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PLANT PATHOGEN IMPACTS - REVIEW

Phytophthora agathidicida: research progress, cultural perspectives and knowledge gaps in the control and management of kauri dieback in New Zealand

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Kauri (*Agathis australis*), which is one of the world's largest and longest-living conifer species, is under threat from a root and collar dieback disease caused by the oomycete pathogen *Phytophthora agathidicida*. The noted incidence of kauri dieback has increased in the past decade, and even trees >1000 years old are not immune. This disease has profound effects on both forest ecosystems and human society, particularly indigenous Māori, for whom kauri is a *taonga* or treasure of immense significance. This review brings together existing scientific knowledge about the pathogen and the devastating disease it causes, as well as highlighting important knowledge gaps and potential approaches for disease management. The life cycle of *P. agathidicida* is similar to those of other soilborne *Phytophthora* pathogens, with roles for vegetative hyphae, zoospores and oospores in the disease. However, there is comparatively little known about many aspects of the biology of *P. agathidicida*, such as its host range and disease latency, or about the impact on the disease of abiotic and biotic factors such as soil health and co-occurring *Phytophthora* species. This review discusses current and emerging tools and strategies for surveillance, diagnostics and management, including a consideration of genomic resources, and the role these play in understanding the pathogen and how it causes this deadly disease. Key aspects of indigenous Māori knowledge, which include rich ecological and historical knowledge of kauri forests and a holistic approach to forest health, are highlighted.

Keywords: *Agathis australis*, disease impact, forest health, kauri dieback, oomycete, traditional indigenous knowledge

Kauri – an Ancient Tree Species Under Threat

Kauri, or *Agathis australis*, is one of the earliest diverging lineages of *Agathis*, a genus of about 17 extant gymnosperm conifer species within the Araucariaceae (Wilf *et al.*, 2014). Kauri is also one of the largest and longest-living tree species, with trunk diameters up to 4.4 m and an average lifespan of 600 years, although the oldest trees reported are well in excess of 1500 years in age (Ahmed & Ogden, 1987; Steward & Beveridge, 2010). Kauri are endemic to New Zealand (NZ), where they have immense cultural significance (Black *et al.*, 2018) and are highly revered. Before European settlement, kauri forest covered >1 million ha, but after more than 200 years of destruction by logging and burning, <1% of the original old-growth forest remains (Steward & Beveridge, 2010). In addition to this, about 60 000 ha of kauri forest that regenerated after the main period of forest exploitation also exists (Halkett, 1983) and much of the existing kauri forest is now protected (Steward & Beveridge, 2010).

The survival of remnant kauri is now threatened by kauri dieback: a lethal root rot disease caused by the oomycete pathogen *Phytophthora agathidicida* (Weir *et al.*, 2015), for which there is no known cure. Kauri dieback was first reported in 1972 on Aotea Great

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Barrier Island in NZ (Gadgil, 1974), but was not recognized on the NZ mainland until 2006 (Beever *et al.*, 2009). The pathogen was subsequently confirmed in many locations within the natural range of kauri (Waipara *et al.*, 2013). Surveillance has revealed the widespread nature of the epidemic (Fig. 1) and kauri are now identified as a threatened species (De Lange *et al.*, 2018).

The symptoms of kauri dieback are excessive resin production (i.e. gummosis, hyper-resinosis; Seyfullah *et al.*, 2018) at the collar and lower trunk region of the tree, and crown decline, usually leading to tree mortality (Fig. 2a,b). These symptoms are only observed during the chronic phase of the disease, and are due to pathogen-mediated dysfunction of the outer vascular tissue (Fig. 2c). Infections of fine roots are likely to occur several years before the onset of aboveground disease symptoms (latency period). The time from symptom development to death is highly variable but it typically takes 1–10 years, with smaller trees generally declining more rapidly than larger trees. The disease trajectory is also strongly influenced by environmental conditions, host predisposition and abundance of the pathogen.

The need for effective management strategies to limit the spread of the pathogen has resulted in a cross-cultural response in NZ, with science, citizen science and indigenous Māori knowledge (*mātauranga Māori*), being used to combat kauri dieback. *Mātauranga Māori* embeds values and culture in a holistic ecological perspective. There is a central role for ecosystem factors such as healthy soils, associated micro- and macroflora, and seasonal observations, in the *mātauranga Māori* approach to sustainable management and forest health (Chetham & Shortland, 2013; Hikuroa, 2017; Lambert *et al.*, 2018). *Mātauranga Māori* thus encompasses a broad systems perspective to forest health and has potential to identify critical factors that could reduce the impacts of kauri dieback and increase health and resilience of forest ecosystems.

Phytophthora agathidicida

Taxonomy and classification

Phytophthora species are Oomycota (Cavalier-Smith, 2018), with many renowned for their impact as primary

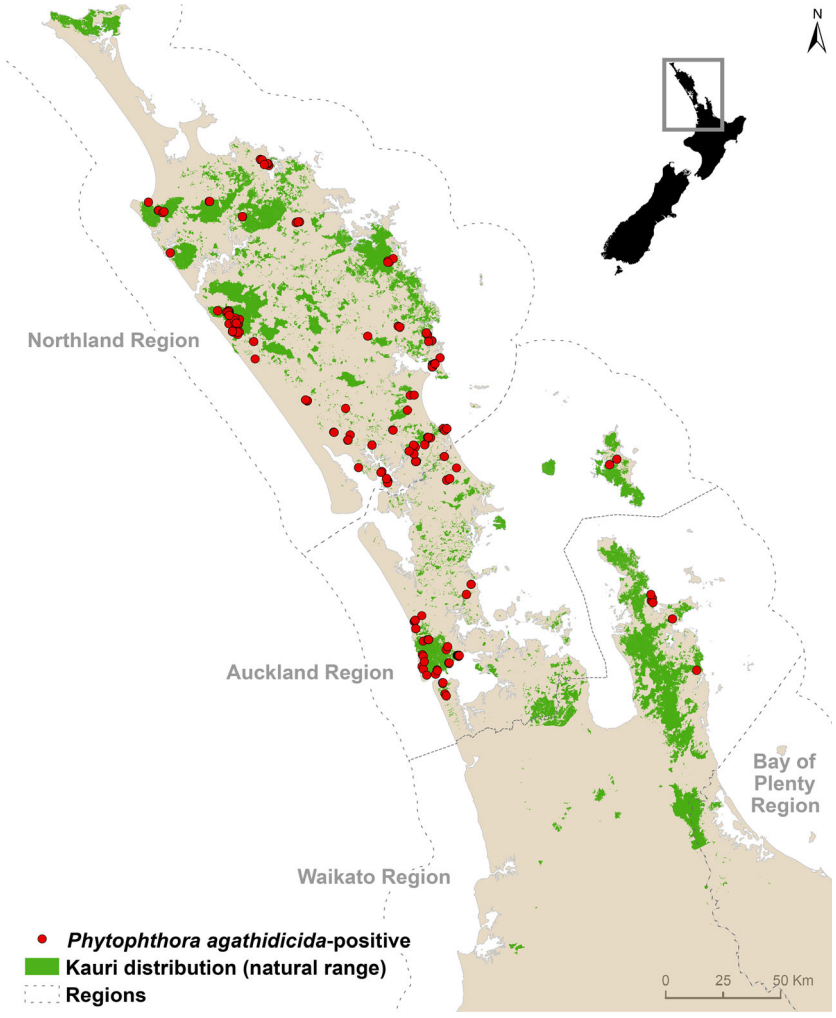

Figure 1 Distribution of *Phytophthora agathidicida* across the natural range of kauri. Red dots indicate where the presence of the *P. agathidicida* pathogen has been confirmed within the native range of kauri in the northern part of New Zealand. The distribution map (Crown copyright) was created by Biosecurity New Zealand (Ministry for Primary Industries; MPI) on 14 August 2019 based on data obtained from various sources available at that time. While all reasonable measures have been taken to ensure accuracy, MPI gives no warranty in relation to the accuracy, completeness, reliability or fitness for purpose of the map and accepts no liability whatsoever in relation to any loss, damage or other costs relating to any person's use of the map. The small New Zealand map is from Wikimedia (Creative Commons CC0 1.0 Universal Public Domain).

Figure 2 Kauri and kauri dieback disease. Two kauri trees standing side-by-side (a). The tree on the left has succumbed to kauri dieback disease, while the tree on the right is healthy or symptomless. The symptoms of kauri dieback disease, which are only observed during the chronic phase of disease, are crown decline (a, left), as well as resin production ('gummosis') at the collar and lower trunk region (b). Symptoms are caused by the dysfunction of the outer vascular tissue, where a lens of discoloration can often be observed (c; white arrow). A diverse epiphyte community growing in the crown of *Tāne Mahuta* (d). Typical active trunk lesion in an untreated tree (e); typical trunk lesion following phosphite treatment, with lesion drying and bark peeling (f). Image credits: (a, b, d, e, f) Dr I. J. Horner (NZ Institute for Plant and Food Research); (c) Dr R. E. Beever (Manaaki Whenua – Landcare Research).

plant pathogens (Erwin & Ribeiro, 1996). Perhaps the most notable is *Phytophthora infestans*, the causal agent of potato blight disease, which was responsible for the 1845 Irish potato famine.

The causal agent of kauri dieback disease was first identified as *Phytophthora heveae* (Gadgil, 1974). However, when the pathogen was isolated again in 2006, the advent of a DNA-based phylogeny for the genus (Cooke *et al.*, 2000) enabled identification of a mismatch between DNA sequences that led to a reassessment of the pathogen's morphology, identifying it as a new species temporarily designated as *Phytophthora* 'taxon Agathis' (PTA) (Beever *et al.*, 2009). PTA was formally described as a new species, *P. agathidicida*, in 2015 based on multigene phylogenies and morphological characters, with its species name meaning '*Agathis* killer' (Weir *et al.*, 2015).

Phytophthora agathidicida belongs to clade 5, a subgroup of *Phytophthora*. Clade 5 has only four described species, fewer than most other clades, although this probably represents a lack of sampling rather than a true paucity of species richness. Most other clade 5 *Phytophthora* species have been isolated from Asia so far (e.g. Japan, Taiwan, China, Malaysia; Weir *et al.*, 2015) but more extensive global surveys of *Phytophthora* species will undoubtedly add to knowledge of clade 5 species and their distributions. *Phytophthora agathidicida* is probably exotic to NZ, but its origins, and how long it has been co-evolving with kauri forest, are unknown (Weir *et al.*, 2015).

Phytophthora agathidicida life cycle

The life cycle of *P. agathidicida* involves the sexual production of oospores, asexual production of motile zoospores produced within sporangia, and vegetative hyphal growth in roots (Fig. 3; Weir *et al.*, 2015; Bellgard *et al.*, 2016).

Phytophthora agathidicida oospores are readily produced within artificially and naturally infected kauri roots (Bellgard *et al.*, 2016) and play an important role in the long-term survival and spread of *P. agathidicida* (Fig. 4a,b). The oospore wall index, which relates

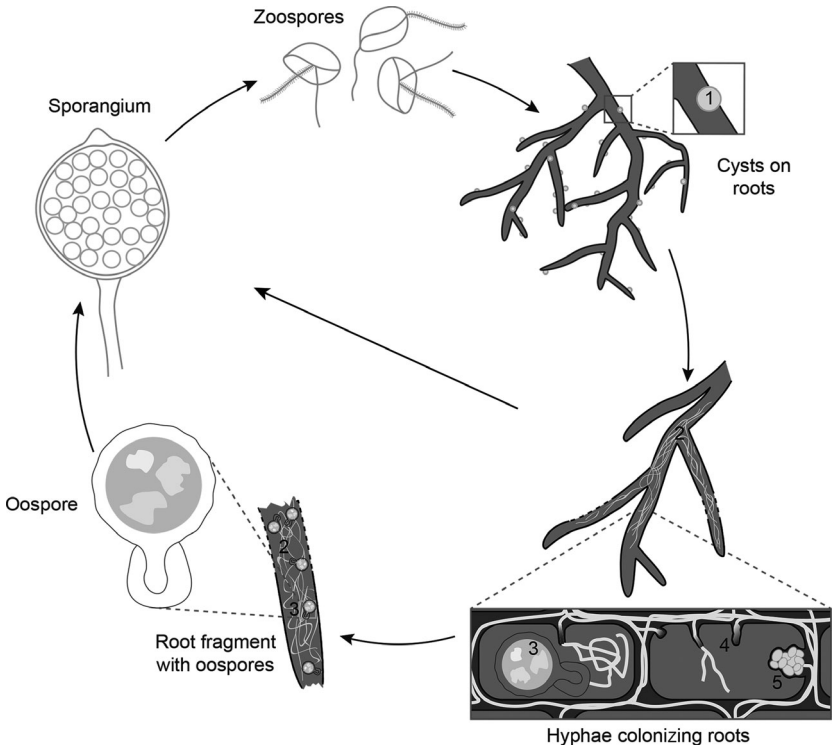

Figure 3 *Phytophthora agathidicida* life cycle. Zoospores are unicellular, short-lived and motile, and move through wet soil along chemotactic gradients towards kauri roots, where they encyst and form a penetration structure, allowing infection of the fine root epidermis and colonization of the cortex. Lignituber formation, as a result of hyphae attempting to enter plant cells, and stromata-like structures, are often observed. Thick-walled and durable oospores are produced via sexual reproduction and germinate to produce sporangia. Sporangia can also be produced directly on colonized roots. Sporangia then release zoospores to complete the life cycle. 1, cyst; 2, hypha; 3, oospore; 4, lignituber; 5, stromata-like structures. Figure not drawn to scale.

oospore wall volume to total oospore volume (Dick, 1990), has been associated with environmental tolerance in some *Phytophthora* species (Scott *et al.*, 2009). *Phytophthora agathidicida* has an above-average oospore wall index of 0.64, compared to an average of 0.41 across the genus (P. Scott, Plant and Food Research NZ, personal communication), suggesting that the oospores may persist within infected root material, like those of other *Phytophthora* species (Fichtner *et al.*, 2011). While not reflective of natural survival, independent analysis of soils stored at 10 °C for 10 years (S. Bellgard, Manaaki Whenua-Landcare Research NZ, personal communication), and 4–6 years (Horner & Hough, 2015), indicate that the pathogen has the potential to survive for extended periods. Kauri roots containing oospores of *P. agathidicida* have been shown to transfer the infection to adjacent clean kauri roots, contributing to both spread and long-term survival of the pathogen (Bellgard *et al.*, 2013). How long *P. agathidicida* can exist in the environment independent of host root material, however, is unknown.

Oospores of *P. agathidicida* germinate to produce modified mycelial stalks bearing sporangia (Fig. 4c,d) that typically contain around 20–30 zoospores (P. Scott, Plant and Food Research NZ, personal communication). Sporangia and zoospores form under ideal conditions within free-standing water (Video S1), then the motile zoospores need to encounter susceptible host material to complete the life cycle. Although the duration of *P. agathidicida* zoospore survival within forest soil is untested, zoospores remained motile for up to 17 h under laboratory conditions (Lawrence *et al.*, 2017).

Initial contact with the host plant is made by the motile zoospores, which actively swim in water and waterlogged soil. They sense chemical signals in the environment (chemotaxis; Tyler, 2002) and move towards favourable conditions. Zoospores of many *Phytophthora* species studied to date are nonspecifically attracted to commonly occurring compounds such as amino acids and sugars (Judelson & Blanco, 2005). However, some species of *Phytophthora*, and especially those with restricted host ranges, exhibit high specificity in their attraction towards host plants. For example, zoospores from *P. sojae* are chemotactically attracted to specific isoflavones exuded by the roots of its host plant (soybean), even at nanomolar concentrations (Tyler, 2007). Unpublished data (M. Gerth, Victoria University of Wellington NZ, personal communication) suggest that kauri root exudates released from the tips of fine roots specifically attract *P. agathidicida* zoospores, but the signals mediating this attraction are currently unknown.

At the root surface, zoospores encyst and produce hyphae that penetrate and colonize the root (Bellgard *et al.*, 2016). *Phytophthora agathidicida* hyphae colonize host vascular tissue with a delay between infection and visible lesion development (Horner & Hough, 2014; Herewini *et al.*, 2018). An early symptomless stage of infection has similarly been identified across a range of *Phytophthora* species and host plants and may be associated with the pathogen suppressing the host defence response (Denman *et al.*, 2009).

Phytophthora agathidicida stromata-like hyphal aggregations, and intracellular hyphae encased by lignin (lignitubers), have been observed in kauri roots (Fig. 3;

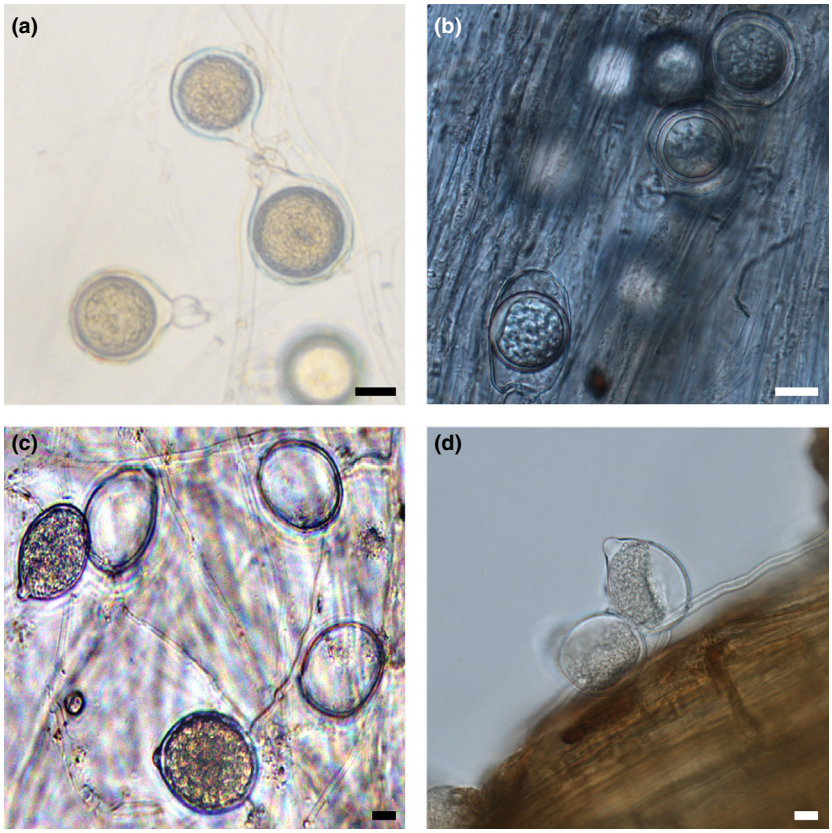

Figure 4 *Phytophthora agathidicida* oospores and sporangia. Oogonia with amphigynous, globose antheridia formed in culture (a), and in the cortical cells of kauri seedlings deliberately inoculated with *P. agathidicida* in a glasshouse experiment (b). Globose and papillate sporangia formed in culture (c), and on the surface of kauri seedlings deliberately inoculated with *P. agathidicida* in a glasshouse experiment (d). In (c), sporangia are shown both prior to, and after, zoospore release. Scale bars = 10 μm. Image credits: (a) Dr I. J. Horner (NZ Institute for Plant and Food Research); (b, d), Dr C. M. Probst (Manaaki Whenua – Landcare Research); (c) Dr R. Lacey (Victoria University of Wellington).

Bellgard *et al.*, 2016). Such structures are important for persistence and survival of other *Phytophthora* species such as *P. cinnamomi* (Crone *et al.*, 2013; Jung *et al.*, 2013). Roots and vascular tissue that are colonized with *P. agathidicida* hyphae and oospores are important propagules that readily dislodge from the hosts and disperse through natural movement in free-flowing water and soil, and can be vectored by humans, animals and vehicles. *Phytophthora agathidicida* can survive passage through feral pig stomachs, although the specific survival propagules have not been identified (Bassett *et al.*, 2017). Hyphal growth of *P. agathidicida* outside the living host is likely to be limited as most *Phytophthora* species are poor saprophytes (Savita & Nagpal, 2012).

Host range of *P. agathidicida* and the potential roles of other *Phytophthora* species

An important knowledge gap for understanding the basic biology of *P. agathidicida* and the ecology of kauri dieback is the extent to which *P. agathidicida* can infect and colonize different plant species in kauri forest, either symptomlessly or as an aggressive primary pathogen. In other forest systems, alternate hosts have been shown to have key ecological roles in the epidemiology of *Phytophthora* pathogens by acting as sporulating hosts, pathogen refugia, terminal hosts or inoculum bridges (Crone *et al.*, 2013).

Mycelial colonization has been demonstrated under both forest and laboratory conditions for kauri, and under laboratory conditions for other indigenous native hosts *Knightia excelsa* (rewarewa) and *Leucopogon fasciculatus* (mingimingi) (Ryder, 2016). The exotic species *Trifolium repens*, *T. ambiguum*, *Lolium perenne*, *L. multiflorum*, *Pinus radiata* and *Lupinus angustifolius* have also been infected in the laboratory (Lewis, 2018). Studies on the susceptibility to infection (both with and without symptoms) of other species in forest conditions are in progress, but early indications suggest that *P. agathidicida* may be a threat to other forest plants, including *Phyllocladus trichomanoides* (tanekaha) (Ryder, 2016). These studies, and the results of glasshouse inoculation trials (Table 1), indicate that *P. agathidicida* is likely to be able to infect and colonize other native NZ plants associated with kauri, and this should be taken into account in future surveillance programmes. The same glasshouse trials (Table 1) suggested that *Agathis robusta* (Queensland kauri) is not susceptible to *P. agathidicida*, but whether other species of *Agathis* are susceptible is not known.

Many other *Phytophthora* species are known to infect multiple host species across a range of forest, agronomic and natural ecosystems, either with or without significant disease expression. Key examples with broad host ranges are *P. cinnamomi* (Shearer *et al.*, 2007) and *P. multivora* (Scott *et al.*, 2009), both of which caused disease lesions on kauri in glasshouse trials (Horner & Hough, 2014) and

Table 1 Glasshouse plant responses to inoculation with *Phytophthora agathidicida*.

Plant species[a]	Family	Root health status after inoculation	DW root control (g)	DW root PA inoculated (g)[b]	PA recovered (plant location)[c]
Agathis australis	Araucariaceae	Dead	86.9	69.5*	Yes (1°, 2°, F, C), oo
Agathis robusta	Araucariaceae	Growth promotion	40.3	46.6*	No
Dacrydium cupressinum	Podocarpaceae	Dessicated	899.0	505.0*	Yes (1°, 2°, F)
Phyllocladus trichomanoides	Podocarpaceae	Healthy	77.3	118.0*	No
Dacrycarpus dacrydioides	Podocarpaceae	Healthy	23.8	42.6*	No
Podocarpus totara	Podocarpaceae	Growth promotion	89.5	117.1*	No
Coprosma arborea	Rubiaceae	Unhealthy	5.2	4.6	Yes (1°, 2°, F)
Coprosma robusta	Rubiaceae	Growth promotion	103.5	134.4*	No
Coprosma grandifolia	Rubiaceae	Healthy	53.9	49.9	No
Metrosideros excelsa	Myrtaceae	Unhealthy	187.4	157.7*	Yes (1°, 2°, F)
Knightia excelsa	Proteaceae	Unhealthy	67.9	52.2*	Yes (1°, 2°, F)
Leptospermum scoparium	Myrtaceae	Dead	21.2	11.9*	Yes (1°, 2°, F, C)
Kunzea robusta	Myrtaceae	Dead	45.3	18.1*	Yes (1°, 2°, F, C)
Myrsine australis	Primulaceae	Healthy	21.1	24.2	No
Hedycarya arborea	Monimiaceae	Unhealthy	68.7	52.7*	Yes (1°, 2°, F)
Corynocarpus laevigatus	Corynocarpaceae	Healthy	13.1	12.4	No
Beilschmiedia tawa	Lauraceae	Healthy	69.2	72.5	Yes (1°, 2°, F, C)
Beilschmiedia tarairi	Lauraceae	Healthy	75.9	80.9	Yes (1°, 2°, F, C)
Corokia buddleoides	Argophyllaceae	Root decline	25.3	18.4*	Yes (1°, 2°, F), oo
Olearia albida	Asteraceae	Unhealthy	273.5	228.4*	No
Nestegis lanceolata	Oleaceae	Health	128.5	144.0	No

[a]Nineteen native plant species of New Zealand, and Queensland kauri (*Agathis robusta*) were screened for the ability to host *P. agathidicida* (PA). Fifteen plant replicates were inoculated with millet colonized by *P. agathidicida* by incorporation into sterile potting medium at a rate of 20%. The plants were grown in a glasshouse at 18 °C for 3 months, then post hoc recoveries were made from all regions of the root system up to the stem collar onto *Phytophthora*-selective media. In this study, a host was defined as a plant on or in which *P. agathidicida* can colonize, not necessarily complete its hemibiotrophic life cycle and produce oospores. These results need field-validation as they represent a 'no choice' test that does not reflect the usual disease pressure experienced in natural settings (Bellgard *et al.*, 2013).

[b]Mean root mass values (DW, dry weight) with an asterisk (*) were significantly different to the uninoculated control ($P < 0.05$).

[c]1°, primary roots; 2°, secondary roots; F, fine roots; C, collar/root crown; oo, oospores.

have been noted to infect other species of Araucariaceae (Bullock *et al.*, 2000; Dos Santos *et al.*, 2011; Puno *et al.*, 2015). Additional *Phytophthora* species that have been recovered from kauri dieback forest sites include *P. cryptogea*, *P. kernoviae*, *P. chlamydospora* and *P. nicotianae* (Randall, 2011; Waipara *et al.*, 2013). Although little information is available on the wider host range of these additional *Phytophthora* species within NZ, they may contribute to biotic stress within kauri forest systems and potentially affect other indigenous plant species.

Societal Impacts of Kauri Dieback

The importance of kauri to indigenous Māori

Kauri is an iconic species for all New Zealanders. However, for indigenous Māori communities in kauri forest regions, kauri are also the centrepiece of cultural and spiritual beliefs. A key kauri forest region is Waipoua within the Te Roroa tribal area. Waipoua is home to the famous *Tāne Mahuta* ('God of The Forest'), NZ's largest kauri tree with a height of >50 m and girth of just over 14 m as of April 2019 (I. Horner, Plant and Food Research NZ, personal communication; Lambert *et al.*, 2018).

To Māori, kauri trees are a treasure of immeasurable and irreplaceable value and are often referred to in speech, dance, song and proverbs (Lambert *et al.*, 2018). Under customary lore, kauri trees have chiefly status and are considered as ancestors. Many Māori feel ancestral obligations to be active guardians of these trees: *Ko te Kauri Ko Au*, *Ko te Au ko Kauri* ('I am the kauri, the kauri is me'), meaning the health of kauri forests and the health of the tribe are inextricably linked (Nuttall *et al.*, 2010; Lambert *et al.*, 2018). For Māori, death of the forest is an existential threat. The health of kauri is linked to the health of numerous other plants and animals within the ecosystem and the health of the local indigenous people. A failure to protect kauri reflects on the mana of the tribe and generations to come.

Economic impacts of kauri

Kauri have significant economic value due to their timber, copal/resin, overall biomass and iconic status. Kauri

timber is amongst those of the highest quality and versatility in the world (Hinds & Reid, 1957). Accordingly, an extensive kauri timber industry exploited this resource from the mid-19th to mid-20th century, leaving a history of impressive engineering feats, bush lore and industry, yet severely depleted natural forests (Orwin, 2004). Given the current protected status of the species, the supply of kauri timber is now scant, although the species has shown high silvicultural potential, suggesting future new plantations of this species warrant investment (Bergin & Steward, 2004). Recognition of the value of kauri forest for carbon markets is now also emerging. Kauri has the fastest carbon sequestration rates to wood of any native conifer in NZ (Kimberley *et al.*, 2014), and kauri ecosystems have the capacity to accumulate extremely large carbon pools over time (Silvester & Orchard, 1999).

Iconic tree species such as kauri evoke strong feelings among the public. In NZ, the decline of kauri trees has received significant and ongoing public attention and media coverage. The social and aesthetic benefits of having large mature trees such as kauri present in urban as well as rural settings are significant and wide ranging, from educational purposes to increased property values (Roy *et al.*, 2012). Kauri are a key tourism-marketing icon for the economy of northern NZ (New Zealand Herald, 2005). Thus, any large-scale disease or dieback of kauri has negative impacts upon these associated benefits.

Ecological Impacts of Kauri Dieback

A specialist forest community is associated with kauri

Kauri is a foundation species of NZ forests (Ellison *et al.*, 2005), and the premature loss of this species may exert broad effects by radically changing the composition of forests in which it dominates (Beever *et al.*, 2009). Kauri-dominated forests are floristically distinct and form the most species-rich forest type in NZ (Wardle, 1991; Ogden, 1995). Established forests are dominated by large kauri, many growing 1–2 m in diameter and 30–50 m in height or larger (Steward & Beveridge, 2010). These forests also commonly contain subdominant canopy associates, including conifer and angiosperm trees, such as those listed in Table S1 (Ahmed & Ogden, 1991), and a sparse but tall (approximately 1–2 m) shrub layer sometimes dominated by large, tussock-forming plants such as *Astelia trinervia* (Table S1; Wardle, 1991). Kauri trees also support abundant and diverse epiphyte communities (Fig. 2d), with those growing on their unusual flaking bark being distinctive from those on other co-occurring tree species (Wyse & Burns, 2011).

Although many plant species are considered to be 'kauri associates' (Table S1), different species exhibit various levels of association with kauri forest (Wyse *et al.*, 2014). Some are found only with kauri, such as the greenhood orchid *Pterostylis agathicola* (Jones *et al.*, 1997), whilst others common in kauri forest also occur abundantly in other forest types, including *Alseuosmia macrophylla* and *Leucopogon fasciculatus*.

In addition to plants, other taxonomic groups contain species associated solely with kauri forest or show high levels of diversity in kauri forest. For example, 264 species of fungi have been identified in kauri forest, with 12 species known to exist only in this ecosystem (McKenzie *et al.*, 2002). Similarly, many species of arbuscular mycorrhizal fungi are present within kauri roots, including some uniquely associated with kauri (Padamsee *et al.*, 2016), and a rich lichen flora has been described growing on the lower 2–3 m of kauri trunks (Hayward & Hayward, 1974). For invertebrates, a distinctive parasitoid wasp community (Kendall & Ward, 2016) and high diversity of beetles (Ward *et al.*, 2014) are found within kauri forests.

The distinctive and diverse character of kauri ecosystems results from how kauri modify their environment (Wyse *et al.*, 2014). Kauri have significant effects on soil processes, creating an acidic, infertile and drought-prone soil through the actions of its slowly decomposing litter layer (Verkaik & Braakhekke, 2007). This layer can accumulate to average depths of 30–40 cm beneath kauri canopies and even up to 2 m immediately around the trunks (Silvester & Orchard, 1999). Kauri forests are thus characterized by deep organic soils dominating the root zone in which tannins immobilize nitrogen (Silvester, 2000) and the low pH affects nitrogenase activity and limits the availability of other nutrients (Wyse, 2012). The organic soil also dries out more quickly than adjacent mineral soil (Verkaik & Braakhekke, 2007). Kauri soils are therefore a powerful ecological filter, allowing the persistence of only species that can tolerate these conditions (Wyse & Burns, 2013). An inevitable conclusion from the importance of kauri to these ecosystems is that if kauri were to be removed from them, the species dependent on that environment could also be lost.

Conversely, species that are naturally associated with kauri may be important for the long-term health of kauri trees themselves. The microbiomes (associated microorganisms) of forest trees can help them adapt to rapidly evolving pathogens, despite the trees' relatively slow rates of reproduction and long lives (Desprez-Loustau *et al.*, 2016). Therefore, in a complex forest environment, restoration of a healthy natural ecosystem is of paramount importance for tree and forest health.

Effects of forest fragmentation and land use changes on *P. agathidicida*

Changes in land use have occurred in and around kauri forest remnants in NZ. A recent study examined the effects of land use change on *P. agathidicida* growth and survival using soils from kauri, pastoral agriculture and planted pine forests immediately south of Waipoua Forest (Lewis *et al.*, 2019). Waipoua Forest, located on the west coast of the Northland region, is one of the three most heavily infested sites in NZ and one of the largest remaining kauri forests (Beever *et al.*, 2009; Waipara *et al.*, 2013).

In laboratory tests, oospore production by *P. agathidicida* grown in pine forest soil was significantly higher than in pasture or kauri forest soils, indicating a potential for pine forest soils to act as pathogen reservoirs (Lewis *et al.*, 2019). These observations warrant further investigation and field confirmation, along with exploration of the potential for a broader range of host species for *P. agathidicida*, including those commonly found in pasture, horticulture and plantation forests, to identify potential risks of pathogen transmission across land-uses.

Disease Surveillance and Diagnostics

The kauri dieback management programme

In 2009, a national Kauri Dieback Programme (KDP) was initiated (www.kauridieback.co.nz) and standardized survey methods were developed to determine the distribution of *P. agathidicida* in NZ forests. Survey sites were prioritized to areas with high conservation value that either contain culturally significant or iconic trees or ensured coverage of the natural geographic range of kauri. A risk assessment to determine current vectors and potential historic pathways of disease spread also led to surveys and sampling in fragmented remnant forest areas containing kauri, historic kauri plantations and nurseries, and at sites of high soil disturbance. Baiting and isolation methods were used to detect *P. agathidicida* in soil and plant tissues (Beever *et al.*, 2010). Both aerial and ground-based surveys were used to locate trees with symptoms, along with a passive surveillance programme whereby the public reported trees with symptoms for inspection and diagnosis. During this time, Māori guardians or *kaitiaki* actively undertook forest health monitoring and surveillance across their regions, which led to a range of Māori-led approaches to manage kauri dieback, such as restricting human access to forests (*rāhui*).

Forest sampling strategies for *P. agathidicida*

Trees infected with *P. agathidicida* have a symptomless period before canopy decline or lesions are evident. Therefore, surveillance cannot rely solely on symptom expression, but requires diagnosis of the presence of the pathogen. Because *P. agathidicida* is a soilborne root pathogen, most current sampling procedures involve taking soil samples and identifying the pathogen using either a soil baiting assay or direct DNA detection methods. *Phytophthora agathidicida* can be recovered year-round, although systematic temporal studies of pathogen inoculum levels have yet to be carried out. Due to the risks of transmitting *P. agathidicida* inoculum while working in the forest, and the shallow nature of the fine roots of kauri, strict operational and hygiene prescriptions must be followed to prevent damage to the roots and transmission of the pathogen among sites (Beever *et al.*, 2010). At the landscape level, sampling work needs to be carried out within a risk management plan that considers the surrounding vegetation, hydrology of the site and proximity to known infestations.

Currently, soil samples are collected from the top 100–150 mm of the soil layer, ideally including feeder roots, and generally comprising a composite of multiple subsamples collected within the root zone of targeted trees. In addition to sampling of soils and roots for routine surveillance, samples can also be taken from the inner bark and primary cambium of infected trees, to confirm diagnosis and to study progression of the disease. However, tree sampling requires special permissions and use of specific protocols that involve excavation of tissue samples using good sanitation practices (Beever *et al.*, 2010).

Soil baiting bioassay for *P. agathidicida*

Soil baiting is a routine method for determining the presence of *Phytophthora* within soil samples and has been used extensively across a range of *Phytophthora* species and soil systems for decades (Erwin & Ribeiro, 1996). Baiting exploits the natural dispersal biology of the pathogen in order to extract and isolate it from bulk quantities of soil. Because it relies on zoospore infection of plant tissue, baiting also confirms that the pathogen is viable and has the potential to initiate infections if conditions are conducive to sporulation. A soil baiting bioassay has been optimized for recovery of *P. agathidicida* (Beever *et al.*, 2010) based on a general *Phytophthora* baiting method (Dance *et al.*, 1975). The method involves drying soil samples then remoistening and incubating them for 4 days. The samples are then flooded with water to induce zoospore formation by any *P. agathidicida* or other *Phytophthora* spp. in the soil samples. Baits, such as *Cedrus deodara* (Himalayan cedar) needles or germinating *Lupinus angustifolius* (blue lupin) seeds, are placed on the water surface to provide a target for the zoospores (Beever *et al.*, 2010). After 2 days of incubation, the bait tissues are placed onto a *Phytophthora*-selective medium (P_5ARPH enriched with V8 juice; Jeffers, 2006). Diseased tissues of forest kauri samples, such as roots and cambium, can also be surface-sterilized and directly plated onto the same medium. *Phytophthora agathidicida* isolates emerging from baits or kauri tissue samples can be identified morphologically (Weir *et al.*, 2015) or with molecular tools as described below. Independent testing across laboratories has shown 96% concurrence between paired analysis of the same soils using the current baiting protocol (I. Horner and P. Scott, Plant and Food Research, NZ, personal communication).

Molecular diagnostics

To complement the baiting bioassay, two PCR assays have been developed to date. One is a hydrolysis probe-based qPCR diagnostic that targets the nuclear ribosomal ITS region (Than *et al.*, 2013). The other is a PCR-based high-resolution melting assay, targeting the β-tubulin gene (R. McDougal, Scion NZ, personal communication). These two tests differ in their specificity. The qPCR diagnostic is unable to differentiate *P. agathidicida* from the closely related *P. castaneae*, although the latter has not been reported in NZ (Weir *et al.*, 2015), whereas

the melting assay distinguishes between *Phytophthora* species commonly reported from kauri forest soils. These tests have been applied to several sample types. For DNA extracts directly from soil, the qPCR assay showed inconsistent results, probably due to differences in starting sample volume, pathogen dormancy, viability or PCR inhibition (McDougal *et al.*, 2014). However, the tests have proved particularly useful for identifying cultures recovered from soil baiting and, more recently, for detecting *P. agathidicida* on the baits themselves (Khaliq *et al.*, 2018). Automation of PCR-based assays (O'Neill *et al.*, 2018) could substantially speed up diagnostics from soil baiting and this approach is now being used for *P. agathidicida* (N. Williams, Scion NZ, personal communication).

Use of portable DNA diagnostics could further decrease analysis times. For example, a loop-mediated amplification assay (Notomi *et al.*, 2015) targeting a mitochondrial locus can distinguish *P. agathidicida* from other clade 5 species and other *Phytophthora* commonly reported from kauri forests. Detection from bait tissues is fast, robust and cost-effective, removing the need for laboratory conditions and enabling community-led testing (R. Winkworth, Massey University NZ, personal communication).

Lipid profiling as an alternative diagnostic approach

Because of wide variation in the structures of lipids, specific fatty acid methyl esters (FAMEs) can serve as biomarkers for specific organisms. Lipid profiling is therefore a common and effective tool for analysing microbial community structure in soils and could potentially serve to complement existing *P. agathidicida* diagnostics (Cavigelli *et al.*, 1995). Lipid profiles have been generated for several *Phytophthora* species including *P. cinnamomi* (Duan *et al.*, 2013). Additionally, *P. sojae* can be identified in soil samples by lipid profiling (Yousef *et al.*, 2012). This method generally involves extraction of lipids from a sample, release of fatty acids, and conversion of these fatty acids to FAMEs (Drenovsky *et al.*, 2004). FAMEs are then analysed via gas chromatography coupled with further identification methods such as mass spectrometry or flame ionization. Lipid profiling is appealing as it is a relatively simple and rapid process when compared with DNA-based techniques and baiting. Lipid profiling is unlikely to replace existing diagnostic tools, but could serve as a supplemental tool in establishing more rapid initial responses to the identification of contaminated soils.

Confidence in *P. agathidicida* diagnostics

The consistency, reproducibility and sensitivity of pathogen detection are fundamental to modelling spatial and temporal variation in pathogen risk, but these parameters remain largely unquantified for *P. agathidicida*. Moreover, sampling scale is a critical consideration if there is to be confidence in diagnostic testing. A study investigating pathogen distribution around a tree with symptoms using traditional baiting detected *P. agathidicida* in 32.5% of the soil samples (Bellgard *et al.*, 2013). Although this may suggest spatial heterogeneity, little has been done to understand how this may vary across trees of different ages and disease levels, and over time.

For *P. agathidicida* the ability to use diagnostics to understand disease risk is further limited by the polycyclic nature of *Phytophthora* reproduction, as well as by knowledge gaps around latency, saprotrophic capacity, host range and the effects of soil and seasonal factors (O'Brien *et al*, 2009).

Current Disease Management Strategies

Many *Phytophthora* pathogens threaten the health of forest ecosystems (Hansen, 2015). Efforts to manage kauri dieback have benefited from prior research on other forest pathosystems such as those associated with *Phytophthora ramorum* in the western USA (Cunniffe *et al.*, 2016). This review outlines progress in efforts to control kauri dieback and highlights practical challenges associated with their implementation.

Containment

In 2008, *P. agathidicida* was declared an 'unwanted organism' under the NZ Biosecurity Act (1993). It was recommended that *P. agathidicida* be treated as an introduced pathogen for management purposes until further research clarified its origin (Beever *et al.*, 2009), and a precautionary disease management programme was initiated in 2009. The primary aim of this programme was to stop further spread of the pathogen by reducing soil movement among kauri stands, based on the assumption that any soil within the root zone of trees with symptoms may be infested with the pathogen. An adaptive management programme has been implemented, which includes hygiene measures such as footwear washing stations at track entrances to reduce spread of the pathogen, control of other vectors such as feral pigs (*Sus scrofa*, an introduced and invasive mammal in NZ) and livestock, upgrading visitor walking tracks and closing public access to some high-value kauri areas. Landowners and community groups play an important role in implementation of this programme and long-term monitoring is underway to assess efficacy of these management methods. A communications and awareness strategy was also initiated to inform the general public of reasons for these measures, but variable levels of awareness and compliance with hygiene measures by the public have probably contributed to the ongoing spread of the pathogen.

In the Waitākere Ranges kauri forest (Te Wao Nui a Tiriwa) west of Auckland, the known area with kauri displaying symptoms typical of dieback more than doubled between 2011 and 2016, with 19% of all kauri in the forest showing signs of infection and *c.* 58% of kauri forest patches >5 ha having trees with symptoms by 2016 (Hill *et al.*, 2017). Disease impacts were associated

with human movement and accessways traversing areas of high pathogen risk (Hill *et al.*, 2017). In response, the Te Kawerau-a-Maki Iwi Tribal Authority placed a customary prohibition or *rāhui* on kauri forest in the Waitākere Ranges in November 2017 (http://www.tekawerau.iwi.nz/node/13). This involved closing forest tracks, with support from the Auckland Council, to keep the public out of the area in order to protect the kauri.

Chemical control

Globally, there are limited chemicals available for control of *Phytophthora*. Phosphite (phosphorous acid) has been used widely for *Phytophthora* control in many horticultural systems (e.g. avocado, citrus, apple and strawberry) and some native ecosystems (e.g. Western Australian forests and scrubland). It works both by direct biocidal activity and by stimulating host defences (Smillie *et al.*, 1989). Phosphite can be applied as a foliar spray, trunk injection or soil drench, and it can move systemically once inside the plant.

Trials on diseased kauri trees showed dramatic healing of *P. agathidicida* -induced lesions following trunk injection with 7.5–20% phosphite (Horner & Hough, 2013; Horner *et al.*, 2015), whereas lesions on untreated trees continued growing (Fig. 2e,f). Phytotoxicity of phosphite was noted in some trees, especially when high doses were used, but factors contributing to phytotoxicity are yet to be determined. Trials with lower phosphite concentrations (4–6%) are in progress, and early results with these suggest minimal phytotoxicity (I. Horner, Plant and Food Research NZ, personal communication). A citizen science project (Kauri Rescue; http://www.kaurirescue.org.nz), in which landowners with kauri dieback problems can treat their trees with various doses of phosphite and collect efficacy data, is also contributing to the knowledge around kauri treatment. This, combined with formal trials looking at lower doses, large trees and alternative application methods, will help clarify some of the unknowns around phosphite treatment, including appropriate concentrations and doses, timing, longevity of treatment effect, factors contributing to phytotoxicity, and the influence of site factors (I. Horner, Plant and Food Research NZ, personal communication).

Phosphite will not eradicate *P. agathidicida* from the soil, and trees could be reinfected once effects wear off. Therefore, long-term control using phosphite will require periodic retreatment. Although treatment is quick, easy and relatively cheap (a few minutes and less than a dollar for most trees, depending on size), repeated treatments over large areas may not be sustainable. In the long-term, there is potential to develop resistance to phosphite, such as that observed in other *Phytophthora* pathosystems with intensive phosphite application (Dobrowolski *et al.*, 2008; Hunter *et al.*, 2018). Although to date there is no evidence for this with *P. agathidicida*, phosphite has not yet been used intensively at regular intervals over a long period of time. However, alternative methods for chemical control are currently being explored (Pasteris *et al.*, 2016; Lawrence *et al.*, 2017, 2019).

Screening for resistance

A key principle of forest disease control involves selection and planting of resistant or tolerant tree genotypes. Kauri naturally regenerate through the establishment of seedlings and saplings on the forest floor, although seed viability is typically short. Kauri regeneration in natural forest occurs irregularly in space and time but highest regeneration densities are noted in large forest gaps caused by fallen trees or other disturbance events such as fire (Ahmed & Ogden, 1987; Ogden & Stewart, 1995). Population demographics are yet to be performed to identify the potential selection of disease resistance within infested stands.

At the time of writing, screening studies to identify resistance had commenced across families of kauri with initial indications of a broad range of responses to infection among families. This screening programme commenced by developing close partnerships with local Māori custodians (*mana whenua*) who authorized and helped collect seed from their kauri trees to be grown for screening (N. Williams, Scion NZ, personal communication). So far, all seedlings have become infected with *P. agathidicida*, as revealed by culturing from surface-sterilized root and collar tissue on selective media. Variation in tolerance was measured by time to death following repeated exposure to the pathogen and reflooding of the plants to encourage infection. Preliminary results showed from 5% to 80% of individuals from each family remaining alive after 106 days exposure to the pathogen in glasshouse trials. This broad range of phenotypes is being compared with genetic data in efforts to identify markers for breeding and selection (N. Williams, Scion NZ, personal communication). If resistance can be bred into kauri populations, long-term recovery of the species could occur within pathogen-affected areas, by planting these genotypes into suitable regeneration opportunities as they arise, or by including resistant genotypes into new kauri plantations.

Although kauri trees with resistance to *P. agathidicida* have not yet been identified, the finding that trees vary in their relative tolerance to the pathogen suggests that tolerant individuals may be present in populations. These early screening results provide hope for the future of kauri, but are by no means a silver bullet for disease management. Given the immense age, morphological and physiological differences between young and mature trees (Steward & Beveridge, 2010), it is not possible to assess whether tolerance would be durably expressed over decades or even centuries. As the life cycle of *P. agathidicida* is comparatively short, increased virulence may be selected within the pathogen population that could overcome disease tolerance in the host. A deeper understanding of the mechanisms involved in disease expression and control, and how *P. agathidicida* interacts with kauri, will help to determine how durable such tolerance could be in the face of future climate change and pathogen-pressure scenarios.

Genome resources for *P. agathidicida*

Whole genome sequencing of *Phytophthora* species can enable rapid pathogen identification and genotyping, as well as providing insights into lifestyle, host preferences and molecular virulence mechanisms that have the potential to lead to new methods of disease control. This genome information can be complemented with gene expression data (i.e. transcriptomes) to identify genes that are differentially expressed during different life stages of a pathogen (oospores, sporangia, zoospores and mycelium) or throughout the host infection process. At the time of writing, draft genome sequences, generated using Illumina technology, are available for two isolates of *P. agathidicida* (Studholme *et al.*, 2016). A further 12 Illumina genome sequences representing *P. agathidicida* isolates from different locations in NZ are also available (NCBI BioProject accession PRJNA486676). So far, these genomes have revealed a low level of genetic diversity among the isolates, with an average of only 0.1% DNA sequence differences compared to the NZFS3770 genome (Studholme *et al.*, 2016; R. Bradshaw, Massey University NZ, personal communication). Based on these genomes, studies are in progress with *P. agathidicida* effector genes that have the potential to activate the plant immune system or to modulate host immune responses (R. Bradshaw and C. Mesarich, Massey University NZ, personal communication), as shown in other *Phytophthora* species (Fawke *et al.*, 2015).

Knowledge Gaps and Future Outlook

Many aspects of kauri dieback require further research (Black & Dickie, 2016). However, research and management of *Phytophthora* pathogens in natural ecosystems elsewhere can help model the response to kauri dieback (Jung *et al.*, 2013; Hansen, 2015; Cunniffe *et al.*, 2016). A high priority is improved surveillance, ideally by following the fates of individual trees over time and integrating pathogen diagnostics with indices of tree decline and landscape factors. Mapping pathogen distribution and landscape-scale modelling of pathogen movement would allow management in relation to disease expression and latency on a regional scale. Critically a centralized, coordinated system is needed for monitoring and surveillance data to enable both local operational responses and regional-level strategic decision-making. Many of these gaps are in the process of being filled, with the implementation of remote sensing technologies showing great promise for further improvements in surveillance (Froud *et al.*, 2019).

Improved surveillance and diagnostics will also improve understanding of kauri dieback dynamics. For example, whether latency periods vary or whether kauri and *P. agathidicida* can co-exist without disease onset. Other critical knowledge gaps include whether *P. agathidicida* has alternative hosts and to what extent co-occurring pathogens such as *P. cinnamomi* and *P. multivora* impact kauri in forests (Waipara *et al.*, 2013; Horner & Hough, 2014). A deeper understanding of pathogen spread within sites and at the landscape level is also critical for understanding both disease progression and population- and stand-scale impacts of the disease on kauri forests. There is little understanding of the rate and direction of spread within a kauri stand, whether all individuals will be affected, and how the disease influences forest composition and structure. Long-term studies of kauri forest demography in the presence and absence of *P. agathidicida* are required.

Better control and management solutions are required for kauri dieback. In the short term a sanitizer that kills oospores effectively is needed to limit human-mediated spread, as well as further research into phosphite and other potential treatments. In the long term, there is an urgent need to understand the biology of *P. agathidicida* and the extent of natural resistance to *P. agathidicida* in kauri. Environmental factors are also important for determining kauri dieback dynamics, hence the effects of plant and microbial community composition, overall soil health and abiotic factors on kauri dieback all require further investigation. Such studies may reveal possibilities for natural disease management, such as biocontrol or companion planting that will be able to provide kauri with enduring protection from *P. agathidicida*, as long as those methods do not compromise ecosystem integrity.

Mātauranga Māori solutions are critical to all aspects of kauri dieback research. Complementary scientific and *mātauranga Māori* solutions based on plant associations and medicinal uses demonstrate practical integration of cross-cultural research streams and this approach provides great promise for managing kauri dieback (Lawrence *et al.*, 2019). *Mahi ngātahi*, 'resilience through collaboration', engenders collaboration with collective responsibility and embraces the diversity of values, knowledge and research priorities necessary to protect kauri forests. Together, it is hoped that the iconic and majestic kauri can be preserved for future generations.

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Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Table S1. Some characteristic/common plant species found in kauri forests.

Video S1. Zoospore release from a sporangium. *Phytophthora agathidicida* zoospores are released from a sporangium under laboratory conditions, shown in real time.