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# Annual and herbaceous perennial native Australian plant species are symptomless hosts of *Phytophthora cinnamomi* in the *Eucalyptus marginata* (jarrah) forest of Western Australia

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Resistant annual and herbaceous perennial plant species were identified as key hosts which allow *Phytophthora cinnamomi* to persist on severely impacted black gravel sites within the *Eucalyptus marginata* (jarrah) forest of southwest Western Australia. Of the annual and herbaceous perennial plant species present on black gravel sites, 15 out of 19 species were found to be hosts of *P. cinnamomi*, and 10 of these were symptomless hosts. In particular, the native annual *Trachymene pilosa* and the two native herbaceous perennials *Stylidium diuroides* and *Chamaescilla corymbosa* were commonly found to be hosts of the pathogen. Species from 12 new genera including three from new families (Crassulaceae, Droseraceae and Primulaceae) are reported for the first time to be hosts of *P. cinnamomi*. The species from which *P. cinnamomi* was recovered were the native species: *Chamaescilla corymbosa, Crassula closiana, Drosera erythrorhiza, Hydrocotyle callicarpa, Levenhookia pusilla, Paracaleana nigrita, Podotheca angustifolia, Pterochaeta paniculata, Rytidosperma caespitosum, Siloxerus multiflorus*, *Stylidium diuroides* and *Trachymene pilosa*, and the introduced annual weeds *Hypochaeris glabra, Lysimachia arvensis* and *Pentameris airoides*.

*Keywords:* dieback, host species, jarrah forest, pathogen survival, *Phytophthora cinnamomi*, susceptibility rating

## Introduction

*Phytophthora cinnamomi* is an oomycete root pathogen with a broad host range which has been spread worldwide (Zentmyer, 1980; Erwin & Ribeiro, 1996). Besides plant losses in agriculture and horticulture, it kills dominant and rare plant species in many natural environments and is an important pathogen in 15 global biodiversity hotspots (Dunstan *et al.*, 2010). Since the identification of *P. cinnamomi*, the number of plant species known to be susceptible has constantly increased. Within the context of Australia's native vascular flora, the most recent list is a compilation of published and unpublished data by McDougall (2005), but this only contains 5% of the Australian vascular flora (Cahill *et al.*, 2008) and 962 of the 12 172 native plant species of Western Australia (Western Australian Herbarium, 1998), with 239 Western Australian species from which *P. cinnamomi* was isolated in the wild. Therefore, 92% of the native vascular flora of Western Australia has an unknown status with regards to its susceptibility or resistance to *P. cinnamomi*. However, for the southwest of Western Australia (which includes the *Eucalyptus marginata* (jarrah) forest), where a Mediterranean climate is conducive for the pathogen, Shearer *et al.* (2004) extrapolated that 40% (2284 out of 5710) of the described plant species are likely to be susceptible to *P. cinnamomi*.

Most research has focused on the pathogen's impact on susceptible plant species and has generated valuable data for conservation purposes in natural environments where *P. cinnamomi* has been introduced, but little is known about the pathogen's potential impact on plant species surviving within infested areas which are considered 'tolerant' or 'resistant'. This is especially the case for annual and herbaceous perennial plant species which can comprise almost 50% of species for the jarrah forest (Western Australian Herbarium, 1998). However, the list of McDougall (2005) highlights an under-representation of annual and herbaceous perennial plant species which have rarely been reported to succumb to the pathogen in natural environments in Australia (McDougall, 2005), or elsewhere in the world (Zentmyer, 1980). As *P. cinnamomi* appears to survive indefinitely on sites where it has killed the majority, if not all, susceptible plant species (McDougall *et al.*, 2002), it is necessary to determine whether it is able to survive in annual and herbaceous perennial species that are able to produce seed rapidly and are likely to do so, even if they become infected during their short life spans. Consequently, the aim of the current study was to test the hypothesis that annual and

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herbaceous perennial plant species are hosts that allow *P. cinnamomi* to persist on sites in the absence of susceptible perennial woody species.

## Materials and methods

### Selection of study sites, plant species and sampling time

Fifty-two sites were chosen in areas of the jarrah forest in south-west Western Australia known as black gravel sites (32°50′ 24·50″S; 116°03′50·65″E) where *P. cinnamomi* persists despite a substantial reduction or total disappearance of susceptible plant species. Characteristic for these landscapes is the presence of 60 –80% gravel (McArthur *et al.*, 1991) of black colour above a lateritic cemented layer with depressions prone to waterlogging and therefore increased chances of root infection (Shea *et al.*, 1984). Previous seasonal soil sampling over a period of 2·5 years using the leaf baiting technique (Erwin & Ribeiro, 1996) as a detection method had confirmed the presence of *P. cinnamomi* adjacent to these sites (M. Crone, unpublished data). Annual and herbaceous perennial plant species in the majority of cases appeared to be unaffected by the presence of the pathogen and were collected from sites prone to temporary waterlogging following rainfall events, and from some free-draining sites. From these 52 sites, 19 plant species (13 annual species and six herbaceous perennial species) from 18 genera and 10 families were collected to determine whether they were hosts of *P. cinnamomi*.

Sampling was undertaken weekly from 28 June (winter) to 1 November 2011 (spring). To determine whether the pathogen remains viable within roots of infected species from the beginning of winter to spring, an emphasis was placed on *Stylidium diuroides* (herbaceous perennial), *Chamaescilla corymbosa* (herbaceous perennial) and *Trachymene pilosa* (annual) which were frequently found to be infected and were present across the study sites in sufficient numbers to enable repeated harvests. Not all species were present at each site to allow sequential weekly harvesting from a site.

During the period from 28 June to 1 November, the monthly rainfall combined (November excluded) was 98·7 mm below the long-term average for these months based on the nearest weather station in Dwellingup (Station 009538, 32·7103°S; 116·0594°E) (Bureau of Meteorology 2011, data not presented).

### Sampling procedure and isolation method

Root systems were carefully removed from the soil with as many roots intact as possible. Each plant was shaken to remove soil particles and immediately transferred into a 50 mL round tub containing distilled water to remove the remaining soil. The majority of plants were plated in the field by drying each root system on a paper towel and immediately placing the whole root system onto plates of a *Phytophthora* selective medium NARPH (Hüberli *et al.*, 2000) but without PCNB (1,2,3,4, 5-pentachloro-6-nitrobenzene), which has been removed from the market. These were sealed with Parafilm and placed in an insulated box for transport to the laboratory.

On average, 170 individuals were collected at each sampling time until 23 August; thereafter between 30 August to 1 November *c.* 56 individuals were collected each week. Plated roots were incubated at 21°C (±1°C) in the dark and examined daily for 3 days, then after 6 days, and intermittently up to 14 days. Outgrowing colonies were examined microscopically for morphological features typical for *P. cinnamomi* (Erwin & Ribeiro, 1996). Sites from which *P. cinnamomi* was recovered were revisited periodically and additional plants collected. A set of eight representative isolates from annuals and herbaceous perennials was prepared for identification by DNA sequencing, using the methods summarized in Aghighi *et al.* (2012), to confirm they were *P. cinnamomi*. Briefly, mycelium on half-strength PDA agar was harvested and genomic DNA extracted according to the method of Andjic *et al.* (2007). The region spanning the internal transcribed spacer (ITS1–5·8S–ITS2) region of the ribosomal DNA was amplified using the primers DC6 (Cooke *et al.*, 2000) and ITS4 (White *et al.*, 1990). The PCR reaction mixture and PCR conditions were as described previously (Andjic *et al.*, 2007). The clean-up of products and sequencing were performed as described by Sakalidis *et al.* (2011) using the ITS4 primer.

## Results

### Host range

*Phytophthora cinnamomi* was recovered from 15 of the 19 annual and herbaceous perennial plant species sampled (Table 1). These represented nine vascular plant families with 12 species native to Australia, each a member of a different genus (Western Australian Herbarium, 1998).

### *Phytophthora* isolations

A total of 219 *P. cinnamomi* isolations (Table 1) was made from 18 of the 52 sites. The ITS region of eight representative isolates from different hosts and/or collection times (MUCC 785, 786, 788–793) was sequenced. A similarity search against the GenBank database using the Basic Local Sequence Alignment Tool for nucleotides (BLASTN) confirmed the identity of these isolates as *P. cinnamomi*. The sequences of these isolates were lodged in GenBank (GenBank accession numbers: JX113308 to JX113315) and the isolates were placed in long-term storage at Murdoch University.

### Disease expression

Ten species from which *P. cinnamomi* was recovered remained symptomless throughout the sampling period and included the annual *Trachymene pilosa* (Table 1). Five species, including *Chamaescilla corymbosa* and *Stylidium diuroides*, developed disease symptoms typical of *P. cinnamomi* in midwinter (August). *Stylidium diuroides*, confirmed to be infected by the pathogen, wilted without necrotic root symptoms (Fig. 1). *Chamaescilla corymbosa* did not show symptoms above ground but water-soaked lesions with discoloration were frequently observed in the tubers (Fig. 2).

### Time of recovery

Frequent sampling of the three Australian native species (*T. pilosa*, *C. corymbosa* and *S. diuroides*) within 10 sites demonstrated that *P. cinnamomi* was present in naturally infected roots of annual and herbaceous perennial

Table 1 Recovery of *Phytophthora cinnamomi* from annual and herbaceous perennial species on black gravel sites known to be infested with *P. cinnamomi*

| Species[a] | Family | New genera | New family | Total harvested | Total positives | Symptoms[d] |
|---|---|---|---|---|---|---|
| Annuals | | | | | | |
| *Centrolepis* sp. | Centrolepidaceae | n.a.[e] | n.a. | 13 | 0 | n.a. |
| ***Crassula closiana*** | Crassulaeae | + | + | 62 | 3 | – |
| ***Hydrocotyle callicarpa*** | Araliaceae | – | – | 68 | 6 | – |
| ***Hypochaeris glabra***[b,c] | Asteraceae | + | – | 26 | 1 | – |
| ***Levenhookia pusilla*** | Stylidiaceae | + | – | 91 | 5 | +(a) |
| *Levenhookia stipitata* | Stylidiaceae | n.a. | n.a. | 8 | 0 | n.a. |
| ***Lysimachia arvensis***[b] | Primulaceae | + | + | 20 | 2 | – |
| ***Pentameris airoides***[b] | Poaceae | + | – | 22 | 1 | – |
| ***Podotheca angustifolia*** | Asteraceae | + | – | 58 | 1 | – |
| ***Pterochaeta paniculata*** | Asteraceae | + | – | 102 | 2 | – |
| *Rhodanthe citrina* | Asteraceae | n.a. | n.a. | 3 | 0 | n.a. |
| ***Siloxerus multiflorus*** | Asteraceae | + | – | 17 | 1 | – |
| ***Trachymene pilosa*** | Araliaceae | + | – | 447 | 74 | – |
| Herbaceous perennials | | | | | | |
| ***Chamaescilla corymbosa*** | Asparagaceae | – | – | 123 | 51 | +(r) |
| ***Drosera erythrorhiza*** | Droseraceae | + | + | 9 | 3 | +(r+a) |
| *Lagenophora huegelii* | Asteraceae | n.a. | n.a. | 6 | 0 | n.a. |
| ***Paracaleana nigrita*** | Orchidaceae | + | – | 4 | 2 | +(r+a) |
| ***Rytidosperma caespitosum*** | Poaceae | + | – | 18 | 2 | – |
| ***Stylidium diuroides*** | Stylidiaceae | – | – | 117 | 65 | +(a) |
| Total | | | | | | |
| **15** of 19 | **9** of 10 | **12** | **3** | | **219** | **10** |

[a]Sampling period 28 June to 1 November 2011. Infected species in bold.
[b]Introduced species.
[c]Sometimes herbaceous perennial.
[d]a = above ground symptoms (stems and leaves); r = root symptoms; +/– = yes/no.
[e]n.a. = not applicable.

Figure 1 A dying *Stylidium diuroides* (Stylidiaceae) with a symptomless *Pentameris airoides* (Poaceae) in close proximity. *Phytophthora cinnamomi* was recovered from both plants (collected 13 September 2011).

Figure 2 *Chamaescilla corymbosa* (Asparagaceae) showing root lesion symptoms in spring (13 September 2011) with water-soaked lesions (thick arrows) and yellow discoloration (thin arrow). *Phytophthora cinnamomi* was recovered from three of the eight tubers. *Chamaescilla corymbosa* has no above-ground disease symptoms.

species during winter through to spring 2011 (Table 2), at which time they started to senescence with the onset of summer. Outgrowth of *P. cinnamomi* from the sampled roots usually occurred within the first 3 days, demonstrating that the pathogen was actively growing during the sampling period.

## Spatial distribution

At each sampling site, not all examined individuals were infected by *P. cinnamomi* (Table 2), suggesting a very heterogeneous distribution across the study sites. Like-

Table 2 Seasonal recovery of *Phytophthora cinnamomi* from *Trachymene pilosa* (annual), *Stylidium diuroides* and *Chamaescilla corymbosa* (herbaceous perennials) in 10 sites prone to temporary waterlogging in 2011. Figures give the number of positive recoveries/number of plants tested from each site

| Species | Sites Code | June 28th | July 5th | July 12th | July 19th | July 26th | August 2nd | August 9th | August 16th | August 23rd | August 30th | September 6th | September 13th | September 20th | September 27th | October 4th | October 13th | October 25th | Nov 1st | Total | Total per species |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Stylidium diuroides* | W2 | | 1/1 | | | | | | | 2/4 | | | | | | | | | | 3/5 | |
| | W4 | | | | | | | | | 0/3 | | | | | | | | | 1/1 | 1/4 | |
| | W7 | | | | | | 2/3 | 2/3 | 1/8 | 0/7 | | 0/1 | | | | | | | 1/1 | 6/23 | |
| | W8 | | | | | | | | | 2/3 | | | | | | | | | | 2/3 | |
| | W12 | | | | | | | 3/3 | 2/3 | 1/3 | 0/2 | 1/1 | | | | | | | | 7/12 | |
| | W14 | | | 1/2 | 2/3 | | | | | | 3/3 | 4/4 | 2/2 | | | | 2/2 | | | 14/16 | |
| | W15 | | | | 0/2 | 2/2 | | | | | | | | | | | | | | 2/4 | |
| | W29 | | | | | 1/3 | 4/7 | | | | | | | | | | | | | 5/11 | |
| | W45 | | | | | | | | | 0/4 | | 2/2 | 3/3 | | | 1/1 | 1/1 | 1/1 | 2/2 | 10/14 | |
| | W50 | | | | | | | | | | | | | 1/1 | 3/3 | | | | | 4/4 | 54/96 |
| *Chamaescilla corymbosa* | W2 | | 0/1 | | | | | 0/5 | | 2/2 | 2/2 | | | | 3/6 | | | | | 7/16 | |
| | W4 | | 1/4 | | 5/5 | | | 1/3 | | 1/2 | | 2/2 | 4/4 | 4/4 | 1/4 | 4/5 | 1/2 | | | 24/35 | |
| | W7 | | | | | | | | | | | | | | | | | | | | |
| | W8 | | | | | | | | | 0/2 | 0/5 | | | 1/3 | 0/1 | | | 0/1 | | 1/12 | |
| | W12 | | | | | | | | | 1/5 | 0/3 | 1/3 | | 0/3 | | | | | | 2/14 | |
| | W14 | | | | | | | | | | | | | | | | | | | | |
| | W15 | | | | | | | 0/2 | | | | | | | | | | | | 0/2 | |
| | W29 | | | | | 1/1 | | 1/3 | 0/5 | 1/4 | 0/5 | 1/1 | 2/3 | 1/3 | | 2/3 | | | 1/1 | 10/29 | |
| | W45 | | | | | | | | | | 1/1 | | 0/1 | | | | | | | 1/2 | |
| | W50 | | | | | | | | | | | | | 1/2 | 4/9 | | | | | 5/11 | 50/121 |
| *Trachymene pilosa* | W2 | 13/37 | | 6/23 | 10/48 | 0/12 | 1/11 | 3/12 | | 1/9 | | 1/8 | | 0/6 | | | 0/4 | | | 35/170 | |
| | W4 | | | | | | | | | | | | | | | | | | 0/3 | 0/3 | |
| | W7 | | 0/1 | | | | | | | | | | | | | | | | | 0/1 | |
| | W8 | | 0/2 | | | | | | | | | | | | | | | | | 0/2 | |
| | W12 | | | | | | | | | | | 0/2 | | | | | | | | 0/2 | |
| | W14 | | | | 1/7 | 0/12 | | 0/13 | | | | 3/6 | | | | | 1/1 | | 3/4 | 8/43 | |
| | W15 | | | 1/9 | 7/29 | 3/6 | 1/6 | 0/14 | | 8/12 | | 1/5 | | | | | | | 1/4 | 22/85 | |
| | W29 | | | | | 0/7 | 0/12 | | 0/13 | 2/18 | | 0/7 | | | | 1/1 | 0/3 | | 0/5 | 3/66 | |
| | W45 | | | | | | | | | | | 0/3 | | | | | 1/1 | | | 1/4 | |
| | W50 | | | | | | | | | | | | | | | | | | | | 69/376 |

wise, infected individuals of *C. corymbosa* frequently had only some of their tubers infected, even though the individual's tubers were only *c.* 5 cm apart from each other (Figs 2 and 3). Even though most sampling focused on depressions prone to temporary waterlogging, *P. cinnamomi* was also recovered from plants growing on relatively free-draining slopes.

## Discussion

With the exception of *Chamaescilla corymbosa* which has been reported to be susceptible in Victoria (McDougall, 2005), but not in Western Australia, none of the other species have previously been reported to be infected by *P. cinnamomi*. Twelve genera previously not known to contain species which harbour the pathogen were found to be hosts of *P. cinnamomi*: *Crassula, Drosera, Hypochaeris, Levenhookia, Lysimachia, Paracaleana, Pentameris, Podotheca, Pterochaeta, Rytidosperma, Siloxerus* and *Trachymene*. The host extension also applied at the family level, as for the first time species from the Crassulaceae (*Crassula closiana*), Droseraceae (*Drosera erythrorhiza*) and Primulaceae (*Lysimachia arvensis*) were shown to host the pathogen.

This extends the host range of *P. cinnamomi* to include 10 annual and five herbaceous perennial plant species. These plant forms were not previously considered to be important in the life cycle of the pathogen (Zentmyer, 1980); however, it has been hypothesized that 'resistant' and symptomless plants could host the pathogen and provide inoculum (Phillips & Weste, 1984; Cahill *et al.*, 2008). As numbers of susceptible woody species were severely reduced on the study area and constant recoveries of *P. cinnamomi* were made from a number of annual and herbaceous perennial plant species throughout space and time, this study strongly supports the hypothesis that annual and perennial herbaceous plants are key host species which allow *P. cinnamomi* to persist on black gravel sites in the jarrah forest. Further experimental inoculations under laboratory conditions of a number of annual species from a range of locations in the jarrah forest (and including some of the species used in this study) gave similar results to those observed in plants collected from the field (M. Crone, unpublished data).

Due to the lack of disease symptoms, these species were previously rated as either 'field resistant' or were not present in the list of McDougall (2005). In the present study, 79% (15) of the tested annual and herbaceous perennial plant species were shown to be hosts of *P. cinnamomi* on black gravel sites. Amongst the herbaceous perennial plant species showing symptoms, the sudden onset of wilting of *S. diuroides* amongst healthy individuals towards the end of winter (August) makes this species a suitable indicator species for the presence of *P. cinnamomi* in areas where it is present. The very heterogeneous distribution of infected plants in dense populations as well as amongst tubers of *C. corymbosa* individuals is similar to the observations of woody hosts, where healthy plants are found in close proximity to infected individuals of the same species (McDougall *et al.*, 2002). In addition, the phenomenon that only up to 30% of the root system of an individual plant is infected even in highly susceptible plant species agrees with the observations of Zentmyer (1980).

*Phytophthora cinnamomi* is traditionally classified as a necrotroph, acquiring nutrients by killing host cells (Cahill *et al.*, 2008) or as a hemibiotroph (Hüberli *et al.*, 2000; Cahill *et al.*, 2008), prior to becoming a necrotroph. The initial biotrophic phase of these biphasic species can be long, with *P. infestans* a classic example of how hemibiotrophs can be overlooked in apparently symptomless plants (Fry, 2008). *Phytophthora ramorum* along with *P. kernoviae* represent recently emerged oomycete threats where evidence suggests that host plant species can be initially colonized without significant symptoms (Fichtner *et al.*, 2012). However, for annuals such as *T. pilosa*, the absence of symptoms suggests that the pathogen does not grow as a necrotroph, although it is possible that necrotrophic symptoms could be masked by senescence late in the season. The annual leaf abscission of the herbaceous perennial *C. corymbosa* after fruiting could be clearly attributed to the life cycle of the species rather than disease impact, as infected individuals were developmentally in synchrony with individuals that tested negative for *P. cinnamomi*.

Recent work has shown that haustoria are produced in some annual and herbaceous perennial plant species (M. Crone, unpublished data). Transmission electron microscope images by Wetherbee *et al.* (1985) are indicative of haustoria and they reported there was an initial biotrophic phase of growth when *Zea mays* was infected with *P. cinnamomi*; however, the present report is the first of haustoria being associated with a continuously symptomless response for *P. cinnamomi*. These special-

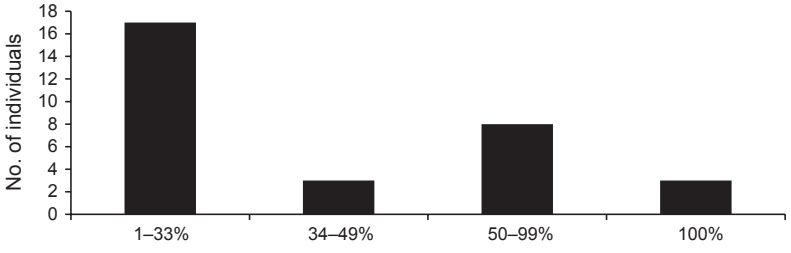


Figure 3 The number of *Chamaescilla corymbosa* plants with 1–100% tubers per plant infected with *Phytophthora cinnamomi* ($n$ = 31).

ized nutrient absorbing haustoria of biotrophs and hemibiotrophs are the reason why *P. cinnamomi* is able to proliferate without symptoms in annual and herbaceous perennial species. With the exception of the *S. diuroides* that died, most of the infected annual and perennial herbaceous species produced seed and persisted on black gravel sites, thus providing host material continuously over time, and hence allowing the pathogen to use these hosts for maintaining inoculum indefinitely. Thick-walled chlamydospores, oospores and stromata are formed in these annual and herbaceous perennial plants (M. Crone, unpublished data), and function as survival structures over the summer.

From a management perspective, the results highlight that efforts to eliminate the pathogen by a period of vegetation removal (Dunstan *et al.*, 2010) will not be successful if annual and herbaceous perennial plant species are allowed to remain.

It will be of interest to determine if *P. cinnamomi* can use annual and herbaceous perennial plant species as hosts in other ecosystems to ensure its survival across seasons. Based on the current study this is likely to be the case, especially as the exotic annual species *Hypochaeris glabra*, *Lysimachia arvensis* and *Pentameris airoides* were found to be symptomless hosts of *P. cinnamomi*. This also suggests that invasive plant species might contribute to the persistence of the pathogen. This would have important implications for disease management internationally, especially in natural environments where annual and herbaceous perennial plant species represent a high percentage of the total vegetation.

This study has for the first time shown the importance of annual and herbaceous perennials, with and without symptoms, as hosts of *P. cinnamomi*. These are important but previously overlooked groups of plants that can allow the pathogen to persist on sites once susceptible species have disappeared or have substantially reduced numbers.

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