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Host removal as a potential control method for *Phytophthora cinnamomi* on severely impacted black gravel sites in the jarrah forest

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Summary

Removal of living plants from an area of *Eucalyptus marginata* (jarrah) forest on black gravel sites infested with *Phytophthora cinnamomi* significantly reduced subsequent pathogen recovery. Vegetation, including trees and annual and herbaceous perennial plants, was killed on the sites by herbicide application. To determine whether this treatment efficiently eliminated *P. cinnamomi*, soil samples were seasonally collected and baited to test for the presence of the pathogen. There were no recoveries on treated sites in autumn, 28 months after removal of all vegetation by herbicide application. To test whether this was the result of the complete elimination of the pathogen or whether inoculum remained, regrowth on sites was not controlled after this period leading to the re-establishment of annual and herbaceous perennial species, some of which are hosts of *P. cinnamomi.* Recovery of *P. cinnamomi* after plant regrowth on the formerly treated sites indicated that for complete pathogen removal, sites need to remain free of vegetation for longer than 28 months. Overall, however, this study confirms that the pathogen is a weak saprophyte, and withdrawal of host material for a period of time may make eventual rehabilitation of these sites possible.

1 Introduction

Phytophthora cinnamomi belongs to the class of *Oomycetes*, a group containing many devastating plant pathogens analogous to fungi in morphology but phylogenetically distinct and therefore less responsive to fungicides (Hardham 2007). It has been demonstrated that copper-based algicides are better-suited chemical control agents for *Phytophthora* species as would be expected due to their closer affiliation with brown algae (Meadows et al. 2011). However, potential use of such algicides might be only applicable for the management of *Phytophthora* species in irrigation water of nurseries. Biological control agents have been considered ranging from rhizosphere organisms found antagonistic to *P. cinnamomi* (Drechsler 1938; Sneh et al. 1977) to higher plants that produce inhibitory root exudates (D'Souza et al. 2005). However, none of these to date have led to control methods applicable to native vegetation, and the delivery of any biological control agent is problematical.

As *P. cinnamomi* depends on living hosts and is a poor competitive saprophyte in soil, temporary removal of vegetation is potentially an effective method of eradication (Dunstan et al. 2010). Withdrawal of living substrate interrupts the pathogen's life cycle and eventually leads to its elimination when all dormant structures including selfed oospores, thick-walled chlamydospores and stromata (Crone et al. 2013) produced prior to the treatment have died or germinated and been unable to colonize new living root tissue. This method has been applied in the horticultural setting, where host destruction has been an integral part of eradicating or containing *P. cinnamomi* in orchards (Erwin and Ribeiro 1996; Gallo et al. 2007). Eradication experiments within a natural environment were first conducted by Weste et al. (1973) in the sclerophyll forest of the Brisbane Ranges, then by Hill et al. (1995) in *Banksia* woodlands and scrub-heaths of south-west Western Australia and recently on heathland sites on the southern sand plains of Western Australia (Cape Riche) and *Eucalyptus* woodland in Tasmania (Narawntapu National Park) in 2007 (Dunstan et al. 2010). Methodology varied considerably among the studies, for example in the monitored type of inoculum (natural infestation (Weste et al. 1973; Dunstan et al. 2010) versus buried inoculated pine plugs (Hill et al. 1995)). Overall, however, all studies reported significant reduction in *P. cinnamomi* recoveries after several months, and all had a combined treatment which involved mechanical manipulation (trenching, stump removal, installation of root barriers), herbicide application and soil fumigation. Only the study by Hill et al. (1995) had an additional comparison using 'herbicides only' as a treatment. Eradication methods have also been applied for spot infections of other *Phytophthora* species in other ecosystems, such as *Phytophthora ramorum* in Californian and Oregon forests (Rizzo et al. 2005). Even though aerial propagules of this species are potentially more difficult to control, the early detection/eradication method has slowed the spread leaving many areas in the infestation zone pathogen free (Kanaskie et al. 2011).

In the current study, the method of resource withdrawal by herbicide treatment was applied to highly impacted sites within the jarrah (*Eucalyptus marginata*) forest, known as black gravel sites. To date, it has not been possible to rehabilitate these kinds of sites using conventional methods (I. J. Colquhoun, personal communication). During this work, several species of annuals and herbaceous perennials were identified as hosts for *P. cinnamomi* even though the infected plants were asymptomatic and able to complete their life cycles and set seeds. This allows the pathogen to persist on sites in the absence of visibly susceptible host species (Crone et al. 2012). Based on this finding, the eradication treatment needs to

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include these species and needs to prevent regeneration from the seed bank for the duration of the treatment to maximize chances for successful eradication.

Therefore, the aim of the current research was to test whether complete removal of all plant species by the application of herbicides will eliminate *P. cinnamomi* from such jarrah forest sites.

2 Materials and methods

2.1 Site selection – Design and size

Two *P. cinnamomi*-infested black gravel sites in the *E. marginata* (jarrah) forest were chosen (Site 1: 32°47′31S 116°04′ 00E; Site 2: 32°50′23S 116°03′49E). Each site was subdivided into two comparable 30 m by 30 m plots with a central 15 m by 15 m zone. Within each site, one plot was cleared of vegetation by the application of herbicides, while the other plot was left as an untreated control. Within each eradication plot, the central 15 m by 15 m zone was used to measure the efficiency of the treatment. The wider 30 m by 30 m treatment zone reduced the chance of living roots penetrating the central 15 m zone from outside as well as the possibility of passive inoculum movement into the central zone. The plots are referred to as 'eradication (treated) plots' (1E and 2E) and 'control plots' (1C and 2C) (Fig. 1).

2.2 Eradication treatments

The foliar herbicide glyphosphate (N-(phosphonomethyl)glycine) was sprayed at 4.8 g/l together with metsulfuron methyl 600 (methyl 2-[[(4-methoxy-6-methyl-1,3,5-triazine-2-yl)aminocarbonyl]aminosulfonyl]benzoate) at 0.1 g/l and EnviroDye Red (Diazo Dyestuff) at 1-1.5 ml/l for visibility. Trees were notched by cutting four wounds equidistant around each trunk at a height of approximately 70 cm and then were treated by immediately applying undiluted glyphosphate (360 g/l) into the notches. The eradication through foliar application was undertaken in January 2010 followed by tree notching in April 2010. Where necessary, the notching process was repeated until all trees had died. To prevent germination from the soil seed bank, simazine 500 (6-chloro-N2,N4-diethyl-1,3,5-triazine-2,4-diamine) at a concentration of 1.52 g/l was applied to the soil surface in August 2010. Glyphosphate was also applied as required to any resprouting plants or germinating seeds of the soil seed bank over the period from winter 2010 to autumn 2012. After this time, there were no additional herbicide treatments, and germination from the soil seed bank was allowed.

2.3 Monitoring of pathogen activity – Collection of samples

All four plots were tested for the presence of *P. cinnamomi* through baiting of soil samples from before eradication (spring 2009 to autumn 2010), through the eradication period (winter 2010 to autumn 2012), and after regrowth on the formerly

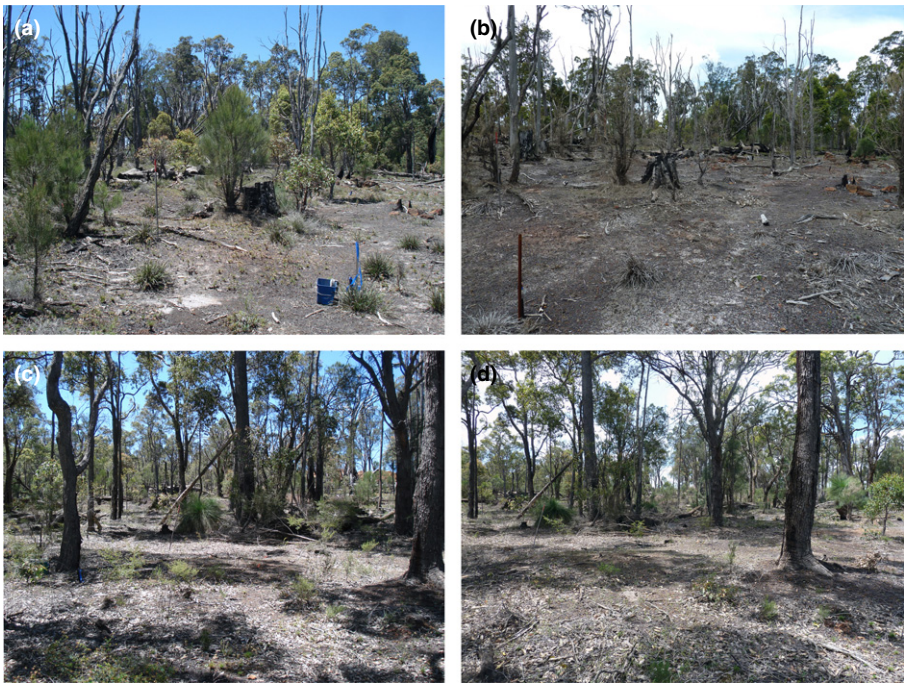

Fig. 1. Site 2, a black gravel area in the *Eucalyptus marginata* (jarrah) forest severely impacted by *Phytophthora cinnamomi* (32°50′23S 116°03′49E). (a) Eradication plot 2E in spring 2009 prior to eradication; (b) plot 2E 1.5 years after eradication in spring 2011; (c) control plot 2C in spring 2009; (d) plot 2C 1.5 years later in spring 2011.

treated sites (spring 2012). To map the presence of *P. cinnamomi* across each plot before and after the eradication treatments, eight transects were established on each plot. Transects were 2 m apart, and soil samples between 10 and 20 cm depth (dependent on depth to duricrust) were collected every 3 m along each transect. This resulted in 40 soil samples per 15 m by 15 m plot for each sampling event. A spade blade cut to a trapezoid shape was used to collect samples and was sterilized with 100% methylated spirits between samples. Approximately, 4 kg of soil was collected per sample. Each sample was placed into a plastic sealable bag (38 cm × 25 cm; Sandvik, WA, Perth, Australia) and stored in the shade. Samples were transported to the laboratory on the same day. When after autumn 2012 germination and growth from the soil seed bank was not controlled, numerous annual and herbaceous perennial plant species re-established themselves. This provided host material to test whether a 28-month fallow period was sufficient to eradicate *P. cinnamomi*. The isolation of the pathogen was also attempted from the root systems of 17 individuals of *Trachymene pilosa*. This species, among other annuals and herbaceous perennials, was previously identified as an asymptomatic host (Crone et al. 2012) and was sampled to verify the importance of such species in the persistence of *P. cinnamomi*.

2.4 Sample processing and detection of *Phytophthora cinnamomi*

Soil from each sample was placed together in 1-L rectangular polypropylene containers (167 mm × 108 mm). Steps were taken to maximize the chance of detecting *P. cinnamomi* if it occurred at a very low inoculum level in each bulk sample: (i) most of the roots present in the collected soil were placed in the container; (ii) the soil was thoroughly mixed; (iii) soil subsamples (total volume = 500 g) were taken from different areas of the bag. Combined, the roots and soil filled one-third of the container. The soil/root mix was then premoistened with distilled water overnight to stimulate pathogen activity, unless it was already sufficiently moist at the time of collection. The next morning, the samples were flooded with distilled water in a 1 : 3 soil/water ratio and baited with young leaves of *Quercus ilex*, *Q. suber*, *Castanea sativa*, *Alnus* sp., *Scholtzia* sp., cotyledons of *Eucalyptus sieberi*, petals of genus *Rosa* and leaves of other plant species, depending on seasonal availability. The baits were incubated at a temperature of 21°C (±1°C); a fibreglass fly screen mesh (hole size 2 mm × 1.5 mm; Cyclone, Dandenong South, Vic., Australia) was used to prevent floating organic particles from coming into contact with the bait leaves.

When lesions were observed on the bait leaves (typically after 3–7 days), they were rinsed in deionized water, blotted dry on paper towelling, cut into 2 by 2 mm pieces and plated on NARPH agar (Hüberli et al. 2000). In early 2010, pentachloro-6-nitrobenzene (PCNB) was withdrawn from the market, so it was removed from the selective medium in subsequent plating. The leaves were incubated at 21°C (±1°C) in the dark and examined under 100 × magnification for the presence of hyphae typical for *P. cinnamomi*. Plates were examined four to five times during the first week and two to three times during the second week. In many cases, mycelial growth on the initial plate could be identified as *P. cinnamomi* due to typical morphological features such as hyphal swelling, chlamydospore formation and branching pattern. When confirmation of initial morphological identification was needed, hyphal tips were transferred to NARPH/NARH and then aseptically subcultured to half-strength potato dextrose agar (half PDA) to morphologically distinguish between *P. cinnamomi* and similar appearing organisms.

When no *P. cinnamomi* cultures were obtained from the flooded samples after approximately 2 weeks, the water was discarded, the soil allowed to dry and then baiting was repeated (double baiting) to increase detection (Jeffers and Aldwinckle 1987; Bunny 1996).

Between spring 2009 and autumn 2012, 13 seasonal samplings were conducted with a minimum of one per season.

2.5 Confirmation of negatives

P. cinnamomi-negative soils from two seasons, summer 2009/2010 and autumn 2010, were each bulked separately, mixed thoroughly and used for live baiting with 6-month-old *Banksia grandis* seedlings (that had never been treated with phosphite) purchased from Apace WA Nursery (Fremantle, Western Australia). Briefly, 10 *B. grandis* were potted into free draining pots (19 cm diameter, 5 l volume) each containing black gravel soil collected in summer. The autumn soil was placed in one free draining 48-l container with three *B. grandis* seedlings as live baits. All potted plants were placed in a temperature-controlled glasshouse (maximum temperatures 24°C) and watered daily to container capacity. As a positive control, five pots were filled with *P. cinnamomi*-positive soil from the autumn 2010 sampling mixed with potting mix (Soil Aint Soils, Perth, WA, Australia) at 1 : 4, v:v, and then planted with *B. grandis* seedlings. As negative controls, five *B. grandis* seedlings were planted in five pots which only had potting mix as the substrate. The plants were monitored for 2 years.

2.6 Analysis of data

A statistical analysis of the variance between *P. cinnamomi* recovery from the eradication and the control plots was conducted using one-way ANOVA with the IBM SPSS Statistics (version 20) software (IBM Corporation, New York, NY, USA).

3 Results

3.1 Accuracy of baiting method to detect *P. cinnamomi*

When soil that initially tested negative by baiting was re-tested with susceptible *B. grandis*, none died over 2 years, a period sufficient to kill *B. grandis* potted in *P. cinnamomi*-positive soil (McDougall et al. 2002). This was also the case for the

negative controls. All *B. grandis* planted in *P. cinnamomi*-positive soil died within one to several months from where the pathogen was recovered by baiting.

3.2 Effectiveness of vegetation removal

Most trees and shrubs died within 2 months after completion of the herbicide treatment, and resprouts were similarly quickly killed. Some woody plant species, for example *Hypocalymma angustifolium* present on 2E, were relatively tolerant of the herbicides and resprouted from lignotubers or roots despite shoots being killed. Mechanical removal of lignotuber and root material helped to eliminate this species, but left some small root fragments which were capable of resprouting. A few seedlings (of both annuals and perennials) emerging from the soil seed bank were missed by the spray treatments. Some individuals of species with tuberous roots (several orchid species and *Chamaescilla corymbosa*) survived despite herbicide applications.

3.3 Effectiveness of treatment

Before the eradication treatments, *P. cinnamomi* was recovered 11 times from the eradication plot (1E) and 10 times from the control plot (1C) for site 1. On site 2, prior to treatment, the pathogen was recovered 15 and 10 times, from the eradication (2E) and control (2C) plots, respectively (Table 1). Thus, prior to treatment, all plots had similar inoculum potentials. Recovery frequency on the eradication sites decreased once treatment was completed. On site 1, *P. cinnamomi* was recovered on the control site 22 times compared with eight times on the treated plot with a similar reduction (23 compared with 9 recoveries) observed on site 2 (Table 1).

On plot 1E, *P. cinnamomi* was never recovered again from six of 10 spots shown to be positive at the start of the experiment. On plot 2E, 11 of 15 spots initially positive never again gave positive results after the eradication treatment (Fig. 2).

A one-way ANOVA test after completion of treatments showed that after 28 months of vegetation removal, there was a significant difference between the number of recoveries in control and eradication areas (p-value = 0.002).

3.4 Testing of pathogen presence after vegetation regrowth

Despite the significant reduction and no detection in autumn 2012, soil testing in spring 2012 did yield *P. cinnamomi* on the formerly treated eradication plots 1E and 2E (1E: two of 40; 2E: 16 of 40 sampling spots) when vegetation was allowed to become re-established after the fallow period of 28 months. *P. cinnamomi* was recovered from four of the 17 root samples of the re-establishing annual *T. pilosa* that is asymptomatic when infected by *P. cinnamomi*.

In general, the lowest recoveries of *P. cinnamomi* were made during the summer, whereas the highest were in spring. Percentages of recoveries on the control plots from the spring sampling periods ranged from 7.5 to 17.5% and were

Table 1. Number of *Phytophthora cinnamomi* recoveries from the control plots and treated plots of both replicates prior to treatment and for the following 2 years. There were 40 samples from each of the four plots for each sampling event. Numbers in brackets are the positive samples obtained by double baiting.

	Site 1		Site 2	
	Total isolations		Total isolations	
Harvest	Control (1C)	Eradication (1E)	Control (2C)	Eradication (2E)
Prior treatment				
Spring 2009	8	7 (1)	6	15
Summer 2009/2010	0	0	0	0
Autumn 2010	2	4 (1)	4	0
Total prior to treatment	10	11	10	15
After treatment				
Winter 2010 (June)	0	0	1 (1)	2 (2)
Winter 2010 (August)	1	0	3	0
Spring 2010 (October)	2 (1)	0	3 (2)	2 (2)
Spring 2010 (November)	4 (3)	4 (1)	2	1 (1)
Summer 2010/2011	0	1 (1)	1 (1)	1
Autumn 2011	2	2 (2)	3 (1)	0
Winter 2011	1	0	2	0
Spring 2011	6	0	4	3 (1)
Summer 2011/2012	3	1	2 (1)	0
Autumn 2012	3	0	2 (1)	0
Total after treatment	22	8	23	9
Regrowth				
Spring 2012	10	2	7	16

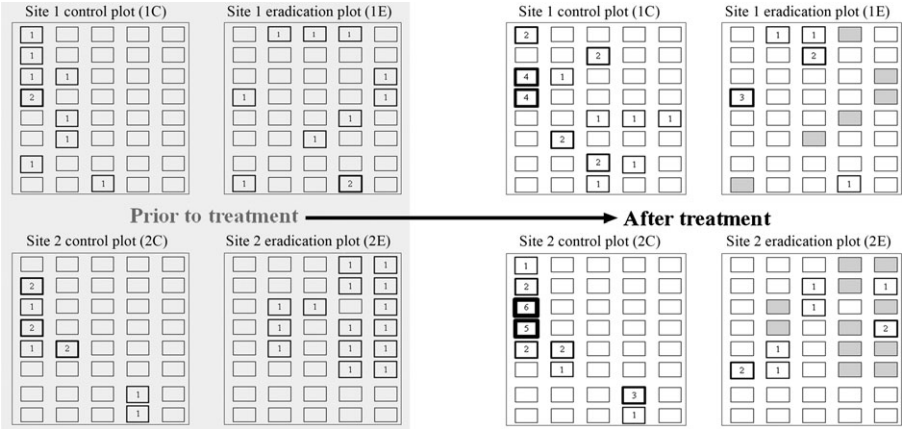

Fig. 2. Spatial recovery of *P. cinnamomi* from seasonal soil sampling prior to (grey background) and after herbicide treatments of eradication sites. Survey period from spring 2009 to autumn 2012. Numbers show the total numbers of recoveries from each locality, empty boxes indicate no recoveries. Thickness of boxes corresponds to higher frequencies of recovery, grey boxes are areas from which the pathogen was only isolated before vegetation removal.

comparable to the normal range of 7.2–35% reported by others working in infected *E. marginata* forest (Podger 1968; McDougall 1996; Davison and Tay 2005). Double baiting increased the number of recoveries by 21.3% (Table 1).

4 Discussion

Vegetation removal was an effective means of reducing the occurrence of *P. cinnamomi* on the black gravel sites. For both sites, from more than half of the sampling spots initially shown to be positive for the pathogen on the eradication plots, *P. cinnamomi* was never recovered again after the herbicide treatments. However, once vegetation was allowed to re-establish, *P. cinnamomi* was recovered again, demonstrating that a period of vegetation removal of longer than 28 months is necessary to achieve complete eradication. Even though *Phytophthora* species such as *Phytophthora lateralis* have been shown to survive for at least seven years inside infected host roots placed in potted soil and buried to ground level (Hansen and Hamm 1996), the duration of *Phytophthora* survival is likely to be shorter under natural conditions and their decline potentially facilitated by removal of any plant material which could play a role in the pathogen's life cycle.

For future studies, a higher replication of sites given vegetation-free periods of 3, 4 and 5 years is needed to determine how long it takes before *P. cinnamomi* is totally eradicated from herbicide-treated plots. During this time, it will be critical to ensure there is no plant recruitment. As there were few or no susceptible woody species on the sites, the recoveries made after vegetation removal are most likely due to a remaining inoculum in the form of oospores, thick-walled chlamydospores and stromata within root material of annual and herbaceous perennial species (Crone et al. 2012, 2013) or woody perennials (Jung et al. 2013) rather than from reintroduction from outside the treated area. It is possible that several conducive seasons are needed before all dormant propagules have germinated and failed to continue growth in the absence of suitable host roots.

Application of simazine to suppress plant germination from the soil seed bank immediately after the winter sampling in August 2010 might have increased sporangial production from germinating survival structures as simazine was reported to increase sporangial production by Kassaby (1985). If so, being on the eradication site, these zoospores would have lacked suitable living host material to infect and colonize. Consequently, simazine might be a useful tool to help speed up the eradication process.

Besides economic and ecological considerations, the sole use of herbicides might be favourable than more robust treatments that include soil fumigation. Even though fumigation has been shown to result in no recoveries of the pathogen after only two to several months, possible reintroductions of the pathogen by vectoring along with re-establishing hosts in the following conducive season would be more problematic, as *P. cinnamomi* with its fast life cycle is able to rapidly build up inoculum and form new survival structures before full re-establishment of antagonistic soil organisms occurs (Gamliel et al. 2000).

Historical records show that *P. cinnamomi* is continuously present within impacted jarrah forest sites. This is a strong indicator that soil temperature and moisture content during the extremes of summer are not detrimental for pathogen survival, even in exposed areas without shade or after high-intensity fires (Shearer and Tippett 1989). Gallo et al. (2007) showed that chlamydospores (produced *in vitro* on agar and most likely to be thin walled) were killed by exposure to 40°C for one to two hours, while mycelium was inactivated after 1–2 h at 38°C. On the black gravel sites, the temperature at 10 cm soil depth never exceeded 36°C (data not presented). At this depth, *P. cinnamomi* survival structures would be buffered by both overlying soil and the root tissues and could be expected to survive over the summer (Crone et al. 2013). From previous research, it is evident that the jarrah forest already experiences suboptimal conditions on black gravel sites (Welker 2008; J. Koch, personal communication; J. Havel, personal communication) and is likely to be highly vulnerable to

any disease pressure. Therefore, under these conditions, it is very important to completely eliminate *P. cinnamomi* inoculum before attempting rehabilitation. This work has shown that these Mediterranean forest sites must be kept vegetation free by herbicide application for at least 3 years to make complete eradication of *P. cinnamomi* likely. This method might also be an efficient tool in other ecosystems or for other primary pathogens of low saprophytic ability.

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