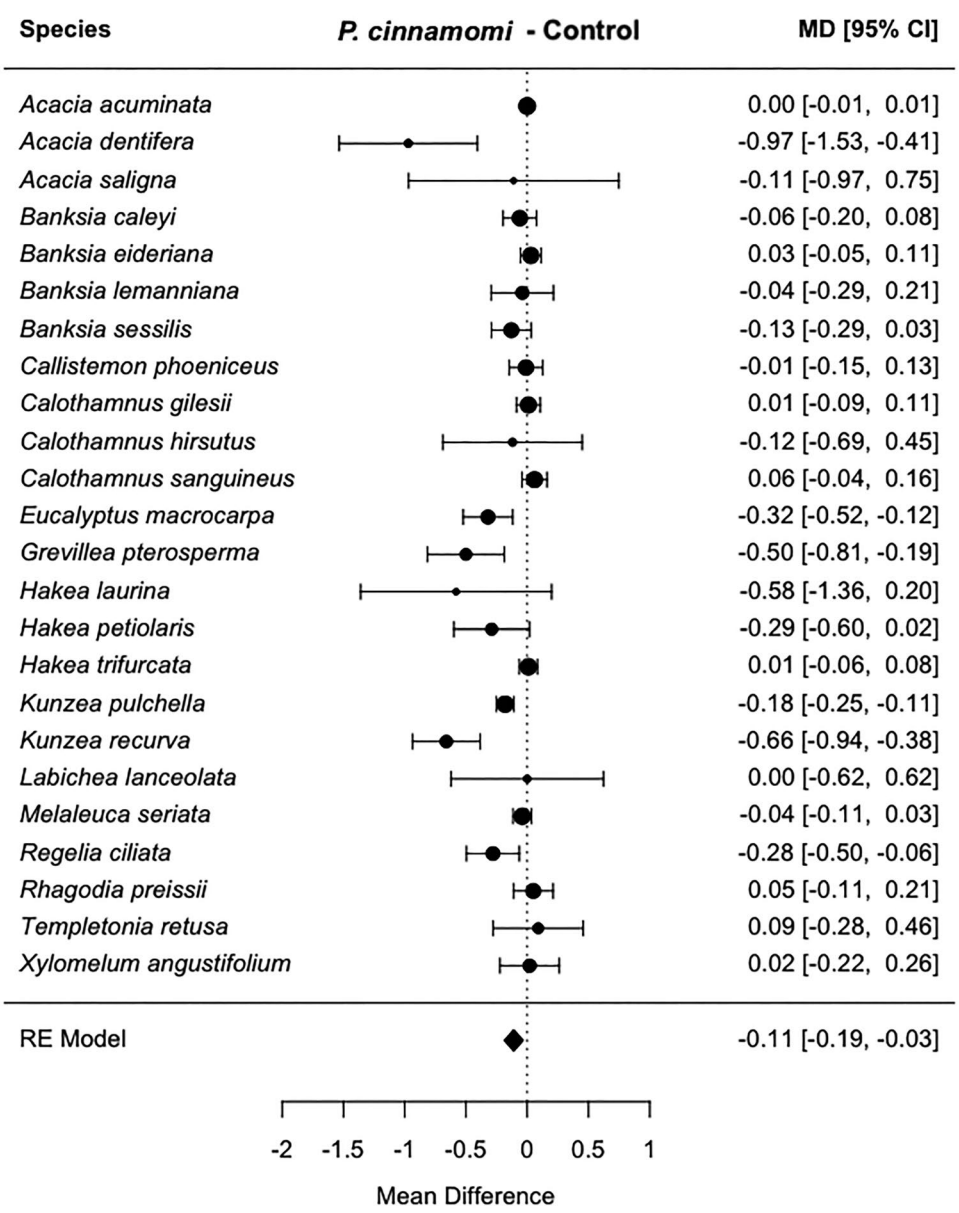


Fig. 2 Root weight of 24 species after inoculation with *Phytophthora cinnamomi* versus control Control and *P. cinnamomi* treatments are significantly ($p < 0.05$) different when the confidence interval for each species does not overlap with the line of no effect (Mean difference = 0). The size of the circle indicates the magnitude of the effect

plants were categorised as resistant. *Acacia acuminata* and *C. gilessii* were the only two resistant species identified. (Table 3). Six species, including *B. elderiana*, *C. phoeniceus*, *C. sanguineus*, *H. laurina*, *M. seriata* and *R. preissii* were classified as moderately resistant to the pathogen (Table 3). No *P. cinnamomi* was isolated from the roots, there was less than 30% mortality after nine months and only up to two measured parameters were impacted.

When *P. cinnamomi* was isolated from the roots species were grouped as tolerant, susceptible, or highly susceptible. *Acacia saligna*, *T. retusa*, and *C. hirsutus* were categorised as tolerant hosts of *P. cinnamomi.* Even though *P. cinnamomi* was present in the roots, no plants died, and the pathogen significantly affected at most two measured parameters (Table 3). Ten species: *A. dentifera, B. caleyi, B. lemanniana, B. sessilis, E. macrocarpa, H. petiolaris, H. trifurcata, L. lanceolata, R. ciliata,* and *X. angustifolium* were classified as susceptible. These showed 11- < 80% mortality in inoculated plants, *P. cinnamomi* was isolated from the roots and up to three measured parameters were affected. Three species: *G. pteroperma*, *K. pulchella*, and *K. recurva* were categorised as highly susceptible to *P. cinnamomi* (Table 3). Mortality was higher than 80%, the pathogen was reisolated from the dead plants, and *P. cinnamomi* significantly affected all or most measured parameters.

Amongst the four species previously reported to be resistant, *C. sanguineus* and *M. seriata* showed moderate resistance in the current study, while *A. saligna* was infected asymptomatically, and *H. petiolaris* was susceptible. Of the eight species previously categorized as susceptible, six were

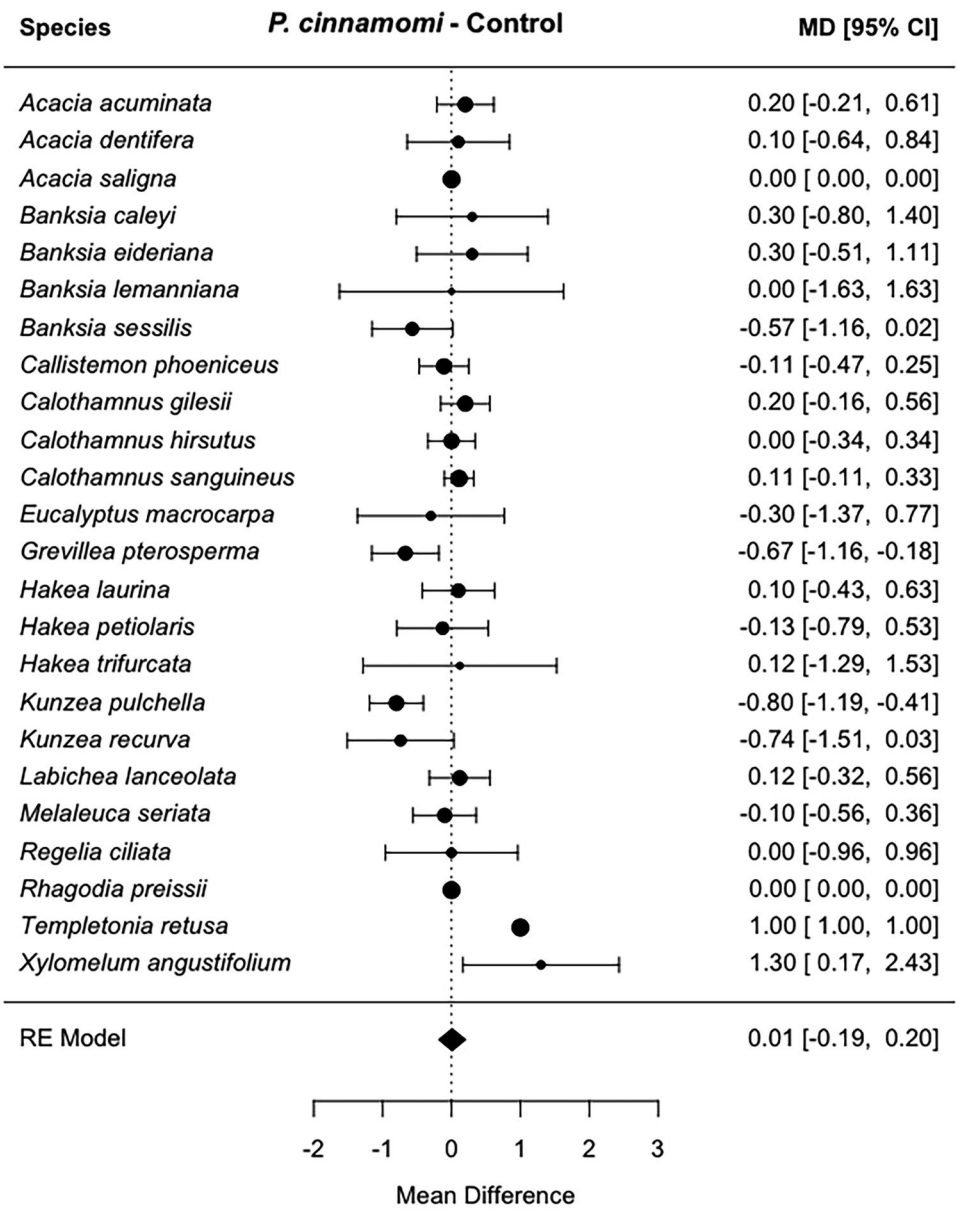


Fig. 3 Root score of 24 species after inoculation with *Phytophthora cinnamomi* versus control Control and *P. cinnamomi* treatments are significantly different ($p < 0.05$) when the confidence interval for each species does not overlap with the line of no effect (Mean difference = 0). The size of the circle indicates the magnitude of the effect

susceptible or highly susceptible, while two appeared moderately resistant.

Discussion

Of the 24 plant species tested for resistance to *P. cinnamomi,* both as young seedlings and when inoculated 5–7-month-old plants, two species were resistant, six were moderately resistant, ten were susceptible, and three were highly susceptible. Three species were tolerant hosts of *P. cinnamomi*.

In the present study, data on the responses of 12 species to *P. cinnamomi* are reported for the first time. These included *A. acuminata* and *C. gilesii,* which were the most resistant to *P. cinnamomi*. Of the six moderately resistant species observed, *C. sanguineus* and *M. seriata* have also been recorded as resistant in the Stirling Range National Park, Western Australia (McDougall 2005; Groves et al. 2009). However, *B. elderiana,* which appeared moderately resistant in the current study, was recorded as susceptible in an experiment that used transplanted 7–9 months old plants in a Banksia woodland site and inoculated with *P. cinnamomi* (McCredie et al. 1985). It is possible that root damage during transplantation resulted in the plant's susceptibility. *Hakea laurina,* which was observed to be susceptible to *P. cinnamomi* in the Stirling Range National Park, Western Australia (McDougall 2005) was moderately resistant in the current study. *Callistemon phoeniceus* and *R. preissii,* for which there is no previous information, were moderately resistant in the present study.

The susceptibility of *B. caleyi*, *B. lemanniana, B. sessilis, H. trifurcata* and *X. angustifolium* to *P. cinnamomi* is consistent with the previous records by McCredie et al. (1985) and Alcoa of Australia (2002). In the present study, many inoculated *H. petiolaris* plants died, and the pathogen was isolated from the roots of dead plants indicating that the species was susceptible to *P. cinnamomi*. This result contradicts McDougall (2005) and Groves et al. (2009) who recorded *H. petiolaris* as resistant to *P. cinnamomi* in the field. This is possibly due to plants being susceptible when young but showing improved resistance when they mature. *Acacia dentifera, E. macrocarpa, L. lanceolata* and *R. ciliata* were susceptible to *P. cinnamomi* in the present study, and no records are available regarding their responses to the pathogen.

Grevillea pterosperma, K. pulchella and *K. recurva* were highly susceptible to *P. cinnamomi,* with more than 85% deaths in the inoculated plants. *Kunzea recurva* has previously been recorded as susceptible to *P. cinnamomi* in the field (McDougall 2005), but this is the first record of the susceptibility of *G. pterosperma* and *K. pulchella*.

No deaths were observed in the inoculated plants of *A. saligna, C. hirsutus,* and *T. retusa,* and only one or two parameters tested were affected by the pathogen. However, *P. cinnamomi* was isolated from the roots of surviving plants indicating that these species were tolerant hosts to *P. cinnamomi*. Crone et al. (2013) revealed that some annual and herbaceous perennial native plant species in the jarrah forest can also survive in dieback areas as symptomless hosts. Similarly, the three species identified in the current study were resistant and able to survive in the *P. cinnamomi* inoculated soil without exhibiting disease symptoms even though the pathogen was present in the roots. Such species should be monitored further to determine if they are appropriate for rehabilitation work or if they may act as a reservoir of *P. cinnamomi* and increase soil inoculum levels. Further investigation of the species which would be valuable for rehabilitation work, but which have shown variable responses to the pathogen should be investigated to determine whether this variation is due to intra-species variation in susceptibility and whether seeds from some regions would be appropriate to use.

The species tested in the present study were mainly from Myrtaceae, Proteaceae and Fabaceae. Most species were resistant within the Myrtaceae and Fabaceae, whereas, within the Proteaceae, most species were susceptible to the pathogen, which is in accordance with previous reports (Kueh et al. 2012; Shearer et al. 2013). All three *Calothamnus* species from the Myrtaceae were resistant to the pathogen, but the *Kunzea* species, *K. pulchella* and *K. recurva* were highly susceptible. Within Fabaceae, *A. acuminata* and *A. saligna* were resistant, and *A. dentifera* was susceptible. The only resistant species in the Proteaceae were *H. laurina* and *B. elderiana*.

Most species susceptible to *P. cinnamomi* as young seedlings were also impacted when plants inoculated at 5–7 months. However, *B. elderiana* was susceptible as young seedlings, but the resistance increased when the plants were older. Shaw (2019) has revealed that the species susceptible at early stages may not be susceptible to the pathogen when they mature or vice versa. In addition, several other studies, including work both on eucalypts and crop species, also reported that the resistance of plants to *Phytophthora* or *Pythium* increased with plant age (Chun and Schneider 1998; Raftoyannis and Dick 2002; Simamora et al. 2017).

This is the first evaluation of species native to Western Australia for their response to *P. cinnamomi* at seedling emergence and early seedling growth. It has shown that some species showing field resistance may be susceptible at early stages and thus unsuitable for use in projects to rehabilitate *P. cinnamomi* infested forest sites. Screening of seedlings of species recorded as resistant from field observation or experiments with mature plants in the glasshouse is highly desirable before species selection for seed-based rehabilitation.

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Author contribution Giles Hardy, Treena Burgess and Shanika Harshani conceived and designed the research. Shanika Harshani performed the gashouse experiments and analysed the data. Shanika Harshani and Jen McComb wrote the first draft. All authors contributed critically to edit the draft.

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Data availability Data are available on request.

Declarations

Conflict of interest The authors have no conflict of interest to declare that are relevant to this article.

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