The impact and control of *Phytophthora cinnamomi* in native and rehabilitated forest ecosystems in Western Australia

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Abstract [Review article]
Botanists have likened the impact of *Phytophthora cinnamomi* in Australian plant communities to that of the last ice age, which affected a large number of plant families, genera and species within these families. *Phytophthora cinnamomi* affects the floristics and structure of many unique plant communities. We discuss the impact of this pathogen and our current knowledge of its biology, genetics and pathology in Western Australian plant communities and the current management strategies used to limit its spread and impact. We hope that the knowledge obtained from some of our experiences in managing this pathogen in Western Australian natural ecosystems will be of some benefit to researchers studying *Phytophthora* diseases in *Quercus, Alnus* and *Castanea* in Europe and America.

Keywords: phosphite, *Phytophthora cinnamomi,* plant communities, pathogen control, Western Australia

1 Introduction

The introduced soil-borne plant pathogen *Phytophthora cinnamomi* is a major threat to Australia's native (natural or wildlands) vegetation and its dependent biota. It has been recognized by the Australian Government in schedule three of the Commonwealth's Endangered Species Protection Act 1999 as a "key threatening process" to Australia's biodiversity. Our discussion will examine the history, impact, biology, genetics, ecology, pathology and control of *P. cinnamomi* in native and rehabilitated forest in Western Australia. It will look at how management practices can be used to reduce the spread of *P. cinnamomi* into non-infested areas with and without phosphite applications. We will also discuss how the movement of infested soil and plant material can change the genetic structure of *P. cinnamomi* populations. Lastly, we will examine the beneficial and detrimental aspects of phosphite that need to be considered by managers when applying it to plant communities in the long-term. It is hoped that the approaches taken in Western Australia can provide stimulus for researchers who now face the task of implementing strategies to control and manage the severe *Phytophthora* disease outbreaks in *Alnus, Rhododendron* and *Viburnum* in Europe (BRASIER 2000, WERRES *et al.* 2001) and *Quercus* in America (HANSEN 2000).

2 History of *P. cinnamomi* in Western Australia

It is generally believed that *P. cinnamomi* is an exotic pathogen to Australia that was introduced with the first European settlers. The first records of root-rot disease in Western Australia are in 1921. However, it was not until 1964 that the disease was attributed to

P. cinnamomi by PODGER *et al.* (1965). During the 1930's, when the timber industry changed from using rail to road transport a massive increase in road construction led to large quantities of infested soils being moved. This resulted in the areas of dead and dying forest increasing to such an extent that there was considerable concern (SHEARER and TIPPETT 1989).

3 Impact

The greatest impact of *P. cinnamomi* tends to be in areas with a Mediterranean climate receiving a mean annual rainfall above 600 mm. These areas include the *Eucalyptus marginata* (jarrah) forest, banksia woodlands and heathlands in the south-west of Western Australia. The impact of *P. cinnamomi* ranges from a high impact or a "graveyard" response in the forest in which many of the susceptible plant species, including jarrah, die, to a low impact where only a very few understory plants die (SHEARER and TIPPETT 1989).

WILLS (1993) estimates that about 2000 out of approximately 9000 plant species from a diverse range of families are at risk in the south of Western Australia. The pathogen attacks a large number of species from a range of genera and families. In Western Australia, PODGER (1968) and SHEARER and DILLON (1995 and 1996) list 100 native plant species belonging to 23 families and 53 genera from which *P. cinnamomi* has been isolated after surface sterilisation of root material and plating onto selective agar. Overall, in Australia *P. cinnamomi* has been directly isolated from 56 families, 145 genera and 256 species (PODGER 1968, PODGER and NEWHOOK 1971, PODGER *et al.* 1990, SHEARER and DILLON 1995 and 1996). In addition, there are many records of dead and dying plants in known *P. cinnamomi* infested areas where no attempts have been made to recover *P. cinnamomi* or from which *P. cinnamomi* was not recovered (WILLS 1993).

Its indirect impact as a consequence of loss of vertebrate and invertebrate pollinators, and loss of canopy and litter cover, for example, has not been measured (NEWELL and WILSON 1993, WILSON *et al.* 1994, NEWELL 1997).

4 Spread of *Phytophthora cinnamomi*

P. cinnamomi is spread as zoospores and/or chlamydospores in soil and water mainly during warm (12–30 °C) moist conditions (SHEARER and TIPPETT 1989). It can spread presumably as mycelial growth through root to root contact and through active zoospore dispersal for short distances, or passively through downslope movement in subsurface or surface flow of water. However, human activities such as road building, timber harvesting, mining, wildflower harvesting, building of firebreaks, and bush walking are the main ways the pathogen is spread (COLQUHOUN and HARDY 2000). These activities have helped to disperse this pathogen widely throughout the landscape. Native and feral animals have also been implicated in its dispersal. How successfully it becomes established at new centers of infestation will depend on the amount of inoculum introduced. Its subsequent survival, establishment and spread varies according to the presence of host tissues and suitable environmental conditions.

5 Genetic diversity

P. cinnamomi is a heterothallic oomycete and requires two compatible mating types (A1 and A2) to be present for sexual reproduction to occur (ERWIN and RIBEIRO 1996). In Western Australia, *P. cinnamomi* is predominantly of the A2 mating type and the A1 type is rarely found. A hierarchical study of three disease fronts, followed by DNA extractions of 640 isolates and analysis with four microsatellite loci, grouped the isolates into three clonal

types, two of the A2 and one of the A1 mating type. Since no recombinants were found (DOBROWOLSKI *et al.* 1999), it was concluded that any variation was asexual in origin and the result of founder effects. Nevertheless A1 and A2 isolates from adjacent soil samples were found at one disease front and the occurrence of both mating types in close proximity to each other without evidence of sexual reproduction has also been recorded in other parts of Australia (OLD *et al.* 1984, 1988). However, under laboratory conditions the A1 and A2 isolates are sexually competent (DOBROWOLSKI *et al.* 1997, 1998). If sexual reproduction does occur in the field, it is possible that the progeny do not persist due to their lack of ecological fitness and competitive ability. However, Dobrowolski *et al.* (unpublished) found genetic variation within clonal types. This finding has significance for disease management as any new introduction of the pathogen has the potential to be genetically different with new capacities to cause disease (TOMMERUP *et al.* 2000).

6 Pathogenic diversity

Although there is no evidence of sexual reproduction of the pathogen in Western Australia, disease-associated phenotypes show considerable variation including isolate aggressiveness, physiology and inoculum production. No phenotypes have yet been associated with any particular genes and no genetic markers have been definitively associated with any phenotypic variation. This is the case even for isolates of *P. cinnamomi* from a narrow geographic range (DUDZINSKI *et al.* 1993, O'GARA *et al.* 1997, HÜBERLI *et al.* 2001a) and from one clonal lineage. Some isolate phenotypes are biotrophic while others are aggressive necrotrophs (HÜBERLI *et al.* 2000, HÜBERLI *et al.* 2001a, b). DUDZINSKI *et al.* (1993) found that the capacity to cause disease varied among isolates inoculated into *P. cinnamomi* resistant *Eucalyptus marginata.* Similar variation has now been observed in France (ROBIN and DESPREZ-LOUSTAU 1998) and South Africa (LINDE *et al.*1999). Environmental factors play major roles in influencing disease responses to host-pathogen isolate interactions even where *E. marginata* clones are used under standardized conditions. In a natural environment, where environmental extremes are more variable, interactions between a host and the pathogen will probably result in more variable disease responses than in controlled environments. Plant-water status and temperature are two factors that have been examined in some detail. High bark and phloem moisture levels favour lesion development by *P. cinnamomi* (TIPPETT and HILL 1983, SMITH and MARKS 1985, 1986, TIPPETT *et al.* 1987, BUNNY *et al.* 1995). Temperature can change the resistance of seedling and clonal *E. marginata* and the expression of pathogenesis of several *P. cinnamomi* isolates (GRANT and BYRT 1984, HÜBERLI *et al.* 1998, 2001a). HÜBERLI *et al.* (2002) used clonal *E. marginata,* selected as susceptible or resistant to *P. cinnamomi,* to show that inoculation method and temperature influence mortality and disease phenotypes. All clones were susceptible to *P. cinnamomi* at 25 and 30 °C when inoculated under the bark. The resistance status of a resistant clone was confirmed with underbark inoculations at 15 and 20 °C and zoospore inoculations at 15 and 30 °C. In contrast, another resistant clonal line and a susceptible clonal line were susceptible under most of the test conditions.

7 Management and control

It is unlikely that *P. cinnamomi* will be eradicated from natural ecosystems where the disease is already established. Therefore, stopping the spread of this pathogen into non-infested but susceptible areas poses a considerable challenge. For example, in Western Australia there are a number of strategic control procedures that are used by forest managers. These include: a) producing up-to-date maps and field demarcations of diseased areas, b) planning high-risk operations, such as timber harvesting and road building, so that it

can take place during dry periods to minimise the spread of *P. cinnamomi,* c) restricting vehicle and water movement from diseased to disease-free areas, d) washing vehicles and equipment prior to their movement from infested into non-infested areas, e) training all field personnel and planners in good hygiene management and f) increasing public awareness about the pathogen and its control (COLQUHOUN and HARDY 2000).

Breeding and selecting for resistance is an option for some key species such as jarrah, but then only to rehabilitate high impact or graveyard areas or mine sites that are infested by the pathogen. In the case of jarrah, clonal seed orchards of resistant jarrah are being established with the aim of collecting seed and sowing it into high impact areas in order to foster more resistant plants into these areas (COLQUHOUN and HARDY 2000). However, breeding and selecting the large range of susceptible species that are present in Western Australia is not feasible in terms of time and cost.

Chemical control

Recently in Australia, the inexpensive systemic fungicide phosphite (phosphonate) has been used as a foliar application to reduce the spread of *P. cinnamomi* in susceptible native plant communities (KOMEREK *et al.* 1997, SHEARER and FAIRMAN 1997a, ABERTON *et al.* 1999, ALI *et al.* 1999, HARDY 2000, HARDY *et al.* 2001). Phosphite, the anionic form of phosphonic acid $(HPO3)^{-2}$, controls many plant diseases caused by *Phytophthora,* even at concentrations *in planta* that only partially inhibit pathogen growth *in vitro* (GUEST and BOMPEIX 1990, GUEST and GRANT 1991, WILKINSON *et al.* 2001a). The mode of action of phosphite involves inducing strong and rapid defense responses in plants infected by *P. cinnamomi.* Our work has shown that phosphite sprayed as a foliar application can contain the spread of *P. cinnamomi* in plants for between six months to more than two years, depending on the method of application, the concentration, the season of application, the plant species, and various environmental factors (TYNAN *et al.* 2001). In contrast, injecting trees with phosphite has a longer-lasting effect on containing *P. cinnamomi.* For example, when naturally growing mature trees of *Banksia grandis* and jarrah were injected with 50, 100 or 200 gL^{-1} phosphite, lesion extension of *P. cinnamomi* in wound-inoculated plants was controlled for at least four years after treatment (SHEARER and FAIRMAN 1997b). Similarly, injecting of *Banksia attenuata* with 100 gL^{-1} phosphite protected trees growing along a disease-front for up to four years.

Phytotoxicity occurs in a range of indigenous species even at recommended rates of phosphite application (ABERTON *et al.* 1999, FAIRBANKS *et al.* 2000, HARDY *et al.* 2001, KOMOREK *et al.* 1997, PILBEAM *et al.* 2000, TYNAN *et al.* 2001). Phytotoxicity is related to growth habit and plant morphological characteristics. In addition, phytotoxicity may be expressed as reduced flowering, pollen viability and seed germination, as well as plant growth malformations (stunting, chlorosis, and leaf rosetting). It is also important to note that phosphite often does not kill the pathogen in the host tissue, but rather contains its rate of spread. In addition, *P. cinnamomi* is able to produce sporangia and release zoospores from contained lesions in plants if moisture and temperature conditions are suitable. Therefore, the chemical is able to contain the pathogen in the host but does not necessarily stop the spread of the pathogen to other plants WILKINSON *et al.* (2001b).

8 Conclusion

The control of *Phytophthora cinnamomi* in natural ecosystems or in the rehabilitation of infested mine sites does pose considerable challenges to land managers. Currently, the strategic use of phosphite together with sound quarantine and hygiene practices are the only

available methods of controlling and containing this devastating pathogen in natural and rehabilitated ecosystems. Since *P. cinnamomi* can survive at depth in the soil profile and in tolerant hosts, it is unlikely that it will be eliminated from natural ecosystems in the long term. However, it is essential that we continue to increase our understanding of the biology, ecology, pathology, genetics and control of this pathogen and how it interacts with its susceptible and tolerant hosts under different environmental conditions across ecosystems. This knowledge will assist us in containing the spread of this pathogen and in developing more effective control methods in the future.

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