MANAGING BIOLOGICAL INVASIONS: THE IMPACT OF EXOTIC DISEASES ON PLANT COMMUNITIES IN AUSTRALIA

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Abstract

Australia's unique flora has evolved in isolation from many of the world's major plant pathogens. As these pathogens have made their way into Australia, their impact on plant species and communities has been dramatic. Two plant diseases, *Phytophthora* root rot and myrtle rust, are used as examples to illustrate the impact diseases can have on individual species, on plant communities, and on the species that depend on those plants. Botanic gardens have a key role to play in protecting plants and enhancing conservation outcomes through surveillance, education, and ex situ conservation programs.

Key words: Biosecurity, invasive species, myrtle rust, *Phytophthora* root rot, plant disease, plant pathogens, quarantine.

Australia has a unique flora of well over 20,000 species, approximately 80% of which are endemic, that have evolved in isolation since the last Gondwanan link (Antarctica) was broken some 38 million years ago. During that period the environment has changed considerably as the continent has moved north, and most notably aridification has increased dramatically. As a consequence there has been substantial species radiation and opportunities for unique adaptations to evolve, but limited opportunities to develop resistance to invasive species, such as those causing plant disease. The flora has evolved in isolation from many of the world's most important plant pathogens and as a consequence when exposed to these pathogens have shown little or no resistance to these diseases. The consequences of these introduced invasive species have been profound and devastating.

Invasive Species

In many parts of the world plants and plant communities are under threat from a range of human-induced factors, including the impact of alien invasive species such as weeds, pests, and plant pathogens. The Global Strategy for Plant Conservation 2011–2020, objective 2 ("Plant diversity is urgently and effectively conserved"), target 10 states, "Effective management plans in place to prevent new biological invasions and to manage important areas for plant diversity that are invaded" (Convention on Biological Diversity, 2010).

Since European colonization of Australia in the latter half of the 1700s there have been repeated incursions of invasive species into the country with varying detrimental impact. Some of these invasive species (for example, foxes, rabbits, and cats) have had dramatic impacts on Australian biodiversity and are well documented. The consequence of these invasions has been a dramatic increase in the number of native species listed as threatened across Australia.

It is difficult to document the impact of invasive species in Australia. Certainly the impact on the Australian agricultural sector is huge, with weeds, pests, and pathogens causing massive reductions in productivity that are estimated at many hundreds of million dollars per annum. It is, however, much more difficult to gauge the impact of invasive species on biodiversity over the last 250 years given the nature and complexity of the impact of each individual invasive species.

Plant pathogenic organisms are often less recognized as invasive species impacting native plant communities, mostly because the impact is often mediated by environmental conditions and is often insidious, not being noticed or obvious until the disease impact is substantial. This has been the case in Australia where diseases in native ecosystems have been undetected, neglected, or not observed until far too late. Control of plant pathogens in these circumstances is extremely difficult; conventional techniques used for the control of plant diseases in agricultural systems are usually not applicable to or unacceptable for use in natural ecosystems. If they could be applied, there is a reluctance to commit the resources necessary because there is no obvious economic return on that investment.

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In Australia there have been a number of incursions of invasive plant pathogens that have had a significant and substantial negative impact on plant diversity. To highlight the impact, the responses to these incursions and the options for control of two plant diseases, *Phytophthora* root rot and myrtle rust, are explored in detail below.

Phytophthora Root Rot

Phytophthora root rot is a disease of trees, shrubs, and herbaceous plants that is caused by a number of species of *Phytophthora*, an oomycete genus (Erwin & Ribeiro, 1996; Burgess et al., 2017b). The most important species in Australia, *P. cinnamomi*, is an aggressive pathogen of trees and shrubs that has for a long time been recognized as a problem affecting some plantation crops, especially avocados, and ornamental species, including many Australian native species, and as causing significant widespread losses in native vegetation in those parts of Australia where the average annual rainfall is greater than 600 mm per annum (Pratt & Heather, 1973; Podger & Brown, 1989; Shearer & Tippett, 1989; Irwin et al., 1995; Burgess et al., 2017b). Worldwide it is one of the most important plant pathogens and has been listed by the Global Invasive Species Database (<http://www.iucngisd.org/gisd/>) as one of the 100 worst invasive alien species (Burgess et al., 2017a).

Phytophthora cinnamomi was first recorded in Australia from pineapple in 1929 and first recovered from native vegetation in 1948 (Gerrettson-Cornell, 1986; Weste, 1994; Irwin et al., 1995). For many decades there was contention about the origin of this pathogen, with two views: firstly, that the pathogen was introduced and, secondly, that it was indigenous to Australia or at least some parts of Australia (Pratt & Heather, 1973; Weste, 1994). This latter viewpoint was based on recovery of the pathogen from remote sites, where it was argued it was unlikely that the pathogen had been introduced, and the relative resistance of plant species in eastern Australia to the disease (Cho, 1983; McCredie et al., 1985). This implied that these species had evolved resistance over long periods of time, clearly prior to European occupancy. However, it has now clearly been shown using a range of population and molecular analyses that there is limited genetic variation and a skewed population ratio that is only consistent with the pathogen being introduced into the country from elsewhere (Dudzinski et al., 1993). Recent research has documented the existence of a number of native species of *Phytophthora* in native vegetation in Australia (Scott et al., 2009; Burgess et al., 2017b). Many of these species are cryptic and difficult to differentiate from better known species of *Phytophthora* but also appear to be less important plant pathogens, causing limited disease issues (Scott et al., 2009; Burgess et al., 2017b).

Global analyses of *Phytophthora cinnamomi* have shown that its center of origin is in highland regions of Southeast Asia (Arentz & Simpson, 1986; Martin & Coffey, 2012), and that it is likely to have been introduced into Australia through the import of plant material for horticulture in the early days of the fledgling colony from the then Dutch East Indies. Regardless of this, the pathogen has been widely spread since then through human-mediated means and as a consequence is now found in most states of Australia where the environmental conditions will allow it to survive (Burgess et al., 2017b).

Phytophthora species are predominantly soil-borne pathogens whose active inoculum—zoospores—swim through soil towards the roots of plants and need high moisture levels to move to and infect a root system. Once roots are infected, mycelium grows through the root, destroying cells and preventing it from extracting moisture or nutrients from the soil (Erwin & Ribeiro, 1996). The pathogen can survive in soil for extended periods by specialized survival structures called chlamydospores; as a result, once soil is infested it will remain that way for considerable periods of time (Weste & Vithanage, 1979).

Phytophthora species can be moved to and spread to new sites via infected plant material; infested soil, which may adhere to equipment, boots, and tires; and through drainage water. As a consequence, it is easy to introduce and spread the pathogen through the native vegetation. Infested soil adhering to tires and machinery can easily be spread considerable distances, and activities such as road construction, logging, and mining have dispersed the pathogen over vast tracts of land in many regions of Australia. A critical component of the control of the spread of this pathogen has been communication programs to promote hygiene practices to ensure that workers, bushwalkers, and the like do not have soil adhering to their boots and equipment before entering a national park, avoid muddy areas, stay on paths, and follow directions regarding this pathogen.

The impact of the disease can be quite variable depending on the susceptibility of the vegetation, environmental conditions, and soil type. For example, in Western Australia jarrah dieback is a disease syndrome caused by this pathogen where large vegetation communities dominated by jarrah (*Eucalyptus marginata* Sm.) can be devastated (Shearer & Tippett, 1989; McDougall et al., 2002). The impact that such large-scale devastation can have on biodiversity can be immense, with not only plants being affected but also the fauna that depends on them (Wilson et al., 1994). Conversely the impact of *Phytophthora cinnamomi* on native vegetation in eastern Australia has for a long time been quite controversial and somewhat confused. It was believed for many years that this pathogen was not important in eastern Australia, and certainly it does not appear to cause the dramatic widespread vegetation losses that are observed in southern and western Australia (Weste, 1997). However, recent research has shown that *P. cinnamomi* plays an important role in dieback of vegetation found in a number of national parks in eastern Australia. In parks in New South Wales, such as Barrington Tops, Werrikimbe, Royal, and Sydney Harbour National Parks, certain vegetation communities have been badly affected by this pathogen (McDougall et al., 2003; Puno et al., 2015; Scarlett et al., 2015). The effect of the pathogen on the New South Wales bushland is different from that observed in Western Australia primarily because in New South Wales the majority of eucalypts appear to be tolerant of the pathogen, so with the notable exception of *Angophora costata* (Gaertn.) Hochr. ex Britton, it is not affecting canopy species (McDougall & Summerell, 2003). Rather, *P. cinnamomi* is causing dieback in understory species, especially the grass trees, *Xanthorrhoea* Sm., and also dominant understory species such as *Oxylobium* Andrews and *Tasmannia* R. Br. ex DC., and a range of rare and threatened species (McDougall et al., 2003).

Symptoms of the disease include yellowing of foliage, wilting, and dieback; infected plants can die very rapidly if stressed by drought (Erwin & Ribeiro, 1996). Diagnosis can be difficult, since the symptoms can be confused with nutrient stress, water stress, and other diseases and pest problems. In very susceptible species the impact is rapid and severe. These species will have extensive root death, and the pathogen can extend into the crown; in these circumstances the plant will rapidly die, and in areas where such susceptible species dominate (e.g., Stirling Ranges National Park) there will be widespread ecosystem decline and death. In less susceptible species the impact is more subtle and can often result in a slow decline over some years. Regardless, the effects of the disease can still be quite profound and the ecosystem impact no less important.

The impact of the disease on ecosystems is complex and varies significantly depending on the ecosystem. There is generally a decline in both the number of species and the numbers of individuals of species; there is often a reduction in both canopy cover and in the diversity of understory species (Kennedy & Weste, 1986). Quite often there will be a replacement of susceptible species by resistant species such as rushes and sedges (Wills & Keighery, 1994; Duncan & Keane, 1996). Consequent to all of this, there is often a negative impact on animals dependent on affected plant species so that their numbers are reduced, and there is a suppression on breeding success and offspring production (Wilson et al., 1994).

Control of the disease in natural ecosystems depends on preventing introduction and spread of the pathogen. There are no fungicides that are registered for use on native vegetation, although there have been some promising developments with the use of potassium phosphonate (Hardy et al., 2001; Scott et al., 2015). Research is underway to better understand a number of aspects of the pathogen, and it is hoped that this may offer some prospects for control in the future. There has been a concerted effort to ensure that plant species, particularly threatened taxa, adversely affected by *Phytophthora* root rot incursions are adequately conserved in seed banks. The Australian government has provided funding to the Australian Seed Bank Partnership to prioritize collection and storage of seed of these species.

THE IMPACT OF *PHYTOPHTHORA* ROOT ROT ON THE WOLLEMI PINE

The Wollemi pine (*Wollemia nobilis* W. G. Jones, K. D. Hill & J. M. Allen) was first discovered in 1994 (Jones et al., 1995); its discovery was much publicized, and the species quickly became iconic. After its discovery a great deal of research was completed on all aspects of its biology, including its susceptibility to diseases. It was shown to be highly susceptible to *Phytophthora* root rot (Bullock et al., 2000). This, combined with initial research showing that the population was close to clonal with no measurable genetic variation (Peakall et al., 2003), raised concerns about the potential for *Phytophthora* root rot to adversely impact the population. Recent studies using next generation sequencing techniques of chloroplast DNA have determined that some genetic variability exists (Greenfield et al., 2016), but whether this will impact susceptibility or resistance to *Phytophthora* species is as yet unknown. The location of the Wollemi pine was kept a secret and legislation brought in to prevent entry to the site. Following the development of techniques for its propagation the Wollemi pine was successfully commercialized in 2004, introduced into the nursery trade, and planted in botanic gardens all over the world (Offord et al., 1999).

Also in 2004, *Phytophthora cinnamomi* was recovered from the wild population site, and two plants in that population were observed with symptoms of the disease; at a later date the related *Phytophthora* species, *P. multivora*, was also detected at the Wollemi pine site and shown to be potentially pathogenic (Puno et al., 2015). The most likely scenario for the introduction of the pathogen into the site was via infested soil adhering to illegal and unauthorized visitors to the site. Scientists visiting the site had recognized the importance of site hygiene and elaborate precautions were taken to ensure that they did not transport the pathogen to the site. It was recognized that this introduction was potentially catastrophic to the Wollemi pine and a number of steps were taken to minimize the impact. Seed banking and commercial horticultural production had ensured that the species was unlikely to become extinct per se, and a complete ex situ representation of the population was maintained at the Australian Botanic Garden at Mount Annan in Western Sydney, Australia. Attempts were made to eradicate *Phytophthora* species from the soil at the site using applications of fungicides, and while this resulted in a reduction in the extent of the infestation, the pathogen was still able to be recovered from the site. Current pathogen research is focused on techniques such as "bark painting" with potassium phosphonate as a noninvasive technique to protect trees from the impact of the disease (Liew, pers. comm.).

It is, however, recognized that there is a possibility of the disease winning, and recent efforts have focused on the establishment of a translocated population in a safer location. An experimental translocation has been attempted with promising results (Zimmer et al., 2016; Rigg et al., 2017), and the search is now on to find an appropriate location to house a translocated population.

Myrtle Rust

Myrtle rust (*Puccinia psidii*) is a plant pathogenic fungus that was accidently introduced into the central coast region of New South Wales, Australia, in 2010 and has since spread along the east coast, from Tasmania in the south to the Northern Territory in the north of Australia (Carnegie & Cooper, 2011). The disease that this pathogen causes is known by different names. Originally known as guava rust in South America, the disease jumped to *Eucalyptus* L'Hér when this tree was planted for logging purposes and was then better known as eucalyptus rust. In Australia the term myrtle rust is used, reflecting that the host range is far greater than just *Eucalyptus* species (Carnegie et al., 2010).

The taxonomic status of *Puccinia psidii* has been controversial and this has led to confusion in the management of incursions. The dual system of naming for fungi that existed prior to 2011 meant that this fungus was known as a *Puccinia* species and an *Uredo* species. The isolate of the rust that was introduced into Australia was initially identified as *U. ranglii* (Carnegie et al., 2010), and this may have implicitly dampened concerns about the potential impact and consequent efforts to eradicate it before the pathogen spread large distances. To date, only one genetic strain of *P. psidii* has found its way to Australia, and this strain appears to be less aggressive than some strains documented in other parts of the world (Brazil, South Africa, and Florida). A natural response would be to assume that once a pathogen has entered a country that border controls for that pathogen can be relaxed; but this is not the case, as the potential for more aggressive strains to be introduced and cause more havoc is still real.

Myrtle rust attacks plants in the Myrtaceae family, in natural vegetation, plantations, and nurseries. Myrtle rust is a potentially devastating disease for Australian Myrtaceae species; as this family includes keystone genera such as *Eucalyptus*, *Melaleuca* L., *Syzygium* P. Browne ex Gaertn., and a range of rainforest species, the potential impact on Australian ecosystems is enormous. Greenhouse and field trials have so far found 350 species to be susceptible to the pathogen, including a variety of ecologically significant and commercially important species (Carnegie & Lidbetter, 2012; Giblin & Carnegie, 2014). However this is only a relatively small proportion of the total number of Myrtaceae species in Australia (1646 taxa), and there is a significant lack of information on the response of many members of the Myrtaceae to the pathogen. Some species, such as the rainforest species *Rhodamnia rubescens* (Benth.) Miq. and *Rhodomyrtus psidioides* (G. Don) Benth., are already on an extinction trajectory because of the impact of the disease (Carnegie et al., 2016).

Subsequent to its introduction the pathogen spread rapidly through the full extent of eastern Australia, and thence to Tasmania and into northern Australia. Outbreaks of the disease have occurred in Indonesia (McTaggart et al., 2016) and recently in Singapore. Western Australia and South Australia are still disease free, but it is likely only a matter of time before the disease is recorded in these states. The extent of the area infested and the lack of a methodology for the early detection of the pathogen, together with no easy method for systematic surveillance of existing outbreaks, make it extremely difficult to monitor changes in distribution and the impact the disease is having.

The symptoms of the disease are classically bright yellow pustules on the leaves, flowers, and developing fruits, usually accompanied by necrotic lesions, especially on the leaves. This is accompanied by defoliation and dieback, and reproductive processes are halted so that no seeds or fruits are produced. Infection on young susceptible plants will often result in death of the plant. Even on less susceptible species, repeated infections over a number of successive years are likely to have a very deleterious impact on the plant so that it slowly declines and eventually dies.

The control options for myrtle rust in Australia are limited. Unlike *Phytophthora* root rot, the myrtle rust pathogen is easily dispersed via airborne spores that are produced in massive numbers. These spores can be dispersed rapidly over large distances by wind and storm events, so quarantine options are to a certain extent ineffective. However, the authorities in Western Australia have put in place stringent quarantine procedures to prevent the importation of Myrtaceae plants, limiting the opportunities for infected material to be brought into the state. There are fungicides that are effective in controlling myrtle rust, both as a preventative option and an eradicant option. The practicalities of using such fungicides at a continental scale are, of course, enormous, and as such this option is only useful in instances of protecting individual plants or small populations of plants of high importance, such as rare and threatened species where it might be practical to do so.

Given that there are limited options for control of the disease and prevention of its spread, a focus at present has been to ensure representative populations of susceptible species are preserved in seed banks and in managed ex situ collections. The collection of seed of susceptible species has been a significant focus of the members of the Australian Seed Bank Partnership. Unfortunately, many of the adversely affected rainforest species in the Myrtaceae are difficult to seed bank; research is underway to develop techniques to improve the success of seed banking and to develop other techniques for germplasm preservation. There are some indications that within a population of a species there can be substantial variability in the level of susceptibility and resistance to the disease, and this offers hope that plant species will adapt to the presence of the pathogen and the selection pressures will result in populations with higher levels of resistance to the disease.

The Role of Botanic Gardens

Botanic gardens are uniquely placed to make an important contribution in the fight against the impact of invasive diseases on plant species and communities. Expertise in ex situ preservation, botanical identification, and practical horticultural skills in plant disease management are the key attributes needed to manage these diseases. Ensuring that well-sourced ex situ collections, both as seed and as living plants, are collected, maintained, and available for research is a critical component of ensuring that species of plants affected by these pathogens do not become extinct.

The other component for which botanic gardens are well placed is providing educational programs and training on how to recognize, detect, and manage plant disease incursions. With the Australian Network for Plant Conservation a number of training and awareness-raising days have been run for reserve management staff, bush regenerators, and botanic garden personnel on both *Phytophthora* root rot and myrtle rust (Makinson, 2014). The Botanic Gardens Conservation International's plant sentinel network program (International Plant Sentinel Network) is a great initiative to detect new incursions, map existing incursions, and generally raise awareness about the importance of plant diseases in biodiversity conservation; it should be a priority to be formally implemented in the botanic garden network in Australia and New Zealand. Legislation relating to the management of the threats caused by diseases like *Phytophthora* root rot and myrtle rust at both a federal and state level will continue to play an important role in minimizing the impact on native vegetation but can be fragmented due to jurisdictional responsibilities, resources, and priorities. Recent reviews of national biosecurity frameworks have pointed to a need to more effectively highlight the importance of environmental biosecurity and develop a framework consistent with that for agricultural biosecurity. It is argued that this will provide a more coherent response to management of incursion of invasive species that impact the environment (Craik et al., 2016).

Conclusions

The impacts of invasive pathogens on plant species and communities are likely to continue to increase in occurrence and frequency due to a range of factors. Some of the key factors are globalization and the extent of international trade and transport, growing plant species in exotic locations with the subsequent exposure to locally adapted pathogens, and the potential impacts of a changing climate. In recent years there have been many examples of such disease outbreaks, and there are a number of potential pathogens known to occur in exotic locations that have the potential to invade unprotected ecosystems. In Australia the prospects of diseases like sudden oak death (*Phytophthora ramorum*, currently in the west coast of the United States) and kauri dieback (*Phytophthora agathidicida*, currently in New Zealand) being introduced are quite likely, and it is difficult to predict the outcomes from such invasions.

Botanic gardens have a key role in the detection and surveillance of disease incursions, in determining susceptibility of host plant species, in education programs, and in ex-situ conservation. This also needs to be reflected by an enhanced awareness of these issues in policy frameworks like the Global Strategy for Plant Conservation.

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