http://dx.doi.org/10.1071/BT14188

Moore, N., Barrett, S., Howard, K., Craig, M.D., Bowen, B., Shearer, B. and Hardy, G. (2014) Time since fire and average fire interval are the best predictors of Phytophthora cinnamomi activity in heathlands of south-western Australia. Australian Journal of Botany, 62 (7). pp. 587-593.

Time since fire and average fire interval are the best predictors of *Phytophthora cinnamomi* activity in heathlands of south-western Australia

Nicole Moore [A B] , Sarah Barrett [A] , Kay Howard [B] , Michael D. Craig [B C D] , Barbara Bowen [B] , Bryan Shearer [A B] and Giles Hardy [B]

[A] Department of Parks and Wildlife Albany District, 120 Albany Highway, Albany, WA 6330, Australia.

[B] Centre for Phytophthora Science and Management, School of Veterinary and Life Sciences, Murdoch University, Murdoch, WA 6150, Australia.

[C] School of Plant Biology, University of Western Australia, Crawley, WA 6009, Australia.

Abstract

Fires are features of ecological communities in much of Australia; however, very little is still known about the potential impact of fire on plant diseases in the natural environment. *Phytophthora cinnamomi* is an introduced soil-borne plant pathogen with a wide host range, affecting a large proportion of native plant species in Australia and other regions of the world, but its interaction with fire is poorly understood. An investigation of the effects of fire on *P. cinnamomi*activity was undertaken in the Stirling Range National Park of south-western Australia, where fire is used as a management tool to reduce the negative impact of wildfires and more than 60% of the park is infested with, and 48% of woody plant species are known to be susceptible to, *P. cinnamomi*. At eight sites confirmed to be infested with *P. cinnamomi*, the proportion of dead and dying susceptible species was used as a proxy for *P. cinnamomi* activity. Subset modelling was used to determine the interactive effects of latest fire interval, average fire interval, soil water-holding capacity and pH on *P. cinnamomi*activity. It was found that the latest and average fire interval were the variables that best explained the variation in the percentage of dead and dying susceptible species among sites, indicating that fire in *P. cinnamomi*-infested communities has the potential to increase both the severity and extent of disease in native plant communities.

Additional keywords: *Phytophthora* dieback, Stirling Range National Park, susceptible.

Introduction

Phytophthora cinnamomi Rands is a threat to a wide range of plants and ecosystems worldwide and is recognised as a Key Threatening Process to the Australian environment (Environment Australia 2001). In natural ecosystems, propagules of *P. cinnamomi* are not uniformly distributed, but occur in a mosaic distribution and are found in the highest concentrations at the surface of unsuberised roots belonging to susceptible species (Dawson *et al*. 1985) and high inoculum loads occur in the soil surrounding the collars of already infected plants, such as *Banksia* species (Shearer *et al*. 2010). Movement of the pathogen occurs downslope in subsurface water flow (Podger 1999) and laterally by root-to-root contact (Hill *et al*. 1994). The cryptic nature of this pathogen makes it difficult to measure the effects of the disease and its spread.

Naturally occurring fire and prescribed burning are important disturbance factors that may complicate the management of *Phytophthora* dieback in native Australian ecosystems. There are many confounding factors when studying the effect of fire on vegetation, including the time since fire, fire frequency (Watson and Wardell-Johnson 2004), fire intensity (Lamont *et al*. 2007), fire-survival strategies of vegetation (Fisher *et al*. 2009), as well as changes in chemical and physical properties of the soil. These factors may also affect survival or virulence of any soil-borne pathogen; however, little is known of the effect of fire on pathogens, such as *Phytophthora* spp., and their interaction with the host after fire. Fire can affect disease activity by directly affecting the pathogen's survival and development (Weste 1974; Schwartz *et al*. 1995; Moritz and Odion 2005) or, indirectly, by affecting the plant (Marks *et al*. 1975) and/or microbial community (Treseder *et al*. 2004) or the physical environment (Podger and Brown 1989; Shearer and Tippett 1989; Bishop *et al*. 2010). Furthermore, plants stressed by fire, low nutrients, drought or defoliation are more likely to succumb to disease (Schoeneweiss 1975).

Studies of the interactions between *Phytophthora* and fire are rare (Beh *et al*. 2012). In Tasmania, impacts from *P. cinnamomi* were found to be greater with increasing vegetation height and age associated with the absence of fire (Brown *et al*. 2002), whereas in the USA, an increase in the incidence of *P. cinnamomi* in relation to fuel-reduction treatments has been observed in forest soils (Meadows *et al*. 2011). One study has been established to monitor the impact of fire and *Phytophthora* in shallow soil communities in south-western Australia (Clarke 2009), but no results have been published. Burrows (1985) and Robinson and Bougher (2003) proposed moderate to high fire intensities as a means to reduce susceptible hosts of *P. cinnamomi* and, thereby, control its spread and impact.

Within the Stirling Range National Park (SRNP) in south-western Australia, 48% of woody plant species, mainly from the Proteaceae, Ericaceae and Fabaceae, are susceptible to *P. cinnamomi* (Shearer *et al*. 2004), whereas 21 of 33 taxa of conservation significance assessed for risk of extinction were threatened by inappropriate fire regimes (Barrett *et al*. 2008). Furthermore, in contrast to other studies, observations within SRNP Threatened Ecological Communities have noted high levels of disease impact in more frequently burnt sites (Barrett and Gillen 1997; Barrett 2000; Barrett 2005).

Prescribed burning is used extensively in south-western Australia, including the SRNP, to reduce the likelihood of devastating wildfires (Bowman 2003; Burrows 2008; Wilson *et al*. 2014). Plant community composition following fire is influenced by fire frequency, intensity and scale, the life-history attributes of the species present, environmental interactions affecting seedling emergence and survival niche, including climate conditions, predation and disease, and the pool of species that can reach the site (Noble and Slatyer 1980; Keith *et al*. 2002). Fires in heathlands provide the only regeneration opportunities for many species (Cheal 2000) and the period immediately after fire is when most regeneration occurs (Bell *et al*. 1984; Keith *et al*. 2002). Studies of post-fire vegetation dynamics in a variety of fire-prone ecosystems consistently report an increase in species richness in the first few years after fire, which then stabilises or declines (Bell and Koch 1980; Watson and Wardell-Johnson 2004; Burrows 2008). Species abundances are also typically greater in the early years after fire (Hobbs and Atkins 1990; Burrows and Wardell-Johnson 2003; Yates *et al*. 2003). Therefore, deviations from these two patterns, particularly if the changes are largely due to a lack of species susceptible to *Phytophthora*, would be indicative of the presence of the pathogen.

Because it is not known whether fire exacerbates the activity and spread of *P. cinnamomi*, an investigation of the effect of fire on *P. cinnamomi* activity on susceptible plant species at infested sites of SRNP was undertaken. Our results will have relevance for those involved in conservation of biodiversity in regions where fire is used as a management tool.

Materials and methods

Experimental design and vegetation survey

More than 60% of Stirling Range National Park, Western Australia (34°23′S, 118°08′E), has been determined to be infested with *P. cinnamomi* (CALM 1999); our eight sites were chosen within areas mapped as infested on the eastern side of the park. These sites were monitored between April 2005 and April 2006 to determine the effects of the pathogen on survival of susceptible plant species after fire (Table 1). The fire history and soil characteristics of each site were also recorded.

At each site, four 5 × 5 m quadrats were randomly located. A species-area curve determined 25 m^2 as an adequate quadrat size (data not shown). A detailed count of the number of individuals of species belonging to families known to be susceptible to *P. cinnamomi* (Proteaceae, Ericaceae, Fabaceae, Myrtaceae and Xanthorrhoeaceae), as well as known susceptible species from the genera *Acacia*(*A. baxteri*, *A. browniana* and *A. chrysocephala*), *Hibbertia* (*H. argentea*, *H. hemignosta*and *H. recurvifolia*), *Calectasia* (*C. grandiflora*) and *Patersonia* (*P. occidentalis*), was undertaken within each quadrat in April 2006. The groups assessed represented the majority of species occurring within the survey sites, with the exception of the families Restionaceae and Cyperaceae. All individual plants were scored as alive, dead (brown and dry, no leaves) and dying (displaying disease symptoms: wilting, chlorosis and/or lesions), identified as seeders or resprouters and determined if known to be susceptible to *P. cinnamomi* (Groves *et al*. 2003; Sage *et al*. 2004; O'Gara *et al*. 2005; Department of Environment and Conservation website (http://www.dec.wa.gov.au/pdf/projects/dieback/dieback_indicators.pdf, accessed December 2012); Project Dieback website (http://www.dieback.net.au/pages/1382/susceptible-species accessed December 2012); NM and SB, pers. obs.). The proportion of dead and dying susceptible species was used as a proxy for *P. cinnamomi* activity. This was supported by confirmation of the presence of *P. cinnamomi* from dead and dying plants and surrounding soil. To calculate this value, the number of all dead and dying individuals of susceptible species was summed for each site and divided by the summed total of all live (asymptomatic) and dead and dying (symptomatic) individuals of susceptible species on each site. This resulted in a dependent variable of proportion of dead and dying susceptible species, with a single value for each of the eight sites.

Fire history and soil characteristics

A fire history for each site was obtained from fire maps of SRNP held by Department of Conservation and Land Management (now Department of Parks and Wildlife), to determine the latest fire interval and average fire interval for each site. Because fire maps extended only back to 1972, the latter variable was the average time between the two most recent fires.

Soil properties are critical to plant survival, so water-holding capacity (which influences water availability to plants) and soil pH (which influences nutrient availability to plants) were measured because we considered these important soil variables influencing survivorship. Furthermore, *P. cinnamomi* requires free soil moisture for active dispersal via motile zoospores and prefers neutral to acidic soils (Erwin 1983; Zentmyer 1983). To obtain these two soil variables, soil samples of 200–500 g were collected from depths between 50 and 300 mm. These were stored in zip-lock plastic bags and placed in insulated containers before processing in the laboratory. Soil texture was determined by sieving fractions (gravel >2 mm, <2 mm sand >500 µm, <500 µm silt >63 µm, and clay <63 µm) of a

500-g dry sample, following the method of Weil (1993). Water-holding capacity was determined by sieving (2 mm) 250 g dried soil samples, which were then weighed, flooded and then allowed to drain freely for 24 h before weighing again.

***Phytophthora cinnamomi* sampling, isolation and identification**

To confirm the presence of *P. cinnamomi* at each site, soil was collected from the base of several symptomatic and dead plants to a depth of 300 mm and stored in zip-lock bags in insulated containers. At room temperature, soil was baited with rose petals in containers flooded with deionised water. After 4–7 days, the rose petals were blotted dry and plated onto NARPH, a *Phytophthora*-selective medium (Hüberli *et al*. 2001) for isolation at 25 ± 2°C. The isolates were stored on half-strength potato dextrose agar (PDA) (Becton Dickinson and Co., Franklin Lake, NJ, USA) at 20 ± 2°C.

To determine whether plant deaths that occurred during the study were caused by *P. cinnamomi*, stem (from around ground level) and root material was collected to isolate *P. cinnamomi* from dead and dying plants. As much material as possible of the stem and root from each dead plant was surface sterilised by dipping into 70% ethanol and immediately flamed, dried and plated onto *Phytophthora*-selective media NARPH (Hüberli *et al*. 2000) for isolation, and incubated in the dark at 25 ± 2°C for 3–5 days. Once clean, isolates were stored on PDA at 20 ± 2°C.

Confirmation of *P. cinnamomi* was achieved using microscopic identification of typical *P. cinnamomi* morphological characteristics by comparison with a known specimen of *P. cinnamomi*. Molecular confirmation was achieved by extracting DNA from selected 10-day-old *Phytophthora* isolates and the rDNA was extracted using an Utraclean® 15 DNA purification kit (MO BIO Laboratories, Carlsbad, CA, USA). The polymerase chain reaction (PCR) mixture and reactions were carried out as described by Cooke *et al*. (2000) and Barber *et al*. (2005), using DC6 primer and the universal primer ITS4. Sequence data were analysed using Sequence Navigator version 1.01™ (Perkin Elmer Applied Biosystems, Waltham, MA, USA) and their identity was established by comparison with known *Phytophthora* sequences in GenBank.

Statistical analysis

To determine whether sites differed in their plant species richness or abundance, or percentage of live plants, seeder species or susceptible species, chi-square analyses were conducted using the average for each variable as the expected value at each site. To determine whether fire had a significant effect on *P. cinnamomi*activity (identified as the proportion of dead and dying individuals of susceptible species on each site), best-subset modelling, a method that assesses all possible combinations of the predictor variables (Burnham and Anderson 2002), was conducted to identify which models provided the best predictor(s) of *P. cinnamomi*activity. Only four predictor variables (latest fire interval, average fire interval, water-holding capacity (%) and pH H_2O; Table 1) were used to avoid over-fitting models (Maloney *et al*. 2012). Each model was run as a generalised linear model with a normal distribution and identity link function. The ratio of sample size to parameters was low in the best-subset models, so the second-order bias-corrected form of Akaike's information criterion (AIC_c) was used as the basis for all model selection (Burnham and Anderson 2002) and all models with an AIC_c value within $\Delta 3$ of the minimum AIC_c value were considered as having good support., The Akaike weight (W_i) was calculated to determine the probability that each model was the best model and, for all well supported models, a multiple regression model was run to see how much variation was explained by these models.

Results

Fire history and soil characteristics

Time of latest fire varied from 1 year at Chester Pass West to more than 30 years at the Chester Pass East[A] site, with five of the sites being burnt within the past 5 years. Average fire interval from the latest two fires ranged from ~8 years for half of the sites, to between 14 and 30+ years for the remaining sites (Table 1). Soil pH was similar for all sites (~5.8), with the exception of Success Ridge with a pH ~5. Soil water-holding capacity was also similar for most sites (between 27% and 39%), with the exception of the long-unburnt Success Ridge Track[A] site at 70% (Table 1).

Phytophthora cinnamomi

Symptomatic plants were present in all quadrats and *P. cinnamomi* was positively identified from soil and infected plant-tissue samples from all vegetation survey sites. The percentage of identified susceptible species was high, ranging between 43% and 67% across the sites. Of these susceptible species, between 5.93% (Chester Pass Road East[A]) and 31.59% (Yungermere Peak) were recorded as showing symptoms of disease (dead or dying) (Table 2).

Vegetation surveys

The percentage of species recorded was adequately represented as determined from species-area curves, with a substantive reflection of the complete flora occurring within the plant communities studied (data not presented). Of the total 146 species identified in the survey, 56% were known to be susceptible to *P. cinnamomi*, 15% resistant and 29% unknown, whereas 66% were obligate seeder species, 23% resprouter species, 3% facultative sprouter-seeder species and 8% were of unknown fire-response strategy. Of the plants surveyed, 68% of resprouters and 85% of seeders were considered to be susceptible to *P. cinnamomi*.

Sites did not differ in terms of species richness ($\chi^2_7 = 10.43$, $P = 0.166$) but did differ significantly in terms of plant abundance ($\chi^2_7 = 1211.49$, $P < 0.001$; Table 2). The 14-year post-fire sites at Bluff Knoll Road and Success Ridge Track had much higher than average abundances, whereas most sites ≤5 years post-fire (except Bluff Knoll Road) had much lower abundances than average. Neither the percentage of seeder species ($\chi^2_7 = 1.03$, $P = 0.994$), nor the percentage of susceptible species ($\chi^2_7 = 13.47$, $P = 0.061$) differed significantly among the sites. However, the percentage of dead or dying susceptible species did differ significantly among the sites ($\chi^2_7 = 40.42$, $P < 0.001$), the long-unburnt Chester Pass Road East site having a much lower percentage than average and the sites ≤3 years post-fire (except Chester Pass Road West) having much higher percentages than average (Table 2).

Predictor model

The two fire variables, namely, the latest fire interval and average fire interval, were the variables that best explained the variation in the percentage of dead and dying susceptible species among sites. A model with both the latest fire interval and average fire interval was the best-supported model, with a 36.4% chance of being the best model. Latest fire interval alone was in the next-best-supported model, with a 26.9% chance of being the best model, and average fire interval alone was also well supported, with a 13.3% chance of being the best model (Table 3). Unsurprisingly, the summed model weights for each variable supported the hypothesis that the fire variables were the best predictors of the percentage of dead and dying susceptible species. Summed model weights for the two fire variables, namely, the latest fire interval (76.2%) and average fire interval (60.2%), were much more influential than was pH H_2O (16.4%) and soil water-holding capacity (10.1%).

Discussion

Latest fire interval and average fire interval were the variables that best explained the variation in the percentage of dead and dying susceptible species among sites, with sites burnt within 5 years of the survey having up to 31.59% of individual susceptible species that were dead or dying, compared with a low of 5.93% in a site unburnt for more than 30 years. It is likely that, immediately after fire, sites will be more open with wetter and warmer conditions for longer periods of time. This, coupled with the presence of germinants and surviving, but potentially stressed, susceptible species makes ideal conditions for the pathogen. Furthermore, after fire, some of these soils were found to be more stimulatory to *P. cinnamomi*chlamydospore and sporangia production and to have increased microbial activity (Moore 2005), and these factors may also contribute to increased *P. cinnamomi*activity post-fire.

In the current study, sites did not differ significantly in terms of species richness, and abundances were greater at sites unburnt for at least 5 years. Other studies on fire have shown that both latest and average fire interval influence species richness (Watson and Wardell-Johnson 2004) and that species richness and abundance typically increase in the first 3–5 years post-fire (Bell and Koch 1980; Hobbs and Atkins 1990; Burrows and Wardell-Johnson 2003; Yates *et al*. 2003; Burrows 2008), after which species richness stabilises or declines. Furthermore most regeneration in heathlands is confined to the period immediately post-fire (Bell *et al*. 1984; Keith *et al*. 2002), when an increase in abundance is particularly true of members of the Proteaceae (Lamont *et al*. 1999). However, both the abundance and species richness of susceptible species have been shown to decline with infestation by *P. cinnamomi* in *Banksia* woodlands of south-western Australia (Bishop *et al*. 2010). Thus, our finding that neither abundance nor species richness increased post-fire is consistent with increased post-fire *P. cinnamomi* activity causing increased mortality in susceptible species.

To further support the finding of increased disease post-fire, Podger and Brown (1989) concluded that disease caused by *P. cinnamomi* in remote forest was dependent on logging or fire disturbance for persistence. In Tasmania, they showed that the pathogen was not recovered from 34 sites in undisturbed forest or remote wilderness, but was frequently recovered from logged forest degraded by repeated burning, recently burnt forest along road verges and disturbed forest recovering from fire. In the present study, the longer-unburnt sites have been burnt previously at average fire intervals of >16 years. Major disturbance to these longer-unburnt communities in the past 50 years has remained relatively low, resulting in greater plant abundances and the lowest proportion of dead or dying susceptible species (<11.5%). In contrast, the reduced species abundance in recently burnt sites along with larger proportions of dead or dying susceptible species may also have been influenced by the previous fire interval and is consistent with fire disturbance and disease (Podger and Brown 1989).

Fire in *Phytophthora*-infested communities has the potential to increase both the severity and extent of disease in native plant communities, and impinge on the regeneration capabilities of susceptible species, particularly obligate-seeder species, given the high level of susceptibility reported in the present study. Because many of these obligate seeders are canopy dominant, changes in density will affect the vegetation structure in the long-term (Bradstock *et al*. 1996). Soil seed banks may persist and provide a means of disease evasion, at least in the short term, for species with persistent seed banks, whereas species with transient and short-lived soil seed banks or canopy-stored seeds will be more rapidly depleted (Meney *et al*.1994; Keith *et al*. 2002). There was little indication that changes in community composition could be reversed, owing to a reduction in juvenile survivorship and the high proportion of existing resprouters that were diseased. Because time since fire can be a strong driver of ecosystem structure and species composition, Moritz and Odion (2005) hypothesised that certain successional stages will be more prone to infection than are others. Therefore, future management of recurring fires and soil-borne disease may mediate stability, or continuing decline, of susceptible species. It is also likely that the predicted change in climate in the south-west of Western Australia (Bates *et al*. 2008), with longer drier periods, will result in more frequent fires, which in turn could exacerbate plant deaths when conditions are warm and wet. The likely increase in *P. cinnamomi* activity post-fire has important implications for the future of plant communities affected and threatened by infestation from *P. cinnamomi*, and land managers should consider this interaction when developing management practices.

Acknowledgements

We thank Renee Hartley, Department of Parks and Wildlife, Peter Dwyer, Susanne and Lynton Moore, and Judy Giles for their invaluable field assistance, and Associate Professor Michael Calver for much appreciated assistance with statistical analysis of the data.

References

Barber BA, Burgess TJ, Hardy GEStJ, Slippers B, Keane PJ, Wingfield MJ (2005) *Botryosphaeria* species from *Eucalyptus* in Australia are pleoanamorphic, producing *Dichomera* syanamorphs in culture. *Mycological Research* **109**, 1347–1363.

Barrett SR (2000) 'Montane heath and thicket of the south west botanical province, above approximately 900 m above sea level (Eastern Stirling Range montane heath and thicket community). Interim recovery plan 1999–2002.' (Department of Conservation & Land Management: Perth)

Barrett SR (2005) 'Montane mallee thicket of the Stirling Range interim recovery plan (mallee–heath and mallee–thicket community on mid to upper slopes of Stirling Range Mountains and hills) 2004–2009.' (Department of Conservation and Land Management: Albany, WA)

Barrett S, Gillen K (1997) Mountain protected areas of south Western Australia. *Parks: The International Journal of Protected Areas and Conservation* **7**, 23–30.

Barrett SR, Shearer BL, Crane CE, Cochrane A (2008) An extinction-risk assessment tool for flora threatened by *Phytophthora cinnamomi*. *Australian Journal of Botany***56**, 477–486.

Bates BC, Hope P, Ryan B, Smith I, Charles S (2008) Key findings from the Indian Ocean Climate Initiative and their impact on policy development in Australia. *Climatic Change* **89**, 339–354.

Beh MM, Metz MR, Frangioso KM, Rizzo DM (2012) The key host for an invasive forest pathogen also facilitates the pathogen's survival of wildfire in California forests. *New Phytologist* **196**, 1145–1154.

Bell DT, Koch JM (1980) Post-fire succession in the northern jarrah forest of Western Australia. *Australian Journal of Ecology* **5**, 9–14.

Bell DT, Hopkins AJM, Pate JS (1984) Fire in the kwongan. In 'Kwongan: plant life of the sandplain'. (Eds JS Pate, JS Beard) pp. 178–204. (University of Western Australia: Perth)

Bishop CL, Wardell-Johnson GW, Williams MR (2010) Community-level changes in *Banksia* woodland following plant pathogen invasion in the Southwest Australian Floristic Region. *Journal of Vegetation Science* **21**, 888–898.

Bowman DJMS (2003) Australian landscape burning: a continent and evolutionary perspective. In 'Fire in ecosystems of south-west Western Australia: impacts and management'. (Eds I Abbott, N Burrows) pp. 107–118. (Backhuys Publishers: Leiden, The Netherlands)

Bradstock RA, Bedward M, Scott J, Keith DA (1996) Simulation of the effect of spatial and temporal variation in fire regimes on the population viability of a *Banksia*species. *Conservation Biology* **10**, 776–784.

Brown MJ, Balmer J, Podger FD (2002) Vegetation change over 20 years at Bathurst Harbour, Tasmania. *Australian Journal of Botany* **50**, 499–510.

Burnham KP, Anderson DR (2002) 'Model selection and multimodel inference: a practical information-theoretic approach.' 2nd edn. (Springer: New York)

Burrows N (1985) Reducing the abundance of *Banksia grandis* in the jarrah forest by the use of controlled fire. *Australian Forestry* **48**, 63–70.

Burrows N (2008) Linking fire ecology and fire management in south-west Australian forest landscapes. *Forest Ecology and Management* **255**, 2394–2406.

Burrows N, Wardell-Johnson GW (2003) Fire and plant interactions in forested ecosystems of south-west Western Australia. In 'Fire in ecosystems of south-west Western Australia: impacts and management'. (Eds I Abbott, N Burrows) pp. 225–268. (Backhuys Publishers: Leiden, The Netherlands)

CALM (1999) 'Stirling Range National Park and Porongorup National Park management plan 1999–2009.' (Department of Conservation and Land Management: Perth)

Cheal D (2000) Seed regeneration in long-unburnt and recently-burnt heathland at Wyperfeld National Park. *Proceedings of the Royal Society of Victoria* **112**, 111–118.

Clarke V (2009) 'Monitoring the impacts of fire and *Phytophthora* within the shallow soil plant communities of the Mt Lindesay Threatened Ecological Community, Denmark WA.' Prepared for Significant Native Species and Ecological Communities – Resource Condition Monitoring Project. (Department of Environment and Conservation: Perth)

Cooke DE, Drenth A, Duncan JM, Wagels G, Brasier CM (2000) A molecular phylogeny of *Phytophthora* and related Oomycetes. *Fungal Genetics and Biology* **30**, 17–32.

Dawson P, Weste G, Ashton D (1985) Regeneration of vegetation in the Brisbane Ranges after fire and infestation by *Phytophthora cinnamomi*. *Australian Journal of Botany* **33**, 15–26.

Environment Australia (2001) 'Threat abatement plan for the dieback caused by the root-rot fungus *Phytophthora cinnamomi*.' (Environment Australia: Canberra)

Erwin DC (1983) Variability among and within species of *Phytophthora*. In '*Phytophthora*: its biology, taxonomy, ecology and pathology'. (Eds DC Erwin, S Barnicki-Garcia, PH Tsao) pp. 149–165. (American Phytopathological Society Press: St. Paul, MN)

Fisher JL, Loneragan WA, Dixon K, Delaney J, Veneklaas EJ (2009) Altered vegetation structure and composition linked to fire frequency and plant invasion in a biodiverse woodland. *Biological Conservation* **142**, 2270–2281.

Groves E, Hardy GEStJ, McComb J (2003) 'Native garden plants resistant to dieback (*Phytophthora cinnamomi*).' (Murdoch University: Murdoch, WA). Available at http://www.cpsm.murdoch.edu.au/ downloads/resources/B_resistantspecies.pdf.[Accessed December 2012]

Hill TCJ, Tippett JT, Shearer BL (1994) Invasion of Bassendean Dune *Banksia*woodland by *Phytophthora cinnamomi*. *Australian Journal of Botany* **42**, 725–738.

Hobbs RJ, Atkins L (1990) Fire-related dynamics of a *Banksia* woodland in south-western Western Australia. *Australian Journal of Botany* **38**, 97–110.

Hüberli D, Tommerup IC, Hardy GEStJ (2000) False-negative isolations or absence of lesions may cause mis-diagnosis of diseased plants infected with *Phytophthora cinnamomi*. *Australasian Plant Pathology* **29**, 164–169.

Hüberli D, Tommerup IC, Dobrowolski MP, Calver MC, Hardy GEStJ (2001) Phenotypic variation of a clonal lineage of two *Phytophthora cinnamomi*populations from Western Australia. *Mycological Research* **105**, 1053–1064.

Keith DA, McCaw WL, Whelan RJ (2002) Fire regimes in Australian heathlands and their effects on plants and animals. In 'Flammable Australia: the fire regimes and biodiversity of a continent'. (Eds RA Bradstock, JE Williams, AM Gill) pp. 199–237 (Cambridge University Press: Cambridge, UK)

Lamont BB, Groom PK, Richards MB, Witkowski ETF (1999) Recovery of *Banksia* and *Hakea* communities after fire in mediterranean Australia: the role of species identity and functional attributes. *Diversity & Distributions* **5**, 15–26.

Lamont BB, Enright NJ, Witkowski ETF, Groeneveld J (2007) Conservation biology of banksias: insights from natural history to simulation modelling. *Australian Journal of Botany* **55**, 280–292.

Maloney KO, Schmid M, Weller DE (2012) Applying additive modelling and gradient boosting to assess the effects of watershed and reach characteristics on riverine assemblages. *Methods in Ecology and Evolution* **3**, 116–128.

Marks GC, Kassaby FY, Fogg PC (1975) Variation in population levels of *Phytophthora cinnamomi* in *Eucalyptus* forest soils of eastern Victoria. *Australian Journal of Botany* **23**, 435–449.

Meadows IM, Zwart DC, Jeffers SN, Waldrop TA, Bridges WC (2011) Effects of fuel reduction treatments on incidence of *Phytophthora* species in soil of a southern Appalachian Mountain forest. *Plant Disease* **95**, 811–820.

Meney KA, Nielssen GM, Dixon KW (1994) Seed bank patterns in Restionaceae and Epacridaceae after wildfire in kwongan in southwestern Australia. *Journal of Vegetation Science* **5**, 5–12.

Moore NA (2005) Role of fire on *Phytophthora cinnamomi* in the Stirling Range National Park, Western Australia. BSc(Hons) Thesis, Murdoch University, Murdoch, WA.

Moritz MA, Odion DC (2005) Examining the strength and possible causes of the relationship between fire history and Sudden Oak Death. *Oecologia* **144**, 106–114.

Noble IR, Slatyer RO (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**, 5–21.

O'Gara E, Howard K, Wilson B, Hardy GEStJ (2005) Management of *Phytophthora cinnamomi* for biodiversity conservation in Australia. Part 2: national best practice guidelines. A report funded by the Commonwealth Government Department of the Environment and Heritage by the Centre for *Phytophthora* Science and Management, Murdoch University, Perth.

Podger FD (1999) A national overview of *Phytophthora cinnamomi* in Australia: Supplementary information to accompany the draft National Threat Abatement Plan. Environmental Australia, Commonwealth Government of Australia, Canberra.

Podger FD, Brown M (1989) Vegetation damage caused by *Phytophthora cinnamomi*on disturbed site in temperate rainforest in western Tasmania. *Australian Journal of Botany* **37**, 443–480.

Robinson RM, Bougher NL (2003) The response of fungi to fire in jarrah and karri forests of south-west Western Australia. In 'Fire in ecosystems of south-west Western Australia: impacts and management'. (Eds I Abbott, N Burrows) pp. 269–289. (Backhuys Publishers: Leiden, The Netherlands)

Sage LW, Blankendaal PA, Moylett A, Agar K (2004) The occurrence and impact of *Phytophthora cinnamomi* in the central western Avon Wheatbelt bioregion of Western Australia. *Journal of the Royal Society of Western Australia* **87**, 15–18.

Schoeneweiss DF (1975) Predisposition, stress, and plant disease. *Annual Review of Phytopathology* **13**, 193–211.

Schwartz MW, Hermann SM, Vogel CS (1995) The catastrophic loss of *Torreya taxifolia*: assessing environmental induction of disease hypotheses. *Ecological Applications* **5**, 501–516.

Shearer B, Tippett J (1989) 'Jarrah dieback: the dynamics and management of *Phytophthora cinnamomi* in the jarrah (*Eucalyptus marginata*) forest of south-western Australia.' (Department of Conservation and Land Management: Perth)

Shearer B, Crane CE, Cochrane A (2004) Quantification of the susceptibility of the native flora of the south-west Botanical Province, Western Australia, to *Phytophthora cinnamomi*. *Australian Journal of Botany* **52**, 435–443.

Shearer BL, Dillon MJ, Kinal J, Buehrig RM (2010) Temporal and spatial soil inoculum dynamics following *Phytophthora cinnamomi* invasion of *Banksia* woodland and *Eucalyptus marginata* forest biomes of south-western Australia. *Australasian Plant Pathology* **39**, 293–311.

Treseder KK, Mack MC, Cross A (2004) Relationships among fires, fungi, and soil dynamics in Alaskan boreal forests. *Ecological Applications* **14**, 1826–1838.

Watson P, Wardell-Johnson G (2004) Fire frequency and time-since-fire effects on the open-forest and woodland flora of Girraween National Park, south-east Queensland, Australia. *Austral Ecology* **29**, 225–236.

Weil RR (1993) 'Laboratory manual for introductory soils.' 6th edn. (Kendall/Hunt Publishing Company: Dubuque, IA)

Weste G (1974) *Phytophthora cinnamomi*: the cause of severe disease in certain native communities in Victoria. *Australian Journal of Botany* **22**, 1–8.

Wilson BA, Kuehs J, Valentine LE, Sonneman T, Wolfe KM (2014) Guidelines for ecological burning regimes in Mediterranean ecosystems: a case study in *Banksia*woodlands in Western Australia. *Pacific Conservation Biology* **20**, 57–74.

Yates CJ, Hopper SD, Brown A, Van Leeuwen S (2003) Impact of two wildfires on endemic granite outcrop vegetation in Western Australia. *Journal of Vegetation Science* **14**, 185–194.

Zentmyer GA (1983) The world of *Phytophthora*. In '*Phytophthora*: its biology, taxonomy, ecology and pathology'. (Eds DC Erwin, S Barnicki-Garcia, PH Tsao) pp. 145–149. (American Phytopathological Society Press: St. Paul, MN)

Table 1. Summary of fire history and soil characteristics for the eight study sites in Stirling Range National Park, Western Australia

Average fire interval was calculated from the latest two fires, and soil pH (s.d.) is the mean of four samples; n.a., s.d. not available because $n = 1$

Site and vegetation type	Latest fire interval (years)	Average fire interval (years)	Soil texture	Soil pH H_20	Soil water-holding capacity (%)
Bluff Knoll Road[A], *Eucalyptus marginata* mallee–heath	14	19	Silt loam	5.9 (0.3)	34
Bluff Knoll Road[B], *E. marginata* mallee–heath	5	9	Silt loam	5.7 (0.5)	31
Chester Pass Road East[A], low woodland	30+	30+	Sandy loam	5.8 (0.2)	27
Chester Pass Road East[B], low woodland	3	16	Sandy loam	5.8 (0.3)	27
Success Ridge Track[A], montane mallee–heath–thicket	14	14	Loamy sand	4.8 (0.2)	70
Success Ridge Track[B], montane mallee–heath–thicket	5	9	Silt loam	5.0 (0.3)	37
Chester Pass Road West, *E. marginata* mallee–heath–scrub heath	1	8	Loamy sand	5.9 (0.4)	27
Yungermere Peak, montane mallee heath–thicket	2	7	Sandy clay loam	5.3 (n.a.)	39

Table 2. Summary of predominantly Proteaceae, Fabaceae, Ericaceae, Myrtaceae and Xanthorrhoeaceae plant species in 100-m^2 vegetation-survey quadrats in Stirling Range National Park, Western Australia, in relation to fire strategy and susceptibility to *Phytophthora cinnamomi*

Total $n = 146$ species

Site	Species richness	Abundance of live plants	Susceptible species (%)	Dead or dying susceptible species (%)	Seeder species (%)
Bluff Knoll Road[A]	43	1407	44.2	9.66	64.8
Bluff Knoll Road[B]	44	1050	43.2	10.88	64.9
Chester Pass Road East[A]	56	1024	50.0	5.93	65.6
Chester Pass Road East[B]	45	744	47.8	29.78	65.0
Success Ridge Track[A]	39	1503	66.7	11.24	63.0
Success Ridge Track[B]	32	437	66.7	18.94	59.6
Chester Pass Road West	38	664	47.5	11.35	68.6
Yungermere Peak	32	501	63.6	31.59	59.6

Table 3. Summary of best-subset modelling statistics ranking all models from the one that explains the most variation in the percentage of dead and dying plant species susceptible to *Phytophthora cinnamomi* to the one that explains the least

Corrected Akaike's information criterion (AIC_c), number of variables in the model (k) and the Akaike weight (W_i) are shown along with adjusted r^2 and probability of resulting multiple regression for the models with the highest W_i

Model variable	AIC_c	k	ΔAIC_c	W_i	Adj. r^2	P
Latest fire interval + average fire interval	60.04	2	0.00	0.364	0.613	0.040
Latest fire interval	60.65	1	0.61	0.269	0.287	0.098
Average fire interval	62.06	1	2.02	0.133	0.150	0.168
Latest fire interval + average fire interval + soil pH	63.96	3	3.92	0.051		
Soil pH	64.27	1	4.23	0.044		
Soil water-holding capacity	64.56	1	4.51	0.038		
Latest fire interval + average fire interval + soil pH + soil water-holding capacity	65.30	4	5.26	0.026		
Latest fire interval + soil pH	65.32	2	5.28	0.026		
Latest fire interval + soil water-holding capacity	66.38	2	6.34	0.015		
Average fire interval + soil pH	67.04	2	7.00	0.011		
Latest fire interval + average fire interval + soil water-holding capacity	67.64	3	7.60	0.008		
Average fire interval + soil water-holding capacity	67.79	2	7.75	0.008		
Soil pH + soil water-holding capacity	69.11	2	9.07	0.004		
Latest fire interval + soil pH + soil water-holding capacity	71.30	3	11.26	0.001		
Average fire interval + soil pH + soil water-holding capacity	73.40	3	13.36	0.000		