Extending the host range of *Phytophthora multivora*, a pathogen of woody plants in horticulture, nurseries, urban environments and natural ecosystems

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Highlights

- *Phytophthora multivora* caused significant root damages on twenty-five plant species common in the urban environment
- *P. multivora* is more commonly isolated than P. cinnamomi in the urban environment
- *Phytopthora* threatens viability and longevity of the urban forest

Abstract

Phytophthora multivora is a recently described species with a global distribution associated with disease of many woody plant species. However, very few pathogenicity studies have been conducted to determine the host range of this pathogen. A soil infestation pathogenicity experiment was conducted using two *P. multivora* isolates with *Phytophthora cinnamomi,* a known virulent pathogen, included for comparison purposes. Twenty-seven plant species were included, 19 native to Western Australia (WA) and eight exotic tree species often used as urban street trees. Plants were harvested 12 weeks after inoculation, damage of root systems were rated and root and shoot dry weight measured. Twenty-four out of twenty-seven tested host species were significantly susceptible to *P. multivora. P. cinnamomi* was often more pathogenic; - despite this, *P. multivora* represents an ecological risk for urban forests of Perth and for the whole of the South West Botanical Province of WA. Additionally, the susceptibility of other common woody plants found globally in cities suggests that *P. multivora* will, in time, become as 'well-known' and damaging as *P. cinnamomi.*

Keywords

Hosts susceptibility; Pathogenicity; *Phytophthora*; Tree decline; Urban trees; Western Australia

Introduction

The South West Botanical Province of Western Australia (SWWA) is an internationally recognised biodiversity hotspot (Shearer et al., 2007), and Perth is the most biodiverse city in the world (Hopper and Gioia, 2004). Perth is a moderately green city with 28% canopy cover across the whole city and some suburbs with over 50% coverage ("202020Vision," n.d.). The SWWA is experiencing a drying climate trend since several decades(CSIRO and Bureau of Meteorology, 2015; Evans et al., 2013; Evans and Lyons, 2013). Climate change is leading to range expansion of many plant pathogens (Desprez-Loustau et al., 2007). Abiotic stress and plant disease are having increased impact across the globe (Fitzpatrick et al., 2008; Lindner et al., 2010), placing both the natural ecosystems and the urban forest under stress. In the urban environment, the plant pathogen *Phytophthora* can be commonly recovered from dead trees or dying stands and its presence, together with variable predisposing and inciting abiotic and biotic factors, can play a key role in the premature decline in health of the urban forest (Barber et al., 2013).

Phytophthora multivora is emerging as a significant pathogen with a wide host range and global distribution found in nurseries, the urban environment and natural ecosystems (Scott and Williams, 2014). It causes fine feeder root damage and stem girdling lesions often leading to the death of its host. Before its description in 2009 and the deposition of verified sequences into global sequence databases, *P. multivora* had routinely been misidentified as *P. citricola.* The *P. citricola* complex now contains several species, *P. plurivora, P. pini, P. pachypleura, P. acerina,* and *P. capensis,* with *P. citricola* being the correct identity only for isolates from citrus in Asia (Bezuidenhout et al., 2010; Hong et al., 2011; Jung and Burgess, 2009). Hence, many reports of *P. citricola* prior to 2009 may in fact be *P. multivora,* and its global distribution, while already widespread, may still be underestimated. In

addition to Australia (Aldaoud et al., 2016; Burgess et al., 2017; Dunstan et al., 2016), *P. multivora* has now been detected in central and southern Europe and North America (mainly in woody plant nurseries)(Cacciola et al., 2000; Jung et al., 2016; Mrázková et al., 2013; Pane et al., 2017), North Africa (Smahi et al., 2017), South Africa (Nagel et al., 2013), New Zealand (Scott and Williams, 2014) and the Canary Islands (Rodrìguez-Padròn et al., 2018). In South Africa it is routinely found in asymptomatic natural vegetation (Oh et al., 2013).

Though first described in WA (Scott et al., 2009), *P. multivora* is now considered introduced to the region. In WA, *P. multivora* is associated with a dieback in *Eucalyptus gomphocephala* (Scott et al., 2012); however, it is also consistently isolated from stem cankers and the rhizosphere of dead and dying plants of numerous endemic and introduced hosts in natural ecosystems and the urban environment (Barber et al., 2013). In fact, *P. multivora* is the dominant and often only species routinely isolated from dead and dying woody plants in the urban environment of Perth (Barber et al., 2013). In SWWA, *P. multivora* has a wider geographical distribution than *P. cinnamomi* and is active on calcareous soils which are inhibitory to *P. cinnamomi* (Scott et al., 2009).

While *P. multivora* has been regularly recovered from dead and dying trees, few pathogenicity trials (to prove Koch's postulates) have been conducted. Species tested to date are *Eucalyptus gomphocephala* and *E. marginata* (Scott et al., 2012), *Corymbia calophylla* (Croeser et al., 2018) and *Banksia grandis, B. littoralis, B. occidentalis, Casuarina obesa, C. calophylla, E. marginata* and *Lambertia inermis* (Belhaj et al., 2018). Due to the regularity of its recovery from dead and dying trees, especially in Perth's urban environment, this current study was undertaken to determine the pathogenicity of *P. multivora* in a range of commonly planted woody plant species.

Materials and Methods

Plant material

Twenty-seven plant species were tested for their susceptibility to *P. multivora* in soil infestation pathogenicity trials (Table 1). Of these, 19 were native to WA and 8 were common exotic tree species used in the urban environment in Perth, WA (Table 1). Within the group of native species, five (*E. gomphocephala, C. calophylla*, *B. littoralis, B. occidentalis, C. obesa)* have been tested previously (Belhaj et al., 2018; Croeser et al., 2018; Scott et al., 2012). Native plants were provided by the Australian Native Nursery, Oakford WA. These were germinated in seedling trays and provided to the Centre for Phytophthora Science and Management (CPSM) in the 2-4 leaf stage for transplanting. Seedlings of the exotic plants were provided by Trillion Trees Western Australia Nursery' LOT 2 Stirling Crescent, Hazelmere WA 6055.

Fungal isolates and inoculum preparation

The trial was conducted using two *P. multivora* isolates (TRH1 and TRH4), (Croeser et al. 2018) and one isolate of *P. cinnamomi* (MP94-48), a known virulent pathogen, included for comparison purposes (as a positive control). Cultures were initially isolated in WA and are maintained at the CPSM, Murdoch University, WA. A volume of 300 mL of vermiculite substrate (substrate composition: 1 L vermiculite, 10 g millet seeds and 600 mL V8 broth) was placed into each 500 mL Erlenmeyer flask, which was sealed with non-absorbent cotton wool and covered with aluminium foil. V8 broth consists of 0.1 L filtered V8 juice, 0.1 g $CaCO_3$, 0.9 L distilled water. The flasks were autoclaved three times at 121 °C for 20 minutes over three consecutive days, and then inoculated on the third day once the substrate had cooled. Inoculum per flask consisted of agar plugs (5 mm diameter) cut from a 7-day-old colony of the specific *Phytophthora* isolates grown on V8 agar (broth with 17 g/l agar). Non-inoculated V8 plates were used for the control flasks. Flasks were shaken and then placed inside zip-lock plastic

Table 1. Host species considered in this study.

Species	Origin	RD		DW	
		TRH4	TRH1	TRH4	TRH1
Acacia dentifera	WA		+ §		§
Acacia rostellifera	WA	/	+		
Agonis flexuosa	WA			§	
Banksia attenuata	WA	+ /	+	/	+ /
Banksia littoralis	WA	+	+ /		+
Banksia media	WA	+	+	/	
Banksia menziesii	WA	+	+		+
Banksia occidentalis	WA	+ /	+ /	/	+ /
Banksia seminuda	WA	+	+		+
Banksia speciosa	WA	/	/	/	+ /
Casuarina obesa	WA				+
Corymbia calophylla	WA	/			+
Eucalyptus gomphocephala	WA				
Eucalyptus kochii	WA	+	+		
Gastrolobium spinosum	WA		+		
Hakea marginata	WA				
Hakea undulata	WA				+ /
Melaleuca brevifolia	WA		+	/	+ /
Patersonia occidentalis	WA	+	/	+ §	
Albizia julibrissin	Iran, E Asia	/	+	/	+ /
Fraxinus griffithii	India, Asia		+		
Magnolia grandiflora	SE United States	+			+
Olea europaea	S Europe, N Africa, W Asia	+ /	+	+	
Quercus ilex	S Europe, N Africa	+	+	+	+
Syzygium smithii	Eastern Australia	+	+ /		+
Triadica sebifera	China	+ §	+	+	+
Tipuana tipu	South America	+ /	+	/	+

bags and incubated at 20 °C in the dark. The flasks were shaken weekly to evenly spread the inoculum. Mycelia rapidly colonised the flasks and the inocula were used after 4 weeks. Colonization of the inocula was confirmed by plating 3 g sub-samples onto *Phytophthora*-selective NARH agar (Simamora et al., 2017). These were incubated at room temperature and checked to ensure the viability of the inocula.

Glasshouse trial

Two experiments were conducted. The first with the native WA plant species, the second with the exotic plant species. The experiments were conducted under evaporative-cooled glasshouse conditions (11-32 °C) in sand-infestation pot trials using sterilised washed river sand as the growth medium. The sand was steam sterilised in hessian bags in an aluminium box for at least two hours at 65 °C. Pots (150 mm, 1.9 L free-draining polyurethane pot; Garden City Plastics Canning Vale, WA) were also sterilised before use. Flywire (Cyclone, OneSteel, Australia) was placed in the bottom of each pot to prevent sand loss. Seeds were germinated in seedling trays and transplanted into the pots at the six-leaf stage. At the time of potting up, two sterile polyurethane tubes (12.5 cm long and 2 cm diameter) were inserted into each pot, one at each side of the seedling.

After two months, the pots were inoculated with one of the 5-week-old isolates of *Phytophthora* by removing the polyurethane tubes and inserting the vermiculite inocula (5 g) into each hole. Control pots received the same amount of non-inoculated vermiculite. The holes were then filled with sterile sand. The first experiment had 10 replicate pots for each combination, while the second experiment had 5 replicate pots per treatment. In order to stimulate the production of sporangia and the release of zoospores from the inoculum source, the pots were placed in a 2L plastic container and flooded with deionised water for 24 hours every two weeks. Pots were arranged in a randomised complete block

design on benches in the glasshouse. Plants were watered as required with deionised water to run-off and fertilized with half strength water-soluble Thrive® (Yates Company, Australia) as required; once for Australian native plants, and every fortnight for the exotic plants. The presence of *Phytophthora* in dead seedlings was confirmed by plating the root collars and roots on NARH.

Twelve weeks after inoculation, surviving seedlings were harvested. The shoots were separated from the roots. Re-isolations were made from surface-sterilized root tissue plated on NARH to confirm Koch's postulates for each treatment. Roots were washed carefully with tap water and blotted dry with paper towels. Whole root systems were visually rated (root damage: RD) for root rot on a scale 0 to 4 (4=no damage, 0=all roots dead). Roots were dried at 37 °C for 20 days, and then weighed once completely dry (dry weight: DW).

Data analysis

To compare the susceptibility of plant species inoculated with *P. multivora* to control plants and to plants inoculated with *P. cinnamomi* (positive control), the response ratio of the root damage scores and the root biomass were calculated. The response ratio measures the proportional change that results from a treatment as compared to the control; therefore, quantifying the effect size of the treatment (Hedges et al., 1999). The response ratio was calculated as follows:

$$RR = \ln\left(\frac{\overline{X}_t}{\overline{X}_c}\right)$$

where $\overline{X}_t$ and $\overline{X}_c$ depict treatment and control mean value, respectively. The response ratio of the root damage scores and the root biomass was calculated in plants inoculated with *P. multivora* (treatment) to that in plants inoculated with *P. cinnamomi* (positive control) and control plants, respectively

(Hedges et al., 1999; Lajeunesse, 2011; Viechtbauer, 2010). The data were analysed using 'metafor' package of the R software ("Team RC (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing," 2017; Viechtbauer, 2010).

Results

Above ground condition and growth

Seedling deaths were observed during the first trial (Table 2). A total of 27 plants died, most of these had been inoculated with *P. cinnamomi. Phytophthora* was always isolated from the roots of the dead plants.

Root damage scores

Response ratio of plant species inoculated with *P. multivora* isolates showed a clear decrease in root health in comparison with control plants. Fourteen host species (six are non-native) inoculated with *P. multivora* isolate TRH4, and eighteen (seven are non-native) host species inoculated with *P. multivora* isolate TRH1 had significantly more damaged roots than the control (respectively Fig 1a,b; Table 1). Overall, the roots of *Banksia* species were the most affected by inoculation with *P. multivora.*

In general, roots were more diseased when infected with *P. cinnamomi* than with *P. multivora* (Fig. 1c, d; Table 1). *P. multivora* isolate TRH4 caused significantly less damage to roots than *P. cinnamomi* for eight species, *Acacia rostellifera*, *Albizia julibirissin*, *B. attenuata*, *B. occidentalis*, *B. speciosa*, *C. calophylla*, *Olea europaea*, and *Tipuana tipu* (Fig. 1c; Table 1). *P. multivora* isolate TRH1 caused significantly less damage to roots than *P. cinnamomi* for five plant species, *B. littoralis*, *B. occidentalis*, *B. speciosa*, *Patersonia occidentalis*, and *Syzygium smithii* (Fig 1d; Table 1). Only *Triadica sebifera*

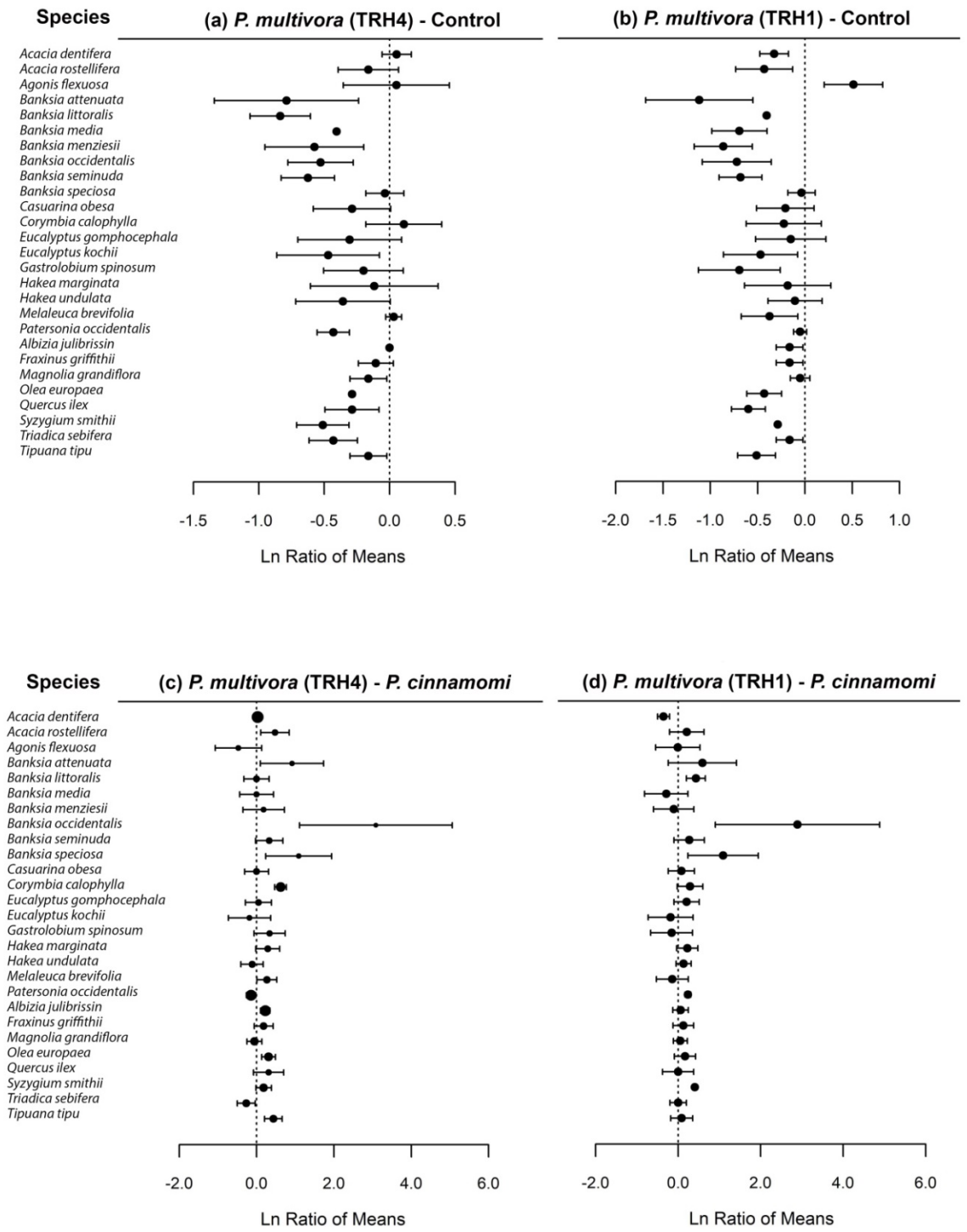

Figure 1. Root damage scores after inoculation.

Table 2. Host species for which plants died before harvest

Species	**control**	**MP94-48**	**TRH4**	**TRH1**
Banksia menziesii	0	1	0	1
Banksia seminuda	0	1	0	0
Banksia attenuata	0	5	1	1
Banksia speciosa	0	7	0	0
Banksia occidentalis	0	9	0	0
Gastrolobium spinosum	0	0	0	1

(Fig. 1c; Table 1) and *A. dentifera* (Fig 1d; Table 1), showed more damage by the inoculation with, respectively, TRH4 and TRH1 than by inoculation with *P. cinnamomi*.

Root Biomass

Phytophthora multivora isolates TRH4 and TRH1 significantly reduced the root weight of four and 16 plant species, respectively, compared to control plants (Fig 2a, b; Table 1). Isolate TRH1 (Fig. 2b) caused an overall greater reduction of root weight than TRH4 (Fig. 2a). In a few cases, the inoculated treatments had a higher biomass than non-inoculated controls, but this was not significant (confidence intervals overlap with the zero line).

Overall, the selected hosts were more susceptible to *P. cinnamomi* than to *P. multivora* (Fig. 2c, d; Table 1). *Phytophthora multivora* isolate TRH4 caused significantly less reduction in root biomass than *P. cinnamomi* for seven species, *A. jubilissin, B attenuata, B. media*, *B. occidentalis, B. speciosa, M. brevifolia,* and *T. tipu* (Fig. 1c; Table 1). *Phytophthora multivora* isolate TRH1 caused significantly less reduction in root biomass than *P. cinnamomi* for six plant species, *B. attenuata*, *B. occidentalis*, *B. speciosa*, *Hakea undulata*, *Melaleuca brevifolia*, and *A. julibrissin* (Fig 1d; Table 1). However, *Agonis flexuosa* and *P. occidentalis* were more susceptible to *P. multivora* isolate TRH4 than to *P. cinnamomi* (Fig. 2c; Table 1) and *A. dentifera* was more susceptible to isolate TRH1 than to *P. cinnamomi* (Fig. 2d; Table 1).

Discussion

Built on the evidence that at least one of the two *P. multivora* isolates produced significant root loss, twenty-five out of twenty-seven tested host species showed significant susceptibility to *P. multivora*. In previous investigations, *P. multivora* was found to significantly reduce the proportion of fine roots of

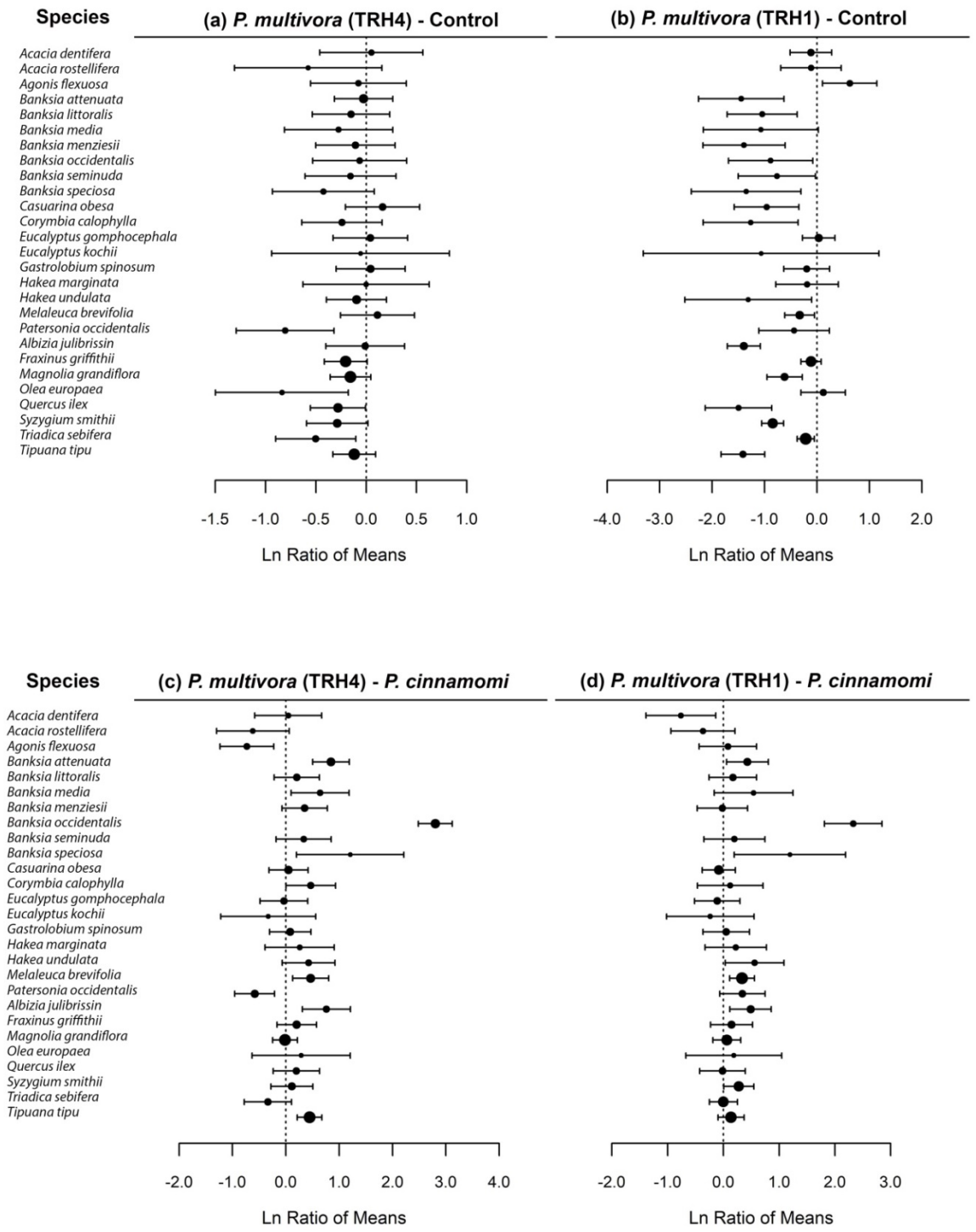

Figure 2. Root dry weight after inoculation.

E. marginata and *E. gomphocephala* (Scott et al., 2012), and overall root volume *E. marginata*, *B. grandis*, *B. littoralis*, *B. occidentalis*, *Lambertia inermis* (Belhaj et al., 2018) and *C. calophylla* (Croeser et al., 2018). Five species in the current study overlap with previous experiments; *E. gomphocephala, C. calophylla, B. littoralis*, *B. occidentalis* and *C. obesa.* In the current study, pathogenicity was confirmed for *C. calophylla, B. littoralis* and *B. occidentalis.* Additionally, one isolate of *P. multivora* (TRH1) caused a significant reduction in root volume of *C. obesa.* The only difference was that neither of the isolates used in the current study were considered pathogenic toward *E. gomphocephala* as a reduction in root volume was not observed. However, Scott et al. (2012) also did not observe a reduction in root volume, they just observed a loss of fine roots.

Plant species highly susceptible to *P. multivora* in our experiment include many *Banksia* species found in natural bushland and forest stands of the SWWA hyperdiverse floristic region and conservation reserves and natural parks within the Perth urban and peri-urban regions. With probably over 200 species in Western Australia (including sub-species and undescribed species) (Florabase, 2018) *Banksia* can be considered a genus with a primary role in the ecology and landscaping of SWWA low bushlands. Risk assessments of *P. cinnamomi* invasion in *Banksia* rich ecosystems like the Swan Coastal Plain had been conducted previously (Hill et al., 1994; Shearer and Dillon, 1996). The capacity of the pathogen to cause a reduction in the host's cover and abundance in infested soils in *Banksia* or *Banksia* rich woodlands has been largely proven (Bishop et al., 2010; Laliberté et al., 2015), and much effort has been undertaken in the last two to three decades to control the damage (Dunstan et al., 2010; McCredie et al., 1985). However, conclusions of field reports (Barber et al., 2013; Scott et al., 2009), together with results from this study, where two of the seven *Banksi*a species tested (*B. seminuda* and *B. menziesii*) were more susceptible to *P. multivora* than *P. cinnamomi,* suggests that the problem is greater than just *P. cinnamomi* alone.

The potential impact of *P. multivora* may also be favoured by the dry Mediterranean climate of the SWWA. The thick-walled oospores and its ability to sporulate within 24 h, may allow it to tolerate the long dry summers (Scott et al., 2012). We hypothesise that the impact of *P. multivora* would be potentially worse than *P. cinnamomi* due to its capability to invade calcareous soils, known to be suppressive for *P. cinnamomi* (Broadbent and Baker, 1974). Calcareous soils are common on the Swan Coastal plain on which the city of Perth is located, especially in the *E. gomphocephala* woodlands. Barber et al. (2013) first observed that *P. multivora* was more commonly isolated within Perth than *P. cinnamomi.* Further examination of isolation data has shown it is 17 times more likely to isolate *P. multivora* from dead and dying urban and peri-urban woody vegetation along the Swan Coastal Plain than *P. cinnamomi* (Barber, unpublished data).

Many of the commonly planted exotic urban street trees and garden ornamentals in Perth tested in our study were moderately to highly susceptible to *P. multivora.* This has global implications, both in other cities (as these are common urban trees across the world), but also from where these trees occur naturally or where they are grown in agricultural systems. Non-native plant species were moderately susceptible (*A. julibrissin*, *Fraxinus griffithii*, *Magnolia grandiflora*) to highly susceptible (*O. europaea*, *Quercus ilex*, *S. smithii*, *T. sebifera*, *T. tipu*) to *P. multivora*. *Q. ilex*, which showed high susceptibility, is common in Europe for crop production and as an ornamental plant. It is also a climax species in natural and semi-natural stands of Southern Europe. To date, European authors have concentrated their attention mostly on *P. cinnamomi*, as this is the most important biological hazard to *Q. ilex* woodlands (Corcobado et al., 2014, 2013; Sanchez-Hernandez et al., 2001; Vettraino et al., 2002). Our investigation has shown that *P. multivora* did not differ in pathogenicity to the most known co-generic species *P. cinnamomi*, leading us to consider it as a potential additional factor in the decline of *Q. ilex* in Europe.

Olea europaea (olive) was also very susceptible to *P. multivora* confirming a recent isolation of *P. multivora* from a sample collected from declining olive growing within a park in the City of Perth. Tolerance to long dry periods and poor soils and its evergreen status make the olive tree an important ornamental plant throughout the Perth urban forest. It is cultivated across Mediterranean-type ecosystems world-wide, and other than its landscaping importance, the olive tree has an incisive financial role: the world-wide export value for oil and olive production in 2016 was estimated at US$ 9,9 Billion (FAO, 2018). Despite no reports of *P. multivora* associated with olive in Europe, previous investigations have found olive trees to be affected by *P. cryptogea, P. inundata, P. megasperma, P. nicotianae, P. oleae,* and *P. palmivora* (Brasier et al., 2003; Cacciola et al., 2000; González et al., 2017; Ruano-Rosa et al., 2018; Sanchez-Hernandez et al., 2001; Vettraino et al., 2009). Additionally, *P. multivora* is already present in the region (Pane et al., 2017). Consequently, there is a need to conduct comparative studies on these species and their pathogenicity including *P. multivora* to olive. Of interest, was the extremely high susceptibility found for the Chinese tallow*, Triadica sebifera.* This species, native to East Asia, is commonly used as an ornamental and street tree in Perth and throughout the world and it is naturalized in many other countries worldwide, including the US where it is a forest weed (Pile et al., 2017). Based on our results, *T. sebifera* could be used as a biological indicator for the presence of *P. multivora*, in particular in the natural areas of the South US where it is very abundant.

In conclusion, despite the overall stronger pathogenicity of *P. cinnamomi*, the capacity of *P. multivora* to cause damage on the wide range of plant species screened, provides strong evidence for it to represent a real ecological risk for urban forests in Perth and throughout the SWWA. Additionally, the susceptibility of other common woody plants found globally in cities suggests that *P. multivora* will, in time, become as 'well-known' and damaging as *P. cinnamomi.* It has been appropriately named as it truly seems to be the 'eater of many'.

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Conflict of interest

The authors declare no conflicts of financial and personal interest.

References

202020Vision [WWW Document], n.d. URL http://202020vision.com.au/ (accessed 7.10.18).

Aldaoud, R., Salib, S., Dinh, S.Q., de Alwis, S., Holmes, R.J., Edwards, J., 2016. Host records for Phytophthora multivora associated with dieback in Victoria, Australia. Australas. Plant Dis. Notes 11, 1–4. https://doi.org/10.1007/s13314-016-0190-9

Barber, P.A., Paap, T., Burgess, T.I., Dunstan, W., Hardy, G.E.S.J., 2013. A diverse range of Phytophthora species are associated with dying urban trees. Urban For. Urban Green. 12, 569–575. https://doi.org/10.1016/j.ufug.2013.07.009

Belhaj, R., McComb, J., Burgess, T.I., Hardy, G.E.S.J., 2018. Pathogenicity of 21 newly described *Phytophthora* species against seven Western Australian native plant species. Plant Pathol. 1140–1149. https://doi.org/10.1111/ppa.12827

Bezuidenhout, C.M., Denman, S., Kirk, S.A., Botha, W.J., Mostert, L., McLeod, A., 2010. Phytophthora taxa associated with cultivated Agathosma, with emphasis on the P. citricola complex and P. capensis sp. nov. Persoonia Mol. Phylogeny Evol. Fungi 25, 32–49. https://doi.org/10.3767/003158510X538371

Bishop, C.L., Wardell-Johnson, G.W., Williams, M.R., 2010. Community-level changes in Banksia woodland following plant pathogen invasion in the Southwest Australian Floristic Region. J. Veg. Sci. 21, 888–898. https://doi.org/10.1111/j.1654-1103.2010.01194.x

Brasier, C.M., Sanchez-Hernandez, E., Kirk, S.A., 2003. Phytophthora inundata sp. nov., a part

heterothallic pathogen of trees and shrubs in wet or flooded soils. Mycol. Res. 107, 477–484. https://doi.org/10.1017/S0953756203007548

Broadbent, P., Baker, K.F., 1974. Behaviour of Phytophthora cinnamomi in soils suppressive and conducive to root rot. Aust. J. Agric. Res. 25, 121–137. https://doi.org/10.1071/AR9740121

Burgess, T.I., White, D., McDougall, K.M., Garnas, J., Dunstan, W.A., Català, S., Carnegie, A.J., Worboys, S., Cahill, D., Vettraino, A.M., Stukely, M.J.C., Liew, E.C.Y., Paap, T., Bose, T., Migliorini, D., Williams, B., Brigg, F., Crane, C., Rudman, T., Hardy, G.E.S.J., 2017. Distribution and diversity of Phytophthora across Australia. Pacific Conserv. Biol. 23, 150–162. https://doi.org/10.1071/PC16032

Cacciola, S.O., Agosteo, G.E., Pane, A., 2000. First report of Phytophthora palmivora as a pathogen of olive in Italy. Plant Dis. 84, 1153. https://doi.org/https://doi.org/10.1094/PDIS.2000.84.10.1153A

Corcobado, T., Cubera, E., Juárez, E., Moreno, G., Solla, A., 2014. Drought events determine performance of Quercus ilex seedlings and increase their susceptibility to Phytophthora cinnamomi. Agric. For. Meteorol. 192–193, 1–8. https://doi.org/10.1016/j.agrformet.2014.02.007

Corcobado, T., Cubera, E., Moreno, G., Solla, A., 2013. Quercus ilex forests are influenced by annual variations in water table, soil water deficit and fine root loss caused by Phytophthora cinnamomi. Agric. For. Meteorol. 169, 92–99. https://doi.org/10.1016/j.agrformet.2012.09.017

Croeser, L., Paap, T., Calver, M.C., Andrew, M.E., Hardy, G.E.S.J., Burgess, T.I., 2018. Field survey, isolation, identification and pathogenicity of Phytophthora species associated with a Mediterranean-type tree species. For. Pathol. 48, 1–15. https://doi.org/10.1111/efp.12424

CSIRO and Bureau of Meteorology, 2015. Projections: Atmosphere and the land, Climate Change in Australia Information for Australia's Natural Resource Management Regions: Technical Report.

Desprez-Loustau, M.L., Robin, C., Reynaud, G., Déqué, M., Badeau, V., Piou, D., Husson, C., Marçais, B., 2007. Simulating the effects of a climate-change scenario on the geographical range and activity of forest-pathogenic fungi. Can. J. Plant Pathol. 29, 101–120. https://doi.org/10.1080/07060660709507447

Dunstan, W.A., Howard, K., Stj. Hardy, G.E., Burgess, T.I., 2016. An overview of Australia's <I>Phytophthora</I> species assemblage in natural ecosystems recovered from a survey in Victoria. IMA Fungus 7, 47–58. https://doi.org/10.5598/imafungus.2016.07.01.04

Dunstan, W.A., Rudman, T., Shearer, B.L., Moore, N.A., Paap, T., Calver, M.C., Dell, B., Hardy, G.E.S.J., 2010. Containment and spot eradication of a highly destructive, invasive plant pathogen (Phytophthora cinnamomi) in natural ecosystems. Biol. Invasions 12, 913–925. https://doi.org/10.1007/s10530-009-9512-6

Evans, B., Lyons, T., 2013. Bioclimatic Extremes Drive Forest Mortality in Southwest, Western Australia. Climate. https://doi.org/10.3390/cli1020028

Evans, B., Stone, C., Barber, P., 2013. Linking a decade of forest decline in the south-west of Western Australia to bioclimatic change. Aust. For. 76, 164–172. https://doi.org/10.1080/00049158.2013.844055

FAO, 2018. FAOSTAT, Crops and livestock products [WWW Document]. URL http://www.fao.org/faostat/en/#data/TP (accessed 7.20.18).

Fitzpatrick, M.C., Gove, A.D., Sanders, N.J., Dunn, R.R., 2008. Climate change, plant migration, and range collapse in a global biodiversity hotspot: The Banksia (Proteaceae) of Western Australia. Glob. Chang. Biol. 14, 1337–1352. https://doi.org/10.1111/j.1365-2486.2008.01559.x

Florabase, 2018. Western Australian Herbarium (1998–). FloraBase—the Western Australian Flora. Department of Biodiversity, Conservation and Attractions. https://florabase.dpaw.wa.gov.au/ [WWW Document]. URL https://florabase.dpaw.wa.gov.au (accessed 7.10.18).

González, M., Pérez-Sierra, A., Serrano, M.S., Sánchez, M.E., 2017. Two Phytophthora species causing decline of wild olive (Olea europaea subsp. europaea var. sylvestris). Plant Pathol. 66, 941–948. https://doi.org/10.1111/ppa.12649

Hedges, L. V, Gurevitch, J., Curtis, P.S., 1999. the Meta-Analysis of Response Ratios in Experimental Ecology. Ecology 80, 1150–1156. https://doi.org/doi:10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2

Hill, T.C.J., Tippett, J.T., Shearer, B.L., 1994. Invasion of bassendean dune Banksia woodland by Phytophthora cinnamomi. Aust. J. Bot. 42, 725–738. https://doi.org/10.1071/BT9940725

Hong, C., Gallegly, M.E., Richardson, P.A., Kong, P., 2011. *Phytophthora pini* Leonian resurrected to distinct species status. Mycologia 103, 351–360. https://doi.org/10.3852/10-058

Hopper, S.D., Gioia, P., 2004. The Southwest Australian Floristic Region: Evolution and Conservation of a Global Hot Spot of Biodiversity. Annu. Rev. Ecol. Evol. Syst. 35, 623–650. https://doi.org/10.1146/annurev.ecolsys.35.112202.130201

Jung, T., Burgess, T.I., 2009. Re-evaluation of Phytophthora citricola isolates from multiple woody

hosts in Europe and North America reveals a new species, Phytophthora plurivora sp. nov. Persoonia Mol. Phylogeny Evol. Fungi 22, 95–110. https://doi.org/10.3767/003158509X442612

Jung, T., Orlikowski, L., Henricot, B., Abad-Campos, P., Aday, A.G., Aguín Casal, O., Bakonyi, J., Cacciola, S.O., Cech, T., Chavarriaga, D., Corcobado, T., Cravador, A., Decourcelle, T., Denton, G., Diamandis, S., Doğmuş-Lehtijärvi, H.T., Franceschini, A., Ginetti, B., Green, S., Glavendekić, M., Hantula, J., Hartmann, G., Herrero, M., Ivic, D., Horta Jung, M., Lilja, A., Keca, N., Kramarets, V., Lyubenova, A., Machado, H., Magnano di San Lio, G., Mansilla Vázquez, P.J., Marçais, B., Matsiakh, I., Milenkovic, I., Moricca, S., Nagy, Z.A., Nechwatal, J., Olsson, C., Oszako, T., Pane, A., Paplomatas, E.J., Pintos Varela, C., Prospero, S., Rial Martínez, C., Rigling, D., Robin, C., Rytkönen, A., Sánchez, M.E., Sanz Ros, A. V., Scanu, B., Schlenzig, A., Schumacher, J., Slavov, S., Solla, A., Sousa, E., Stenlid, J., Talgø, V., Tomic, Z., Tsopelas, P., Vannini, A., Vettraino, A.M., Wenneker, M., Woodward, S., Peréz-Sierra, A., 2016. Widespread Phytophthora infestations in European nurseries put forest, semi-natural and horticultural ecosystems at high risk of Phytophthora diseases. For. Pathol. 46, 134–163. https://doi.org/10.1111/efp.12239

Lajeunesse, M.J., 2011. On the meta-analysis of response ratios for studies with correlated and multi-group designs. Ecology 92, 2049–2055. https://doi.org/10.1890/11-0423.1

Laliberté, E., Lambers, H., Burgess, T.I., Wright, S.J., 2015. Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. New Phytol. 206, 507–521. https://doi.org/10.1111/nph.13203

Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R.,

Delzon, S., Corona, P., Kolström, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. For. Ecol. Manage. 259, 698–709. https://doi.org/10.1016/j.foreco.2009.09.023

McCredie, T.A., Dixon, K.W., Sivasithamparam, K., 1985. Variability in the resistance of Banksia L.f. Species to Phytophthora cinnamomi rands. Aust. J. Bot. 33, 629–637. https://doi.org/10.1071/BT9850629

Mrázková, M., Černý, K., Tomšovský, M., Strnadová, V., 2013. and Phytophthora plurivora in the Czech Republic 49, 155–164. https://doi.org/10.17221/74/2012-PPS

Nagel, J.H., Gryzenhout, M., Slippers, B., Wingfield, M.J., Hardy, G.E.S.J., Stukely, M.J.C., Burgess, T.I., 2013. Characterization of Phytophthora hybrids from ITS clade 6 associated with riparian ecosystems in South Africa and Australia. Fungal Biol. 117, 329–347. https://doi.org/10.1016/j.funbio.2013.03.004

Oh, E., Gryzenhout, M., Wingfield, B.D., Wingfield, M.J., Burgess, T.I., 2013. Surveys of soil and water reveal a goldmine of Phytophthora diversity in South African natural ecosystems. IMA Fungus 4, 123–131. https://doi.org/10.5598/imafungus.2013.04.01.12

Pane, A., Granata, G., Cacciola, S.O., Puglisi, I., Evoli, M., Aloi, F., Spada, F., Zambounis, A., 2017. First Report of Root Rot of White Mulberry Caused by Simultaneous Infection of Phytophthora megasperma and P. multivora in Italy. Plant Dis. 101, 260. https://doi.org/https://doi.org/10.1094/PDIS-07-16-0993-PDN

Pile, L.S., Wang, G.G., Knapp, B.O., Walker, J.L., Stambaugh, M.C., 2017. Chinese tallow (Triadica

sebifera) invasion in maritime forests: The role of anthropogenic disturbance and its management implication. For. Ecol. Manage. 398, 10–24. https://doi.org/10.1016/j.foreco.2017.05.006

Rodrìguez-Padròn, C., Silvero, F., Pèrez-Sierra, A., Rodriguez, A., 2018. Isolation and pathogenicity of Phytophthora species and Phytopythium vexans recovered from avocado orchards in the Canary Islands, including Phytophthora niederhauserii as a new pathogen of avocado. Phytopathol. Mediterr. 57, 89–106. https://doi.org/DOI: 10.14601/Phytopathol_Mediterr-2202

Ruano-Rosa, D., Schena, L., Agosteo, G.E., Magnano di San Lio, G., Cacciola, S.O., 2018. Phytophthora oleae sp. nov. causing fruit rot of olive in southern Italy. Plant Pathol. 67, 1362–1373. https://doi.org/10.1111/ppa.12836

Sanchez-Hernandez, E., Munoz-Garcia, M., Brasier, C.M., Trapero-Casas, a, 2001. Identity and pathogenicity of two Phytophthora taxa associated with a new root disease of olive trees. Plant Dis. 85, 411–416. https://doi.org/Doi 10.1094/Pdis.2001.85.4.411

Scott, P., Williams, N., 2014. Phytophthora diseases in New Zealand forests. NZ J. For. 59, 14–21.

Scott, P.M., Burgess, T.I., Barber, P.A., Shearer, B.L., Stukely, M.J.C., Hardy, G.E.S.J., Jung, T., 2009. Phytophthora multivora sp. nov., a new species recovered from declining Eucalyptus, Banksia, Agonis and other plant species in Western Australia. Persoonia Mol. Phylogeny Evol. Fungi 22, 1–13. https://doi.org/10.3767/003158509X415450

Scott, P.M., Jung, T., Shearer, B.L., Barber, P.A., Calver, M., Hardy, G.E.S.J., 2012. Pathogenicity of Phytophthora multivora to Eucalyptus gomphocephala and Eucalyptus marginata. For. Pathol. 42, 289–298. https://doi.org/10.1111/j.1439-0329.2011.00753.x

Shearer, B., Dillon, M., 1996. Impact and Disease Centre Characteristics of *Phytophthora cinnamomi* Infestations of *Banksia* Woodlands on the Swan Coastal Plain, Western Australia. Aust. J. Bot. 44, 79. https://doi.org/10.1071/BT9960079

Shearer, B.L., Crane, C.E., Barrett, S., Cochrane, A., 2007. Phytophthora cinnamomi invasion, a major threatening process to conservation of flora diversity in the South-west Botanical Province of Western Australia. Aust. J. Bot. 55, 225–238. https://doi.org/10.1071/BT06019

Simamora, A., Paap, T., Howard, K., Stukely, M., Hardy, G.E.S.J., Burgess, T., 2017. Phytophthora contamination in a nursery and its potential dispersal into the natural environment. Plant Dis. 102, PDIS-05-17-0689-RE. https://doi.org/10.1094/PDIS-05-17-0689-RE

Smahi, H., Belhoucine-guezouli, L., Franceschini, A., Scanu, B., 2017. Phytophthora species associated with cork oak decline in a Mediterranean forest in western Algeria. IOBC-WPRS Bull. 127, 123–129.

Team RC (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, 2017.

Vettraino, A.M., Barzanti, G.P., Bianco, M.C., Ragazzi, A., Capretti, P., Paoletti, E., Luisi, N., Anselmi, N., Vannini, A., 2002. Occurrence of Phytophthora species in oak stands in Italy and their association with declining oak trees. For. Pathol. 32, 19–28. https://doi.org/10.1046/j.1439-0329.2002.00264.x

Vettraino, A.M., Lucero, G., Pizzullo, P., Franceschini, S., Vannini, A., 2009. First Report of Root Rot and Twigs Wilting of Olive Trees in Argentina Caused byPhytophthora nicotianae. Plant Dis. 93,

765. https://doi.org/https://doi.org/10.1094/PDIS-93-7-0765B

Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. J. Stat. Softw. 36. https://doi.org/10.18637/jss.v080.b01