The Potential Impacts of Phytophthora Species on Production of Kiwifruit and Kiwiberry in New Zealand

| A literature review |

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April 2019

Zespri Innovation Project BS1950

Contents

Acknowledgements

We thank Italian colleagues for their help in providing information about *La Moria*, particularly Maria Aragona and Giannia Tacconi of CREA, and Francesco Savian of the University of Udine; Wan Min of CABI for her assistance with literature searches in China; and Lesley Ragab for general literature searches.

1 Executive summary

This report presents detailed information on the potential threat posed by *Phytophthora* species to kiwifruit production in New Zealand. It is based on a thorough review of all published information the authors had available, including both scientific and grey literature. The main finds are:

- Several *Phytophthora* species are already known to infect kiwi fruit plants, causing root and collar rot, causing marked reductions in fruit yields and sometimes plant death. *Phytophthora* diseases have been reported in most of the major kiwi fruit-producing countries, including New Zealand.
- The most important *Phytophthora* species affecting kiwi fruit, based on frequency of reports, appear to be *P. cactorum*, *P. cinnamomi*, *P. citrophthora, P. cryptogea* and *P. megasperma.*
- Kiwifruit vine decline (La Moria) is currently causing concern to growers in Italy, although the cause is unclear. Waterlogging is a major issue in La Moria, however, and is probably associated with infections by *Phytophthora* and/or other Oomycota.
- There are 30 species of *Phytophthora* known to be present in New Zealand, several of which are capable of infecting kiwi fruit. Some of these species, such as *P. captiosa, P. fallax* and *P. kernoviae* are probably native to New Zealand, and it is highly likely that further species also occur naturally but have not, as yet, been identified.
- The risks posed to kiwifruit vines by other species of *Phytophthora* already known to occur in New Zealand require testing in rigorous experiments.
- The oceanic climate of New Zealand makes most of the land mass highly suitable for *Phytophthora* species to cause damage on host plants. Apart from at the highest elevations, New Zealand ideal temperature and rainfall conditions exist for the development of *Phytophthora* species. Climate change is likely to result in further development of conditions conducive to disease development.
- Biosecurity NZ, the organization that protects New Zealand against incursions of potentially harmful organisms, has some of the most stringent regulations for the prevention of introduction of invasive alien pests and pathogens. Following the incursion of *Pseudomonas syringae* pathovar *actinidiae* (PSA), probably between 2005-2009, border controls on kiwifruit are particularly tight. The arrival of PSA in New

Zealand, however, indicates that problems may still enter the country and establish, despite the best of efforts by biosecurity at the borders.

- Detailed case studies of three long-known damaging problems caused by *Phytophthora* are presented, including *P. cactorum* on apples, *P. cinnamomi* on avocado and *P. fragariae* on strawberry. These studies gave information on the conditions under which *Phytophthora* cause major problems on crop plants, current diagnostic procedures, the potential losses caused and management and control protocols that can help alleviate disease problems when they occur.
- The most useful general cultural tool in the fight against *Phytophthora* diseases is to establish good drainage in the growing area; *Phytophthora* species are 'water moulds', requiring high soil or atmospheric moisture to grow, reproduce and cause disease.
- The most effective chemical control of *Phytophthora* diseases is the application of chemicals based on phosphonate. On woody plants, the chemicals can be applied by trunk injections, although this procedure is damaging to the plant and cannot be repeated regularly.
- Great efforts have gone into finding host plants with resistance to *Phytophthora*. In woody crop plants such as apple and avocado, work has focused on the resistance status of the rootstocks onto which the scions are grafted, and several clonally lines are available for field deployment.

Recommendations for further research are included, based on the findings reported here. The most important general conclusions are that

- New Zealand should be in a state of alert for *Phytophthora* attacks on kiwifruit
- Biosecurity NZ should have state-of-the-art facilities to examine incoming plants and plant materials, particularly any that also include soil or other plant growth substrates, for Oomycota.
- The abilities of all *Phytophthora* known to attack woody plants and present in New Zealand should be tested on kiwifruit plants under controlled conditions conducive to development of 'water mould' diseases.

2 General introduction

This report gives the results of a literature review and assessment of the possible impacts of *Phytophthora* species on production of kiwifruit and kiwiberry in New Zealand. The work was co-funded by the Kiwifruit Vine Health/Zespri Biosecurity Research Portfolio and Biosecurity New Zealand under the Government Industry Agreement (GIA) (Project BS1950).

Steve Woodward focused on the biology and pathology of *Phytophthora* species and their inter-relationships. Eric Boa investigated *Phytophthora* diseases affecting *Actinidia* species grown for commercial production and management practices.

The work began in late 2018 and literature searches were completed in March 2019. Both authors worked closely on the final report. Eric Boa visited Italy to find out more about research on vine decline (*La Moria*) and its impact on kiwifruit production.

References have been stored in Endnote, a popular piece of software used to organise, search and link scientific publications to relevant text in research papers. Copies of publications and the Endnote database are provided separately.

3 Review outline and expected results

The principal findings are presented in the main sections shown above in the table of contents. More detailed technical information is available in the annexes. The aim is to balance the need for precise information about the biology and pathogenic behaviour of Phytophthora with direct access to the main conclusions based on scientific knowledge. Original sources of information are provided in the annexes and, where relevant, in the main sections.

Section 4 explains the scope of information searches. This is followed by an overview of *Phytophthora* diseases of Actinidia (Section 5) then general findings from the disease case studies (Section 6). Section 7 examines the disease risks to *Actinidia* spp. in New Zealand based on current knowledge of the genus *Phytophthora* and more specifically from past records of disease outbreaks.

The overall conclusions are presented in Section 8 with recommendations for further research provided in Section 9.

4 Literature searches

In addition to broad searches carried out through open access search tools, such as Google and Google Scholar, we queried CABI databases, Scopus and China Academic Journals. FAO Agris revealed little relevant information. Phytosanitary portals were also largely unrevealing, at least in attempting to track disease incursions. There was only one report of root and crown rot of kiwifruit on Pro-Med mail, a service which offers a global overview of new diseases and significant outbreaks. There was only one general report, from China, on *Phytophthora* root rot. Queries of databases maintained by the European Plant Protection Organisation (EPPO) also revealed little information of value.

The most useful and up to date global overview on *Phytophthora* diseases of *Actinidia* forms part of a chapter on cultivation and management in *Kiwifruit: the genus Actinidia* (Huang, 2016). Attempts to obtain information directly from Chinese plant pathologists working on *Actinidia* were unsuccessful, though there was little suggestion from wider searches of much research on *Phytophthora*. No Japanese publications for *Phytophthora* and *Actinidia* were found, including the CABI database, which has the broadest historical coverage of plant diseases. Two papers were found on *Phytopythium* spp. associated with root rot disease in Japan (Shimuzu et al. 2005; Yano et al., 2011).

It is possible that more information on *Phytophthora* might be revealed through wider literature searches for root rots of *Actinidia* spp., for example prior to the late 1980s, when clear evidence of its role in disease development began to emerge. Such searches would also uncover publications concerning *Armillaria* and other root pathogens and distinguishing a role for *Phytophthora* would be difficult, even if early reports (e.g. Dingley, 1969) suggest a long association with *Actinidia*.

5 Global overview of *Phytophthora* on *Actinidia* spp.

Country records: The earliest record found of *Phytophthora* on kiwifruit is from New Zealand in 1969 (Dingley, 1969). Since then 12 countries have reported at least 15 different species on Actinidia, mostly affecting *A. chinensis* or *A. deliciosa* (Table 1). We were unable to find any references to *Phytophthora* infecting *Actinidia* in Japan, though there is little doubt that it is associated with root and crown rots. Shimizu et al. (2005) reported two other oomycetes, originally ascribed to *Pythium* but now known as *Phytopythium vexans* and *Phytopythium helicoides*.

TABLE 1: Earliest country records found of *Phytophthora* on *Actinidia*

Country	Year	Reference	Note
New Zealand	1969	Dingley, 1969	
Italy	1979	Zuccherelli, 1979	
USA	1987	Wilcox and Mircetich, 1987	
France	1988	Baudry, Morzieres and Ellis, 1991	
Iran	1989	Binesh and Pourabdollah, 1889	
China	1990	Wang, 1990	Cited in Huang, 2016
Chile	1991	Lattore, Alvarez and Ribeiro, 1991	
Brazil	1992	Valdebenito-Sanhueaz, 1992	Original paper not available
Korea	2001	Lee et al., 2001	
Portugal	2005	Sofia, 2005	
Turkey	2011	Akilli et al, 2011	
Spain	2014	Pintos et al, 2014	

No information was available on the species of *Phytophthora* reported from Brazil in 1992, and early records from China (e.g. Wang, 1990 and Fang and Wei, 1992) also appear to have only identified to genus level. Other country records provide a more detailed record of the 15 species known to be associated with diseases of *Actinidia* (Table 2). Known records for Brazil and Portugal only noted *Phytophthora* spp. while other papers (e.g. Conn et al, 1991 from the USA) referred to 'four unknown species'.

TABLE 2: Phytophthora species on *Actinidia* recorded from different countries

Scientific name	Countries	Major regions
P. cactorum	China, Italy, New Zealand, USA	E Asia, Europe, N America, Oceania,
P. cinnamomi	China, New Zealand, Spain	E Asia, Europe, Oceania
P. citricola	New Zealand	Oceania
P. citrophthora	Chile, Italy, New Zealand	Europe, S America
P. cryptogea	Chile, Iran, Italy, New Zealand [1]	W Asia, Europe, Oceania, S America
P. drechsleri	Korea	Asia
P. gonapodyides	New Zealand	Oceania
P. lateralis [2]	China, New Zealand	Asia, Oceania
P. megasperma	New Zealand, Turkey, USA	W Asia, N America, Oceania
P. megasperma var. *megasperma*	New Zealand	Oceania
P. megasperma var. *sojae*	Iran	W Asia
P. nicotianae	USA	N America
P. nicotianae var. *nicotianae*	Italy	Europe
P. nicotianae var. *parasitica*	Italy	Europe
P. palmivora	Turkey	W Asia

1: The earlier record of *P. cryptogea* attacking kiwifruit vines in New Zealand preceded reclassification of the complex into three species. It is unknown which of the three species was the subject of this work. In the absence of information a precautionary approach has been taken to include *P. cryptogea* on the 'not present in New Zealand' and of concern to kiwifruit pending any new information to the counter.

2: *P. lateralis* attacking kiwifruit is believed to be from a single report of experimental inoculation of *Actinidia deliciosa* cv. Hayward using an imported isolate of this species.

Phytophthora cactorum and *P. cryptogea* have the widest known geographic range, according to Table 2, followed by *P. megasperma*. New Zealand has the largest recorded diversity of species affecting kiwifruit, with seven recorded, followed by the USA (six species) and Italy and Turkey, both of which have four known species. One possible explanation for the widespread distribution of a species is that *Phytophthora* is being spread in either planting material, or more probably in potting compost. The high diversity of *Phytophthora* species found on kiwifruit within a country could be due to several factors. Kiwifruit orchards may be grown in close proximity to other plant hosts affected by the same or similar pathogenic *Phytophthora* species. Alternatively, *Phytophthora* species associated with plants growing in nearby natural environments may attack kiwifruit, once the orchards are established.

High diversity of *Phytophthora* species recorded on kiwifruit for a country or widespread distribution of a named species does not necessarily suggest a greater risk to production of kiwifruit and commercial relatives. There is clearly a difference in the amount of damage that *Phytophthora* species cause (e.g. Conn et al, 1991), as reported for a particular country.

That is not to say that a species which is a low risk in one country will behave in the same way in different growing conditions, including use of different host cultivars. The possibility also exists that, in a region with a high diversity of *Phytophthora* species, there is a greater chance of host jumps and the formation of interspecific hybrids with unknown impacts. Further work is needed to explore these issues and matters relating to the diversity of *Phytophthora* species associated with *Actinidia* around the world.

6 *La Moria* (vine decline), *Phytophthora* and associated diseases of kiwifruit vines in Italy

La Moria, literally 'the death', of kiwifruit plants was first seen in the Verona region in northern Italy in 2012 (Tacconi et al 2014). The delay in announcing the disease, translated as 'vine decline' in English, could suggest sensitivity about reporting a new problem. Kiwifruit production has expanded considerably in northern Italy, often replacing the less profitable peach. Farmers have invested a lot of money and effort in kiwifruit and by all accounts it is a popular crop.

But the delay could also simply be related to gathering of scientific information. Eric Boa visited Dr Tacconi at the CREA research station in Fiorenzuola (north of Bologna), where brief but helpful discussions enabled him to gather publications and other details of interest relevant to the present review.

Phytophthora is clearly associated with La Moria, a damaging problem which has affected 1600 ha of orchards out of a total 2500 ha in Verona (Tacconi et al. 2014), yet is not believed by Italian researchers to be the main cause. They point out that there is no consistent association between the oomycetes (several *Phytophthora* species as well as *Phytopythium vexans* have been isolated) and the presence of symptoms (see Tacconi et al. 2015 and Tosi et al. 2017).

The pronouncement about limited or weak causality appears in the above citations and others concerning vine decline and needs more careful analysis. Few hard scientific data have been published about pathological investigations. The main response to vine decline, as seen from published research and personal discussions, has been an emphasis on developing control measures. Although it is difficult to confirm, this review's authors believe that a strong grower imperative has limited extended scientific studies. This is,

however, only speculation, though there is at least two clear conclusions about the cause of vine decline: much still remains to be discovered; and the role of *Phytophthora* may well be more important than stated in print.

There is a much longer association of *Phytophthora* with kiwifruit in Italy than suggested by recent literature on vine decline. The earliest record found (Zuccherelli 1979) said that *Phytophthora* was associated with collar root, root death and dying kiwifruit plants. In 1982 D'Ercole and colleagues reported a collar rot of *Actinidia*, though it is unclear from available information if *Phytophthora* was involved. Five years later unsuccessful attempts were made to inject trunks with fungicides to control collar rot associated with *P. cactorum* and *P. nicotianae* var. *parasitica* (Caccioppo 1987). Foot and root rots associated with *Phytophthora* were observed on kiwifruit vines growing in Puglia and Basilicata (Ciccarese et al. 1992) shortly afterwards, then *P. cryptogea* from Campania, an adjacent region in southern Italy (Cristinizio and Iannini 1996).

No other publications mentioning *Phytophthora* on kiwifruit in Italy were found until a brief account of crown rot in the Piedmont, the adjacent region to Verona (Cotroneo 2009). Again few details are available – the articles cited are from bulletins and newsletters that appear intended mainly for growers and technical staff – though Cotroneo does write about water-logging and heavy soils leading to 'asphyxiation' and contributing to infection by *P. cactorum*.

The Piedmont record of *Phytophthora* from 2009 is not explicitly mentioned in articles on vine decline published post reporting of vine decline in 2014. Crown rot symptoms and root decay and malfunctioning are, however, frequently noted as distinctive features of vine decline. The reports from 1979 onwards show that *Phytophthora* has a long association with kiwifruit in Italy, further enforcing the suggestion of a significant role in the damaging losses resulting from vine decline. It is difficult to be more exact because of weak knowledge about what pathogen species were involved and other experimental information and scientific analysis – if indeed much experimentation was done or was possible.

A 1991 paper by Magliulo and colleagues investigated the decline and death of kiwifruit linked to waterlogging and persistent anaerobic soil conditions. The authors do not consider a possible role for *Phytophthora*. All the reports and articles on vine decline make persistent mention of increased rainfall and conditions leading to soil saturation and waterlogging (e.g. Sorrenti et al. 2019) and while there is strong evidence to support a link between persistent anaerobic conditions in soil and root death, the role and interplay with

Phytophthora infections has yet to be fully investigated. Italian researchers clearly believe that *Phytophthora* and waterlogging are linked, though they also point out that vine decline occurs in well-drained soils where conditions would appear to be less conducive to infection.

More consideration has been given to the effect of irrigation methods. The use of overhead watering ('l'irrigazione per scorrimento') is associated with increased incidence of vine decline, as is poorly functioning use of microjets and other ground-based methods for delivering water. Yet the over-riding difficulty in stating what is known about vine decline, and with what certainty, is in the lack of scientific detail. The largely narrative accounts of where the disease occurs, and associated conditions and weather phenomena are informative but inconclusive. Research being carried out at the University of Udine (northwest Italy) aims to correct gaps in knowledge but as of early 2019 detailed pathogenicity trials with *Phytophthora* isolates have still be performed.

There has been much discussion and debate about vine decline in Italy, a disease (syndrome?) which occurs from Calabria in the south to the Piedmont and Friuli Venezia Giulia bordering Slovenia. Further collaborations with Italian scientists on the identity of *Phytophthora* species isolated from kiwifruit, their behaviours and untangling of multiple possible causes of vine decline are needed in order to understand and estimate the future risk to New Zealand and beyond. Modern methods for high throughput testing of soils would provide more data on the presence of *Phytophthora* species, overcoming the limitations of baiting and other direct isolation methods.

PCR methods have been used to sample plant tissues directly (Tosi et al. 2015) but there is a still a sense that more emphasis should be placed in future on extended scientific research. This may not be possible without additional funding to those channelled through the Italian research councils. The regions have been quick to provide funds for researchers though, as already noted, this has appeared to favour empirical studies and quick-fix suggestions for limiting the disease (e.g. avoid overhead watering; better drainage of soils). More detailed laboratory work is needed with publication of results in scientific journals.

7 *Phytophthora* species known to be present in New Zealand

There are at least 30 species of *Phytophthora* recorded in New Zealand, including several presumed native species (Table 3). The presence of these pathogens has a long history, with *P. cinnamomi* recorded before 1950 (Smith, cited in Newhook and Podger 1970).

Table 3. *Phytophthora* species present in New Zealand (updated from Scott and Williams 2014).

***Phytophthora* species with known hosts in New Zealand**	**Clade[1]**	**Main land use type affected**			
		Agriculture	Forest plantations	Horticulture/ amenity plantings	Natural ecosystems
Phytophthora aleatoria	1		√		
Phytophthora cactorum		√	√	√	√
Phytophthora infestans		√			
Phytophthora nicotianae		√		√	√
Phytophthora citricola[2]	2	√	√		√
Phytophthora citrophthora		√			√
Phytophthora meadii				√	
Phytophthora multivesiculata				√	
Phytophthora multivora			√	√	√
Phytophthora plurivora		√		√	
Phytophthora pluvialis[3]	3				√
Phytophthora agathidicida	5				√
Phytophthora asparagi	6			√	
Phytophthora gonapodyides		√			
Phytophthora megasperma		√	√		
Phytophthora chlamydospora				√	√
Phytophthora x *cambivora*	7			√	
Phytophthora cinnamomi		√	√	√	√
Phytophthora europea					√
Phytophthora fragariae		√			
Phytophthora brassicae	8	√			
Phytophthora erythroseptica		√		√	
Phytophthora hibernalis		√		√	√
Phytophthora lateralis[4]				√	
Phytophthora medicaginis		√		√	
Phytophthora porri		√			
Phytophthora primulae				√	

Phytophthora species with known hosts in New Zealand	Clade[1]	Main land use type affected			
		Agriculture	Forest plantations	Horticulture/ amenity plantings	Natural ecosystems
Phytophthora pseudocryptogea[5]		√	√	√	√
Phytophthora syringae		√	√		
Phytophthora capitosa	9		√		
Phytophthora fallax			√		
Phytophthora kernoviae	10	√		√	
Totals in each land use system		**18**	**10**	**17**	**12**

1: Clades according to Martin et al. (2014)

2: Unclear, as many species formerly classified as *P. citricola* are now known as *P. multivora.*

3: Clades with the species were defined in Reeser et al. (2013)

4: Referred to by Robertson (1982) on kiwifruit; now thought to have been a deliberately imported isolate for use in experimental inoculations on *Actinidia*.

5: Originally identified as *P. cryptogea* which preceded reclassification of the complex into three species. It is unknown which of the three species was the subject of this work. In the absence of information a precautionary approach has been taken to include *P. cryptogea* on the not present in New Zealand and of concern to kiwifruit pending any new information to the counter.

Several species of *Phytophthora* present in New Zealand attack woody hosts, and all of these taxa are potential threats to the kiwi fruit industry. A lack of knowledge of some species, particularly their host range, makes it difficult to clearly state the risk to kiwifruit (ie. the likelihood that a particular species is pathogenic). It is much easier to greatly minimise if not eliminate the threat of well-known species such as *P. infestans* or *P. fragariae* to *Actinidia*, where a long history of research enables a more detailed assessment of the host range.

Several of the species listed in Table 3 are already known to attack *Actinidia* species (Table 2) and will not be considered further in this sub-section. The apparent detection of *P. lateralis* affecting kiwifruit in New Zealand (Robertson 1982) may have been a mis-diagnosis. *Phytophthora* species that are known to attack woody plants in New Zealand are the most likely threats to kiwifruit, as these species are capable of overcoming defences in woody hosts. It is also important to note that species of *Phytophthora* native to New Zealand are only now being discovered; it will be many years before the full range of native species is known.

Potential Phytophthora threats to *Actinidia* in New Zealand

Excluding species currently recorded in New Zealand and not listed in Table 3, the following additional *Phytophthora* species are considered potential threats to kiwifruit plants:

P. agathidicida *P. x cambivora* *P. captiosa* *P. fallax*

P. gonapodyides	*P. kernoviae*	*P. medicaginis*	*P. multivora*
P. plurivora	*P. syringae*	*P. cryptogea*	

The selection of species is based on knowledge of their known host range. Further tests are required to confirm it they are pathogenic on *Actinidia* spp. and under what conditions. Extended host testing for pathogens is useful but is still no guarantee that such infections (of new hosts) will actually occur.

Phytophthora multivora, one of the potential threats to *Actinidia*, was first isolated from the rhizosphere of *Eucalyptus* species in Western Australia (Scott et al. 2009), but was also present in roots of other Myrtaceae and Proteaceae. The known host range of this species was considerably expanded soon after the publication of this research, particularly as contemporaneous research confirmed that *P. multivora* occurs in Europe (Jung and Burgess 2009). *Phytophthora plurivora*, closely related to *P. multivora*, also attacks a wide range of woody plant species (Hansen & Delatour 1999; Jung et al. 2000; Vettraino et al. 2002; Balci & Halmschlager 2003a,b; Jung & Burgess 2009), including both roots and young shoots (Nechwatal et al. 2011).

Phytophthora agathidicida, also considered here as a potential threat to *Actinidia*, causes a lethal dieback disease of *Agathis australis*, an iconic tree in Maori culture (Bevan et al. 2015). The species appears to be native to Oceania, but other hosts have yet to be identified. *Phytophthora agathidicida* does not appear to affect other plants in the kauri forests. It is possible that *P. agathidicida* has been a low-level pathogen on *A. australis* for some time (e.g. Gadgil 1974), only becoming damaging with changes in soil moisture and structure (more rain and waterlogging), for example.

Species in *Phytophthora* clade 6, such as *P. gonapodyides* and *P. megasperma* (Table 3), are generally considered saprotrophs, occurring naturally in watercourses (Brasier et al. 2003) and colonising dead plant material. Many of these species have been discovered causing disease on plants growing outside watercourses where there has been periodic waterlogging of the soil. *Phytophthora gonapodyides*, for example, is a pathogen component in decline of *Quercus ilex* in the dehesa communities of the Iberian Peninsula (Corcobado et al. 2010) and kills young seedlings of *Q. robur* (Jung et al. 1996; Balci and Halmschlager 2003a).

Species in clade 7 include those with wide host ranges, such as *P. cinnamomi* (covered in detail in Annex 2). A hybrid species in the clade, *P.* x *cambivora*, is also considered highly damaging to woody species in many different families, notably the Fagaceae and Rosaceae

(see Plantwise Technical Factsheet for a list of known hosts). *Phytophthora* x *cambivora* is a major problem on woody plants in Europe, where it is frequently associated with sites with compacted soil and, in some sweet chestnut (*Castanea sativa*) stands, manured (Fonseca et al. 2004). *Phytophthora* x *cambivora* also occurs in North America (Rizzo and Fichtner 2009).

Phytophthora syringae is a long-known species, placed in clade 8 (Martin et al. 2014), first isolated from lilac (*Syringa* sp. – hence the specific epithet) in Germany (Klebahn 1905). Since its description in 1905, *P. syringae* has been found to infect 24 genera of plants in 14 families (Cline et al. 2008), notably in the Rosaceae. It causes collar rot and storage rot of apples and canker on the stems of almond.

P. captiosa and *P. fallax* , the two clade 9 *Phytophthora* species known in New Zealand on *Eucalyptus* species (Dick, et al., 2006), are unusual in that they are not root diseases. Infections occur in the crown, where humidity is normally lower than at ground level or in the soil. The molecular analyses reported by Dick et al. (2006) suggested that *P. captiosa* and *P. fallax* were intermediate between the then accepted clades 9 and 10. More recent phylogenetic work, based on concatenated sequences of seven nuclear genetic markers, placed both species in clade 9 (Yang et al. 2017). Symptoms include the presence of necrotic lesions on the foliage, thinning of the crown and dieback of affected twigs.

Phytophthora capitosa and *P. fallax* are closely related, but infect distinct host plants in the Myrtaceae. It is unclear to date whether these pathogens are indigenous to New Zealand, or were imported with *Eucalyptus* plant materials. The more recent discovery of *P. fallax* in Victoria, Australia, suggests that species may be exotic in New Zealand, particularly as the organism was only recovered from soils, with no indications of *Eucalyptus* infections (Cunnington et al. 2010).

There is a report suggesting that *P. medicaginis* causes root rot on *Prunus* 'Mahaleb' [1]. As *Prunus* spp. are woody plants, it is possible that *Phytophthora medicaginis* may pose a threat to *Actinidia* spp., and should be included in tests of virulence.

Phytophthora kernoviae was first discovered in New Zealand in 1953 (Beever et al. 2006, cited in Ramsfield et al. 2009), but was initially listed as an undescribed '*Phytophthora* sp.'. Isolates were fortunately maintained in culture collections, enabling later use of advanced tools to identify the species. Further isolates of what is now called *P. kernoviae* were also recovered from soils and roots in *Pinus radiata* plantations in the early 1960s (Newhook 1961). When

[1] http://www.phytophthoradb.org/species.php?a=dv&id=290277

the unknown *Phytophthora* isolates were re-examined using molecular methods in the early 21st century, it was discovered that *P. kernoviae* was apparently present in several regions of New Zealand (Beever et al. 2006, cited in Ramsfield et al. 2009). Morphological and molecular data were similar to those published for the 'newly reported' *P. kernoviae* in the UK (Brasier et al. 2005). Further investigations strongly suggested that the isolate of an incompletely characterized *Phytophthora* obtained from a *P. radiata* plantation in Tokoroa was also *P. kernoviae*, and that the same species had been shown to be infecting *P. radiata* roots without causing notable problems to the trees in the early 1960s (Newhook 1961).

Other hosts for *P. kernoviae* include custard apple (cherimoya; *Annona cherimola*). No infections have been detected in native New Zealand vegetation. Analysis of the genetic diversity present in the ITS region of New Zealand *P. kernoviae* isolates clearly shows that this species is native to the southern hemisphere (Ramsfield et al. 2009). More recent work carried out in western regions of South America, including native forests in Chile (Sanfuentes et al. 2016) demonstrated that *P. kernoviae* was also present in western parts of South America.

A number of *Phytophthora* species not known to be present in New Zealand have been reported attacking *Actinidia* species outside the state, including (Table 2):

P. cactorum sensu stricto	*P. cryptogea*	*P. drechsleri*
P. lateralis	*P. palmivora*	

Clearly, these species pose significant threats to production of kiwifruit and kiwiberry in New Zealand and Biosecurity New Zealand should be informed through the GIA partnership.

What *Phytophthora* species are native to New Zealand?

It is difficult to say which species shown in Table 3 evolved in New Zealand without further sampling and testing of plants and soils. Many species have undoubtedly been introduced. Future work using state-of-the-art high throughput sequencing technologies may reveal the presence of other *Phytophthora* species in New Zealand's varied ecosystems, but large scale sampling and a representative ranges of isolates will be required to determine the genetic variation within each species, to determine which are native to New Zealand.

8 Climatic suitability of New Zealand for *Phytophthora*

The occurrence of plant diseases has long been associated with climate, and is strongly tied to seasonal weather patterns (Coakley et al. 1999). It is important, therefore, to consider how *Phytophthora* species are affected by the current and predicted future climate of New Zealand.

Oomycota were traditionally known as 'water moulds', referring directly to the requirement for free water for growth, the production of sporulating structures and the dispersal of the motile zoospores. Infection of host plants also requires very high humidity, although infection is also promoted under conditions of drought followed by inundation (Erwin and Ribeiro 1996). The classical research on weather and climate impacting on *Phytophthora* is from modelling potato blight outbreaks. Several useful models have arisen through this research, enabling regular predictions of the likelihood of an outbreak of potato blight, based on simple temperature and humidity readings taken in potato crops during the growing season. The 'Smith Period' and the 'Beaumont Period' were developed based on very simple humidity criteria and used with great accuracy in the UK (Beaumont 1947; Smith 1956). A model commonly used in the USA is known as 'Blitecast' (MacKenzie 1981). A model developed to predict potato blight outbreaks developed in Switzerland during the 1990s (Cao et al. 1997) used 'crucial weather conditions' based on:

1. 'At least 6 hours of precipitation when air temperatures were over 10°C; and
2. A minimum of six successive hours with a relative humidity of over 90%.'

This model accurately predicted outbreaks of potato blight in susceptible varieties growing under Swiss conditions. Many other models for predicting potato blight outbreaks based on weather conditions exist.

An illustration of the significant effect of precipitation has on incidence of plant diseases caused by Oomycota followed a period of heavy rainfall in Florida in 2015 – 16 (Campoverde et al. 2017). Following these heavy rains, samples submitted by commercial growers of ornamental plants to the University of Florida Plant Diagnostic Clinic included significantly more examples of *Pythium* and *Phytophthora* root and crown rots and foliage blights than in previous years.

Apart from *P. infestans*, the *Phytophthora* that has received the most attention in terms of climate modelling is *P. cinnamomi*. Many of these models were focused on particular regions (e.g. Podger et al. 1990; Bergot et al. 2004; Marçais et al. 2004; Desprez-Loustau et al. 2007;

Thompson et al. 2014; Duque-Lazo et al. 2016), with more limited attempts to model distribution on a global scale (Brasier and Scott 1994). A recent publication (Burgess et al. 2017), however, modelled the probably changes in the distribution of damage caused by *P. cinnamomi* based on predicted global climate change. Based on the CLIMEX Ecoclimatic Index, changes in the suitability of New Zealand for *P. cinnamomi* to cause disease on suitable hosts were included in the predictions. The current distribution of damage reportedly due to *P. cinnamomi* includes much of the northernmost parts of North Island, plus the north of South Island. With predicted climate change, the suitability of other areas of both islands for *P. cinnamomi* activity increased, with only the highest elevation regions of South Island remaining unsuitable for the pathogen to cause damage by 2080.

When *P. ramorum* was first recognised as a threat and described, it raised particular alarm for biosecurity practitioners globally (Werres et al. 2001; Rizzo et al. 2003; Davidson et al. 2003; Tooley et al. 2004), leading to the production of a number of models to predict the damage it was likely to cause with further spread, mainly in the horticulture trade on hardy woody ornamental plants (e.g. Venette and Cohen 2006; Kelly et al. 2007; Václavík et al. 2010). A UK-based model (Harwood et al. 2009) suggested the importance of the horticulture trade in distribution of the pathogen, and stated that the precise climatic parameters that led to disease development were incompletely understood. Later attempts to model the climatic suitability of regions for *P. ramorum* were able to use a greater breadth of climatic data, and produce arguably more realistic models (Ireland et al. 2013; Cunniffe et al. 2016).

It is important to note that, although many of the *P. ramorum* models predicted the pathogen would spread and cause serious problems in many regions of the globe, these predictions have rarely, if ever, arisen in reality. For example, the pathogen is occasionally found in the nursery trade in Greece, but there is no indication that it has caused any problems in that country (Tsopelas, P., 2019, personal communication). It is clear that some of the climatic parameters thought to be important in the establishment and activity of *P. ramorum* remain to be elucidated. *P. ramorum* has caused major damage only in regions where there is more-or-less continuous high humidity, coupled with suitable temperatures, such as in the coastal regions of California, Oregon and Washington State, and in parts of the UK and Ireland. Caution should be applied, however, as the current understanding of this pathogen suggests the range it occupies may continue to expand in the absence of drastic management measures (Ireland et al. 2013). The model of Ireland et al. (2013) indicates that, with the exception of the higher elevations in the Southern Alps, most of the

territory of New Zealand will be highly favourable to establishment of *P. ramorum*. Moreover, New Zealand has both native and introduced plants that are suitable hosts for the pathogen (Hüberli et al. 2008), including *Pinus radiata* and species of *Nothofagus*.

The climate of New Zealand is strongly oceanic, with three temperature and eight rainfall regions (Salinger and Mullan 1999) based on climatic data from 1930 – 1994. On North Island, temperature ranges from lows of 4-16°C in winter to 12-25°C in summer. South Island is cooler, with average winter temperatures 1-12°C and in summer 10-22°C. The higher altitude peaks on both North and South Islands retain snow throughout the year. Rainfall is between 640 – 1500 mm per year, and is usually evenly spread throughout the year. The high rainfall and moderate temperatures are ideal for survival, reproduction and infection by *Phytophthora* species throughout most of the New Zealand land mass (e.g. Ireland et al. 2013; Burgess et al. 2017). *Phytophthora* species less likely to thrive in New Zealand are those generally associated with high temperatures, such as *P. parsiana* (Mostowfizadeh-Ghalamfarsa et al. 2008) or with lower temperatures, including *P. psychrophila* (Jung et al. 2002). Survival of most species at high altitudes will be limited.

9 Biosecurity in New Zealand

The economy of New Zealand is highly reliant on agriculture, horticulture, aquaculture and forestry, making biosecurity of the utmost importance in order to avoid significant losses in plant production capacities (Jones et al. 2012). For example, agriculture and fruit production alone contribute some 4.6% to New Zealand gross domestic product[2]. In parallel with the importance of these industries, biosecurity measures applied at New Zealand's ports of entry are amongst the strictest of such systems used globally. With increasing travel and global trade, however, all states and regions are faced with immense difficulties in dealing with the problems posed by biosecurity.

New Zealand's approach to biosecurity is enshrined in The Biosecurity Act (1993), which allows biosecurity personnel, under the auspices of The Ministry for Primary Industries, to 'exclude, eradicate and effectively manage pests and unwanted organisms', using all appropriate methods available (Ram et al. 2016). Within this role, there is an aim to prevent unwanted organisms entering New Zealand and, when considered feasible, to eradicate

[2] www.stats.govt.nz/information-releases/tourism-satellite-account-2017

unwanted organisms that have entered New Zealand and may become a serious pest if allowed to establish. In terms of the threat of *Phytophthora* species to kiwifruit and kiwiberry production, both of these aims apply.

It has been estimated that 'pests' (undefined) cost the New Zealand primary sector approximately NZ$2.1 billion per annum, including 40% in defending the territory against potential invasive pests, and lost outputs of some 60% (Giera and Bell 2009, cited in Dalziel and Hulme 2016). What proportion of this total is due to plant pathogens, and specifically *Phytophthora* species is not documented, although the estimated losses of NZ$885 million over a four year period due to the outbreak of *Pseudomonas syringae* pathovar *actinidiae* (PSA; see below) indicates that invasive pathogen have the capacity to cause severe losses to the impacted industry.

Despite the biosecurity efforts at New Zealand ports of entry, problems still get through the barriers, establish and cause problems. Of particular relevance to the kiwifruit industry is that of PSA, a bacterial pathogen that causes dieback and death of *Actinidia* species (Everett et al. 2011; www.kvh.org.nz). Following the first report of this pathogen being present in New Zealand, in 2010, it was rapidly recognised within the same growing season that the pathogen had spread throughout kiwifruit growing regions of the country. With the estimated losses in mind, a small group of kiwifruit growers took legal action against the New Zealand Government, seeking compensation for negligence by Biosecurity NZ[3]. The organism was first officially reported from Japan in 1989 (Takikawa et al. 1989), although it soon became clear that a disease of *Actinidia chinensis* found in China in the mid-1980s was caused by the same organism (Fang et al. 1990). Within ten years, PSA was reported in Korea (Koh et al. 1994) and Italy (Scortichini 1994), and was causing problems in Portugal and France by 2010 (Balestra et al. 2010; Vanneste et al. 2011), and in Spain and Australia by 2011 (Balestra et al. 2011; Anon. 2011). Spread into New Zealand is suspected of coming via plant material of *Actinidia chinensis*, which the claimants of this legal action believe should have been either intercepted, or checked more thoroughly by Biosecurity NZ.

Despite the concerns shown by these kiwifruit growers in New Zealand, it is difficult to detect pathogens in plants during trade. In the absence of visible symptoms, or known high susceptibility to a given agent, the biosecurity personnel are likely to either pass the plants as 'clean', or sample a small proportion for further, laboratory-based analyses. The proportion

[3] http://thekiwifruitclaim.org/page/about

of plant consignments sampled in the USA is estimated to be approximately 2% (Margaray et al. 2009), due to the sheer numbers of plant imported. The availability of highly sensitive and accurate molecular tools for diagnostics has revolutionized the process (Vannini et al. 2013). State-of-the-art diagnostics based on high throughput sequencing (HTS) is, hypothetically, capable of detecting DNA of all organisms present in or on a sample.

For the screening of soil samples, this process should be invaluable. Soil contains immense diversity estimated at billions of micro-organisms per gram (Bardgett and van der Putten 2014), making accurate detection of a problematic fungus or bacteria extremely difficult in this substrate. HTS gives the capacity to find the 'needle in the haystack' when applied to commodities that include soil. As most *Phytophthora* are soil-borne, HTS could be used routinely in tests of soil for this genus (e.g. Sapkota and Nicolaisen 2015; Puertolas et al. in preparation). Application of this technology to imported plants and plant products could markedly reduce the probabilities of introducing *Phytophthora* through this route. It can also be used to delimit the spread of *Phytophthora* species from a known outbreak, through field surveys and sampling. HTS does, however, require costly equipment and reagents, plus trained personnel for both the running of the machinery and interpretation of the data obtained (bioinformatics). The online databases used to identify species based on sequences can be inaccurate, meaning that currently, it is safer to establish an 'in-house' database, adding further costs at least to the set up period. Application of HTS, therefore, has to be balanced with perceived risks and the funding available for the work. In the near future, however, this approach will become the industry standard for biosecurity work involving microorganisms.

Biosecurity New Zealand now endorses the 'Government Industry Agreement for Biosecurity Readiness and Response' (GIA) partnership[4], signatories to which include Kiwifruit Vine Health [5] and New Zealand Kiwiberry Growers Incorporated [6]. In fact, Kiwifruit Vine Health was amongst the first signatories to the partnership, in May 2014; New Zealand Kiwiberry Growers Incorporated signed in June 2016. The aim of GIA is to improve on existing biosecurity, to secure the future of all agriculture, horticulture and forestry sectors in New Zealand through the joint efforts of different producer and grower associations. Signatories are encouraged to determine the (predicted) most important potential threats to their sectors and help set out protocols for minimising the risks and

[4] http://www.gia.org.nz/

[5] www.kvh.org.nz

[6] www.nzkiwiberry.com

impacts of incursions. A significant change in policy heralded by the GIA partnership is enabling the various industry partners to have direct inputs into biosecurity decision making at all levels.

Comparison of New Zealand and European Union Biosecurity

Globally, it was estimated that between 1995 and 2010, there was a 13-fold increase in the numbers of plant-infecting fungi (Oomycota are included under this term) reported in ProMED (www.promedmail.org; Fisher et al. 2012). This high rate of increase illustrates the scale of the problem regional and national biosecurity services are facing, with global trade. Examining only invasions of tree pathogens into Europe, Santini et al. (2013) demonstrated the increasing numbers now impacting on tree health in the continent. The role of global trade in this increase is also clear (e.g. Santini et al. 2018), and has led to calls for increased legislation, policy and management protocols to deal with these potentially highly destructive problems (Roy et al. 2016).

Until recently, EU biosecurity was considered weak, compared to the systems in place in North America and Australasia. Weaknesses recognised in the EU Plant Health Regime were detailed in a report published in 2010 (Anon 2010) and subsequently, improvements were made to biosecurity protocols and the legislation surrounding plant health, previously enshrined in Council Directive 77/93/EEC and Directive 2000/29/EC, was tightened in the publication of regulation (EU) 2016/2031[7]. These laws require member states to '*to carry out adequate and efficient control measures*', specifying the measures for inspection and, if required, destruction of the contaminated plants or plant products. Lists of known problematic organisms are maintained by the European Environment Agency (Directorate General SANCO), often based on recommendations from the European and Mediterranean Plant Protection Organisation (EPPO), the regional plant health authority under the auspices of the International Plant Protection Convention (IPPC). A previous weakness in the legislation was that action could only be taken to prevent the movement of formally named organisms; as many of the problems appearing in EU states were caused by previously undescribed organisms, this idea was clearly of little validity. Another problem of great concern was that, once a plant went through the EU biosecurity protocols in ports of entry, it then became a 'European plant'; it was difficult to determine the history of the plant, where it was propagated, which agrichemical treatments it received and how it was transported into Europe.

[7] https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:32016R2031&from=EN

Public awareness of plant health issues was also a factor in determining how state governments viewed biosecurity. The confirmation of the presence of ash dieback in the UK in 2012 was a striking example of how a public outcry led to government action (e.g. Woodward and Boa 2013). Some of the new EU legislation derives from British action following the arrival ash dieback (e.g. Gilligan et al. 2013).

Much of this updated legislation will parallel similar tools used elsewhere, including New Zealand.

In a multi-state region, such as the EU, the biosecurity of the whole trading area is reliant on how the state with the weakest ability to implement biosecurity measures operates. Dealing with these weaknesses on a practical level is difficult. Legislation gives individual states direction, in terms of how their biosecurity agencies should operate, but funding is ultimately the factor determining how stringent the measures implemented can be.

In comparison with the measures adopted in the European Union, those in New Zealand are arguably simpler, but stricter. The work of Biosecurity NZ, as an agency in the Ministry of Primary Industries, is led by the Biosecurity Act 1993, which specifies the duties of the service in terms of risk management, standard setting, response to incursions and long term management of incursions[8]. At ports of entry, biosecurity is focused on risk reduction based on known problems, including any pests/pathogens recently observed by biosecurity agencies elsewhere. All imported goods require biosecurity clearance before release into the country. There are also powers to confiscate and destroy property considered to be of risk, regardless of ownership, in order to prevent entry, establishment or spread of harmful organisms. If a harmful organism establishes in the territory of New Zealand, policies for the development of specific management plans exist[9].

The EU provides over-arching advice to individual member states, but legislation differs from that operational in New Zealand due to the number of individual states concerned. The internal movement of plants and plant materials within the EU occurs without many barriers, as it is a component in internal trade: no unreasonable barriers to this trade are allowed in the EU, although individual states can, with suitable justification, refuse to import goods considered of potential risk.

[8] https://www.biosecurity.govt.nz/law-and-policy/legal-overviews/biosecurity/

[9] https://www.biosecurity.govt.nz/dmsdocument/9464/loggedIn

The UK Plant Health Risk Register

One major recommendation from the UK Tree health and Plant Biosecurity Taskforce, set up by the British Government after the discovery of ash dieback, was for a Plant Health risk Register to be prepared[10]. The register was planned to include all **known** agents posing a risk to health of plants in the British Isles, with an estimate of the relative risk posed. Risk is rated in a matrix designed to capture:

- Likelihood of the risk arising
- Potential impact of the risk, should it enter Britain
- Threat to the sector (likelihood x impact)
- Value of the host plant in the UK.

Each rating is given a numerical value of 1 – 5, based on expert judgement. Mitigations against the invasion and establishment of the pest or pathogen can also be modelled using this approach. The maximum score (relative risk rating) a potentially harmful organism can attain is 125.

It also enables hypothetical quantification of the overall potential impact of a given harmful organism on the UK economy[11]:

- *Cost of risk (UK£, per annum) = likelihood (probability) x impact x crop/ecosystem value (GBP per annum)*

It is unlikely that this calculation would give sufficient accuracy in assessing the monetary impact of an invading organism. The system is not without pitfalls. For example, *Sirococcus tsugae*, a pathogen on a number of conifers (*Cedrus atlantica, C. deodara*, *Tsuga* spp.), initially was given a low risk relative rating of 19; in the two years following establishment of the risk register, however, the pathogen has proved to be highly destructive to host trees, and the relative risk rating was revised to 60.

Phytophthora ramorum, already widespread in the UK, has a relative risk rating of 125 in the absence of mitigation, and 80 with mitigation. A problem with *P. ramorum* is that it has a very wide host range, and has already spread within the UK, where the climatic conditions

[10] https://secure.fera.defra.gov.uk/phiw/riskRegister/

[11] https://secure.fera.defra.gov.uk/phiw/riskRegister/Summary-of-Guidance-for-phase-1-Public-Ver2.pdf

are conducive to disease development. With fewer known hosts, *P. kernoviae* has a lower relative risk rating of 100, in the absence of mitigation.

Local measures to reduce spread

Measures can be introduced within New Zealand to reduce the probability of spread of *Phytophthora* species. For example, producers of grafted varieties should be aware of, and take measures to and eliminate or avoid any *Phytophthora* problems on the production sites. This approach is basic to phytosanitary practice with all plant pests and diseases.

It is important to take measures to prevent the further spread of *Phytophthora* already present in New Zealand in order to reduce the threat to kiwifruit production. Distribution of species already known in New Zealand and causing problems to growers (see: Global overview of *Phytophthora* on *Actinidia*) should be determined with accuracy and measure implemented to prevent further spread. This process would require regular surveys of *Actinidia*-growing areas, not only on the farms themselves, but also of the surrounding land. A contingency plan similar to that recently developed in Australia for *P. cinnamomi* is relevant to containment of *Phytophthora* on kiwifruit in New Zealand. [12]

Kiwifruit growers can adopt more stringent phytosanitary measures within and between orchards, such as either cleaning footwear in a suitable disinfectant (e.g. quaternary ammonium) and using different footwear when visiting other orchards. Sterilizing all equipment that is used in pruning or other management actions is also standard practice. Vehicle wheels and the under chassis should be cleaned with a suitable sterilant when leaving orchards where *Phytophthora* has been diagnosed. These measures sound drastic, but have proven useful in Western Australia, when applied to reduce the risk of spread of *Phytophthora cinnamomi* (Colquhoun and Hardy 2000).

Given the high tolerance of saturation of *Phytophthora* species, imports of aquatic plants or animals carry the risk of introducing these damaging organisms. Unfortunately, biosecurity measures, wherever applied, can rarely be all-encompassing: freedom of movement for people and goods, given reasonable precautions, must still be allowed. Eradication measures can be applied to new outbreaks of *Phytophthora*, if the conditions, including topography and soil types, are suitable. It is extremely difficult to eradicate pathogens once established, however, and the process requires a detailed cost-benefit analysis prior to initiation.

[12] https://nzfungi2.landcareresearch.co.nz/WebForms/LiteratureDetails.aspx?RefUPK=59a1d0d0-9183-4c24-b041-41e2f5d3a065

10 Main findings from three *Phytophthora* case studies

The three case studies (Annex 2) demonstrate general principles for spread of *Phytophthora* infections in crops and in natural ecosystems. For infections to occur, *Phytophthora* requires favourable conditions, which broadly include high soil humidity and moisture, sometimes coupled with alternating drier periods. The dry spells render potential host plants less able to resist infection. Some *Phytophthora* species, such as *P. fragariae*, appear to be highly host-specific. Others, of which *P. cactorum* and *P. cinnamomi* are good examples, have wide host ranges and have resulted in long-distance spread of many pathogenic species through trade and other pathways in cryptic infections, or as dormant propagules in soil.

P. cactorum occurs throughout temperate regions of the globe. It has over 200 known host plants, but has for long been regarded as the dominant or principal *Phytophthora* disease affecting apple production, affecting both orchard-grown plants and apples in storage. Symptoms produced on plants and spread of the pathogen under waterlogged or high soil water conditions are typical of a root-infecting *Phytophthora*. Spread also occurs in the atmosphere, as the asexual propagules (sporangia) are easily detached from sporangiophores (=caducous) and can be dispersed in rain splash from aerial mycelium. Saturated soil conditions enable rapid infection of host roots and rapid spread to other host tissues, due to the reduced ability of the plant to respond to infections under these conditions.

Phytophthora cactorum is placed in Clade 1a of the genus, along with *P. pseudotsugae*, *P. heidraiandra* and *P. idaei*. Other clade 1 species that have been fully described and attack woody plants include *P. quercina* and *P. nicotianae*. The highly destructive potato blight pathogen, *P. infestans,* is in Clade 1c. It has recently become clear that *P. cactorum* is a species complex, including at least three other taxa, of which *P. heidraiandra* and the hybrid *P. x serendipita* are notable examples (see Annex 3). The full host range of the species within the *P. cactorum* complex requires further elucidation.

The pathogen was considered relatively easily recognised in culture, though the discovery that it represents a species complex makes morphological identification less certain.

Phytophthora cinnamomi is the most destructive of all known species in the genus, and arguably of all known plant pathogens (see Annex 3). The species almost certainly evolved in the New Guinea-Sulawesi-Malaysia region, possibly stretching as far east as Taiwan (Ko

et al. 1978). It is highly damaging to avocado production wherever the crop is grown, including South Africa, California, Mexico and Colombia. Despite the pathogen having origins in tropical and sub-tropical regions, *P. cinnamomi* has also established and become a problem in temperate regions.

P. cinnamomi is in clade 7, along with *P.* x *cambivora*, *P. fragariae*, *P. pistaciae*, *P. sojae* and *P. neiderhauseriae.* Phytophthora root rot was first recognised as a problem in California in the 1920s, and now affects approximately 60-75% of avocado groves in the state. The most recent published estimate of losses in avocado groves in California, in 2013, was over US$ 40 million annually (Ploetz 2013).

Strawberry *Phytophthora* crown rot disease, caused by *P. fragariae* var. *fragariae* is commonly known as red core, reflecting the discoloration in the root stele following infection. *P. fragariae* var. *fragariae* is highly host specific and strawberry is the only known natural host. Artificial inoculations of other host genera in the Rosaceae have, however, been successful. As with other *Phytophthora*, the pathogen is highly persistent once established in strawberry crops, most likely through spread of cryptic infections in stock plants which are then traded regionally and internationally. The pathogen has a number of races which vary in virulence on different cultivars and varieties of strawberry. Under conducive conditions, which include cool and wet weather, particularly in the late growing season and into early winter, copious asexual sporangia are produced on infected roots. The sporangia release huge numbers of zoospores capable of spreading infection rapidly within a crop.

Phytophthora fragariae is in clade 7a of the genus, which also includes: *P. fragariae* var. *rubi, P.* x *cambivora, P. europaea, P. uliginosa, P. alni* subsp. *alni* and *P. uniformis*. The sister clade, 7b includes *P. vignae, P. cajani, P. melonis, P. pistaciae, P. sojae, P. cinnamomi, P. parvispora* and *P. neiderhauseri.*

Diagnosis: Initial or field diagnosis of any *Phytophthora* disease is based on visual recognition and interpretation of symptoms on (crop) plants. The majority of root-infecting *Phytophthora* species result in the production of small, chlorotic foliage, failure to flush in the growing season, dieback of distal twigs and branches and eventual death of the whole plant. There may be dead patches of bark at the root collar and necrosis in the inner bark tissues when exposed. *Phytophthora* species primarily infecting aerial plant parts will usually result in foliar necrosis and shoot dieback.

Rapid, sensitive and highly accurate molecular methods are now commonly used in identification of pathogenic *Phytophthora* species. Quantitative PCR and other modifications

of standard PCR protocols are used in many diagnostic laboratories; specific primers have been published for many of the most damaging *Phytophthora* spp. Molecular methods mean that *P. fragariae* can be identified in a single day, according to Bonants et al. (2004), where previously it would take up to a week from sampling to result.

11 Managing *Phytophthora* disease risks

There are several generic measures which can be used for management of all *Phytophthora* diseases. These include:

- fumigate soils used in nurseries producing plants for horticulture and forestry
- avoid wounding of plant roots or shoots
- treat all irrigation water, including that from water courses, to remove (filters) or kill (UV light) *Phytophthora* contaminants
- grow plants in containers raised above ground level
- establish good drainage in orchards (for example) prior to planting

Ensuring good soil drainage is the most important. Additional protection can be obtained by ensuring the growing substrate is less than pH 4. Fertilisers that reduce substrate pH can also help to prevent infections. In contrast, high levels of some fertilizers, particularly those containing nitrates or ammonium, can increase the likelihood of infection and severity of disease attack.

Managing *Phytophthora* diseases in nurseries and in crops such as strawberry, which can be grown in similar conditions, is relatively straightforward compared to field sites with a long history of *Phytophthora* infections. Here management is complicated by the presence of pathogenic species with a wide host range, combined with the longevity of propagules and hyphae in soil and in plant root debris. Attempts to eradicate *Phytophthora* in infested soils have had mixed success. Trenching and chemical barriers, including fumigation, have resulted in temporary reduction of *P. cinnamomi* inoculum in soils in Western Australia. Recent aggressive interventions in Western Australia and Tasmania have included removal of host materials (including root debris), the application of fungicides, soil fumigation and introducing physical barrier to root spread. These successfully reduced *P. cinnamomi* inoculum in soils in Western Australia, and appeared to eradicate the pathogen in Tasmania. The methods used, however, are highly labour intensive and expensive to apply.

Phytosanitary legislation is an important way of preventing spread of *Phytophthora* spp., yet regulations are often incomplete and enforcement ineffective. Phytosanitary officers examine incoming plants and plant products at ports of entry into a state, and reject any materials that are clearly infected by a pathogen or affected by a pest. This process of visual diagnosis is reasonably effective, but can be backed up by sending samples for laboratory analysis, now using culture coupled with molecular methods. The process is most rapid and efficient when diagnostics can be applied directly to the plant tissue sample itself. The methods used, however, can only detect a pest or pathogen if the affected tissue is analysed. Moreover, it is unlikely that apparently clean plants will be sampled, despite the fact that they can carry cryptic infections; plants with soil or other growing substrates increase this risk enormously, as we have only a limited understanding of micro-organism biodiversity in soils.

The growth in plant trading via the internet has created new difficulties in regulating movement of particularly soil-borne pathogens. In some countries it is an offence to sell strawberry planting material infected with *P. fragariae*, yet this is difficult to enforce through remote sales. The recent introduction of highly sensitive molecular methods for detecting soil-borne propagules and cryptic infections of *Phytophthora* and other plant pathogens has made it easier to limit their spread, providing that sampling is of sufficient intensity. Previous detection methods for *Phytophthora* relied on visual inspections and baiting methods and were much less reliable in detecting pathogens.

Other management options: In addition to the generic methods noted above, other more specific measures have been developed to manage *Phytophthora* diseases.

Biological control: Both antagonistic bacteria and fungi have been proposed for use in reduction and elimination of *Phytophthora* diseases, but efficacy varies according to soil conditions and other environmental factors. Biological control agents that are effective under the more controlled environmental conditions of experimental glasshouses do no always prove valuable under field conditions.

Agrichemicals: Heavy reliance on the fungicide metalaxyl, introduced in the 1970s, to reduce the impacts of *Phytophthora* in nurseries and field crops, eventually led to resistance in a number of key species. Agrichemicals based on phosphonate (e.g. phosphite; fosetyl-Al), have proven more durable in managing *Phytophthora* diseases. Current developments in use of these compounds have focused on foliar applications. Trunk injections of woody plants are highly effective as preventative and curative measures but have several

disadvantages, not least the cost of treating individual trees. It is still unclear how phosphonate compounds work against *Phytophthora*, but these compounds remain an effective and control option compared to many other agrochemicals and are relatively more benign in the environment (e.g. Long et al. 1989).

Host resistance: In apple and avocado a number of rootstocks have been selected and marketed which show resistance to their respective *Phytophthora* pathogens. Examples for avocado include Duke 7, G6 and Dusa. For apple, resistant rootstocks are produced regionally and used as required. In selecting resistant materials, however, it is important to ensure that resistance is not related to the age of the plants, and that a wide set of *Phytophthora* isolates is tested. This is particularly true for apple, where *P. cactorum* is now known to be a species complex.

12 Further research and actions

Recommendations for further investigations and actions are noted, based on the findings reported here.

- New Zealand should be in a permanent state of alert for *Phytophthora* attacks on kiwifruit.
- Biosecurity NZ should have state-of-the-art facilities (High-Throughput Sequencing) to examine incoming plants and plant materials, particularly any that also include soil or other plant growth substrates, for Oomycota.
- The abilities of all *Phytophthora* known to attack woody plants and present in New Zealand should be tested on kiwifruit plants under controlled conditions conducive to development of Oomycete diseases.
- Further investigation and characterization is needed of the *Phytophthora* species associated with La Moria (vine decline) in Italy, the most potentially worrisome threat to kiwifruit from this genus.
- Kiwifruit rootstocks should be tested for resistance to *Phytophthora* attack; any genotypes showing resistance must be field tested extensively prior to general deployment.

ANNEX 1 | Taxonomy of *Phytophthora* and related genera

Introduction

Phytophthora is a genus of eukaryotic, fungus-like plant pathogens in the Kingdom Chromista (super kingdom Stramenopila; Heterokonta) and Phylum Heterokontophyta. Many species cause major plant diseases throughout the world. Numbers of confirmed species are uncertain, but are at least 142 (Yang et al. 2107) and some suggest that the genus may contain as many as 600 species (e.g. Brasier 2009). Ho (2018) reported 313 species from mycobank.org, although it is likely that many of the species listed are synonyms. Wikipedia suggests that 170 species are fully described but does not give a source of this estimate. As of early March 2019, the Phytophthora Database web site (www.phytophthoradb.org) includes data for 123 formally described species and 23 provisional species. A general consensus is that approximately 140 species have been fully described to date (add ref.).

Although at least 15 species of *Phytophthora* (Table 2) are known to infect and damage *Actinidia* spp. it is important to consider other species, both for insights on how *Phytophthora* diseases have spread globally and on general pathogen biology.

The *Phytophthora* literature focuses on a relatively small number of highly destructive plant diseases, including potato (and tomato) late blight, caused by *P. infestans*, root rot of soybeans (*P. sojae*) and citrus gummosis (*P. citrophthora* and *P. parasitica*). Some *Phytophthora* diseases appear to be predominantly host-specific, while other have wide host ranges. Further investigation may reveal that reported host-specific species are, in fact, polyphagous. Arguably the most damaging taxon in the genus, *Phytophthora cinnamomi*, causes damage, often mortality, on over one thousand plant species, including kiwifruit (Stewart and McCarrison 1991; Conn et al. 1991; Lattore et al. 1991; Mahdavi 2013). Other species with a wide host range include *P. ramorum*, *P. kernoviae*, *P. cactorum* and *P. pluvialis*.

There are other highly damaging but lesser known diseases caused by *Phytophthora,* such as *P. cinnamomi* killing cinchona trees (quinine tree) in DR Congo (Boa, pers. comm.) and *P. austrocedri* causing dieback of *Austrocedrus* in Patagonia (Greslebin et al. 2007). The same species also appears responsible for mortality of *Juniperus* spp. in Northern Britain (Green et al. 2015).

At least 30 *Phytophthora* species occur in New Zealand (see Scott and Williams, 2015), infecting plants in agriculture, horticulture, commercial forestry and natural forest ecosystems. A prominent example of current concern is *P. agathidicida* (formerly known as *Phytophthora* taxon *Agathis*), causing widespread mortality of kauri (*Agathis australis*) (Bellgard et al. 2016). Although the problem on kauri is considered recent, the pathogen may have been causing damage on a smaller scale for many years (cf. Gadgil 1974) [13].

P. kernoviae was first described from isolates obtained from dying beech (*Fagus sylvatica*) trees in the south-west of England (Brasier et al. 2005), yet it is probably native to Pacific Rim countries (Jung et al. 2018), including New Zealand. The same pathogen also infects non-native plants in New Zealand, causing damage but not death (Ramsfield *et al.* 2009). Following the original description of *P. kernoviae* (Brasier et al. 2005), subsequent work showed that it was identical to an incompletely described *Phytophthora* first isolated in New Zealand from *Annona* plantations and in healthy native forest ecosystems in the 1950s (Newhook 1970).

There is wide concern in the New Zealand Primary Industries that globalisation of trade is leading to further incursions of *Phytophthora* (and other) pathogens into the territory, despite the stringent biosecurity measures in place at ports of entry. It is likely that *P. pluvialis,* now causing serious red needle cast (RNC) on *Pinus radiata* (Dick et al. 2014) is a recent incursion into New Zealand, for example, though the precise pathway remains obscure.

[13] Peter Gadgil identified the causal agent as *Phytophthora heveae*, at a time when advanced diagnostic tools were unavailable.

Taxonomy of *Phytophthora*

For many years, *Phytophthora* and species in the related genera *Pythium*, *Peronospora*, *Saprolegnia, Aphanomyces* and *Achlya* were considered 'unusual' fungi because they produce motile spores, unlike true fungi, which do not. These genera were originally placed in an artificial taxonomic grouping, the Phycomycetes, which also contained species now transferred to taxa in the Zygomycotina and the Chytrids. The Phycomycetes were renamed Oomycota in the late 1960s and placed with the Chytrids in the Mastigomycotina (Ainsworth, 1966; Webster 1970). The production of a biflagellate zoospore by many Oomycota, along with the absence of chitin in the cell walls, continued to raise doubts about their relatedness to true fungi.

In the 1980s, Cavalier-Smith (1981) proposed placing the Oomycota and (true) fungi into separate kingdoms. The Oomycota are now a phylum in the kingdom Chromista (Cavalier-Smith 1986), which also includes the marine algae, golden algae and diatoms. The common feature of Chromista is the presence of four membranes around plastids (Cavalier-Smith 2018).

The phylum Oomycota includes a range of non-photosynthetic Chromista that superficially resemble true fungi, but differ in their life cycles and physiologies. Within the Oomycota, the order Peronosporales encompasses three families, the Albuginaceae, Peronosporaceae and Pythiaceae. A common feature of species in these families is their ability to cause disease, mainly on plants, but also on other organisms. Along with *Phytophthora*, the Peronosporaceae family includes downy mildews in the genera *Peronospora* and *Bremia*. *Pythium* and *Phytopythium* species are placed in the Pythiaceae. The Albuginaceae includes a range of 'white rusts', such as species of *Albugo*, *Pustula* and *Wilsoniana*.

The importance of *Phytophthora* diseases, and the lack of suitable keys for identification, led Grace Waterhouse of the Imperial Mycological Institute in London to propose a novel system of grouping for *Phytophthora*, based on combinations of morphological similarities (Waterhouse 1963).

Groups I and II comprised species producing papillate sporangia; groups III and IV included semipapillate species. In contrast, species lacking papillae were placed in groups V and VI. Further separation depended on how the antheridium (structure delivering male gametes) attached to the oogonium (female gamete; receives DNA from the antheridium). Species in groups I, III and V have paragynous antheridia (attaching to the side of the oogonium), whereas those in groups II, IV and VI have amphigynous attachment (around the stalk of the oogonium).

The scheme was updated in 1990, to include new species (Stamps et al. 1990). Flaws in the groupings were recognized by Waterhouse herself, who stated that the system did not necessarily reflect phylogenetic relationships between the different species. The system was, however, a useful basic tool for determining species of *Phytophthora* known until 1990.

The advent of molecular biology enabled the relationships within the Oomycetes and with other kingdoms to be elucidated with much greater certainty. Cooke et al. (2000) proposed a molecular phylogeny of *Phytophthora* species which divided the genus into eight clades or sub-groups. A recent genus-wide taxonomy of *Phytophthora* in 2014 utilized 11 loci in 92 fully described species, plus 17 provisional species (Martin et al. 2014). The phylogeny was later updated (Yang et al. 2017), utilizing 142 described *Phytophthora* species and 43 provisional taxa. There are now ten delineated clades in the genus. Species relationships supported by the most recent analysis evolved from previously published systems based on molecular analyses (Cooke et al. 2000; Martin and Tooley 2003; Kroon et al. 2004; Blair et al. 2008; Martin et al. 2014).

There are at least 38 genera currently recognized in the Oomycota (e.g. Uzuhashi et al. 2010; Jung et al. 2017).

Clades in the genus *Phytophthora*

The current taxonomy of *Phytophthora* includes 10 separate clades or sub-groups (Figure 1). Some of these clades might in the near future become split into separate genera, but the current consensus is to maintain *Phytophthora* a single genus. In this review, all species will be named in the genus *Phytophthora*. Smaller sub-divisions of species within the clades are also recognized, based on multi-gene sequence analyses, reflecting the presumed evolutionary trajectory of species in the genus.

Full descriptions of newly recognized species now include the clade with which the novel species is most closely aligned, based on molecular analyses.

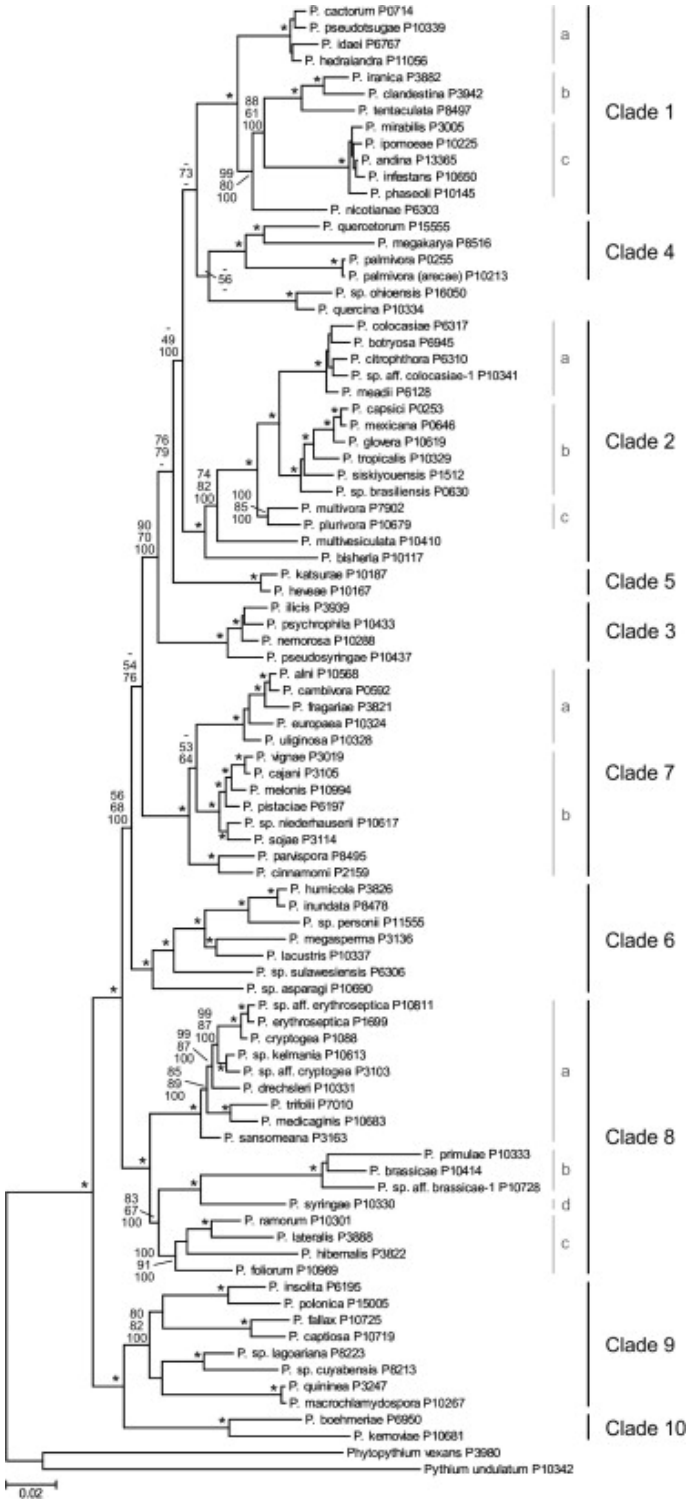

Figure 1. Genus wide phylogeny for *Phytophthora* using seven nuclear and four mitochondrial loci. Maximum likelihood branch lengths shown. Numbers on nodes represent bootstrap support values for maximum likelihood (top), maximum parsimony (middle) and Bayesian posterior probabilities as percentages (bottom). Nodes receiving significant support (>95%) in all analyses are marked with an asterisk (*). Scale bar indicates number of substitutions per site. [From Martin et al. 2014]. The later phylogeny of Yang et al. (2017) gives matching results, but includes 142 fully described species and 43 provisionally named taxa.

Hybrid *Phytophthora*

Given the long history of research on the genus, the concept of inter-specific hybrids between different *Phytophthora* is relatively recent (e.g. Boccas, 1981; Brasier 1991; Brasier et al. 1993). It was suggested prior to the advent of molecular tools that hybrids might be difficult to find or rare in both the true fungi and in the Oomycota. The first unequivocal proof of the existence of hybrids between *Phytophthora* species came with the publication of Man in't Velt et al. (1998). Isozyme and molecular analyses demonstrated that serious damage to *Spathiphyllum* and *Primula*, ornamental plants grown in The Netherlands was caused by hybrids between *P. nicotianae* and *P. cactorum*. Previous work (Goodwin and Fry, 1994; Érsek et al. 1995) had reported the artificially induced formation of *Phytophthora* hybrids under laboratory conditions. Prior to that time, it was speculated that certain described species of *Phytophthora* were, in fact, interspecific hybrids (e.g. Sansome et al. 1991), but the techniques to generate supporting evidence were not available.

Since the 1990s, numerous additional interspecific hybrids of *Phytophthora* have been identified (e.g. Brasier 2001; Martens and van der Peer 2010; Goss et al. 2011; Nagel et al. 2013; Burgess 2015). Where interspecific hybrids occur, it was assumed that the two parental species are recently diverged from the same common ancestor, but that genetic divergence to date was insufficient to prevent compatibility in mating (Man in't Velt et al. 1998). The increasing numbers of publications on hybrid *Phytophthora* in the last 15 years suggests that such events may be quite common both in nature, and in environments heavily influenced by humans, such as plant nurseries (e.g. Bertier et al. 2013; Safaiefarahani et al. 2016).

Arguably, the best known of these hybrids is the alder *Phytophthora*, which has caused widespread mortality of *Alnus* species in riparian zones in northern Europe (Gibbs et al. 1999; Brasier et al. 1999). Until the mid-1990s, the genus *Alnus* was believed to be unaffected by *Phytophthora* infections, but the discovery of dying *A. glutinosa* trees along the River Stour in Kent, England led to the discovery of a novel and virulent *Phytophthora* (Brasier et al. 1995). The problem spread rapidly in Northern Europe on the roots of contaminated *Alnus* plants raised in nursery fields (Jung and Blacksche 2004). Recent work suggests that the same pathogen is also the most common *Phytophthora* taxon present in or on roots of species of ornamental woody plants other than *Alnus* (Puertolas et al. in prep.).

Initial analyses suggested that the parents of *Phytophthora* x *alni* were *P. cambivora* and an unknown species similar to *P. fragariae* (Brasier et al. 1999). Subsequent examination suggested a more complex background to the emergence of this highly damaging hybrid (Ioos et al. 2006). Three sub-species in the complex were proposed by Brasier et al. (2004): *P. alni* subsp. *alni*, *P. alni* subsp. *uniformis* and *P. alni* subsp. *multiformis*, differing in chromosome numbers and the numbers of alleles at certain single loci (Ioos et al. 2006). Amongst these variants, *P. alni* subsp. *alni* is the most aggressive pathogen; the other two subspecies were considered far less damaging to *Alnus*.

The status of these apparent hybrids has been further elucidated (Ioos et al. 2007a,b; Husson et al. 2015). Examination of ploidy in the complex demonstrated that *P. alni* subsp. *alni* is a hybrid between *P. alni* subsp. *uniformis* and *P. alni* subsp. *multiformis*. More recently it was confirmed that the variant previously named *P. alni* subsp. *uniformis* is a diploid *Phytophthora* species in its own right (Husson et al. 2015),. This work enabled the three taxa to be renamed as *P.* ×*alni*, *P.* ×*multiformis* and *P. uniformis*. *P. uniformis* was found in Alaska in soils around *Alnus incana* subsp. *tenuifolia* (Adams et al. 2008).

The potential for interspecific hybrids to produce novel *Phytophthora* variants with damaging effects on hitherto relatively unaffected plants cannot be overemphasized (Brasier 2001). The international trade in ornamental and horticulture plants has clearly led to the spread of many species of *Phytophthora* from their centres of evolution to native environments (Santini et al. 2013; 2018), causing serious damage to local flora. With the possibility of hybridization between species that diverged in different environments, the threat of damage by *Phytophthora* spp. is further magnified. Moreover, the apparently rather complex nature of the hybridization events that led to the formation of *P.* x *alni* underlines the genetically plastic potential of *Phytophthora* and further highlights the threat these taxa pose to plants.

Other Genera of Peronosporales

The genus *Pythium* originally included at least 138 species and was known for many years to include a number of different clades based on both morphological (ref?) and molecular analyses (e.g. Levesque and de Cock 2004; Bala et al. 2010). The genus was then divided into several genera: *Pythium sensu stricto, Ovatisporangium*, *Globisporangium* and *Pilasporangium* (Uzuhashi et al. 2010). *Ovatisporangium* was eventually rejected as the name *Phytopythium* had precedence for species previously place in *Pythium* clade K (de Cock et al. 2015). Some *Pythium* species are serious pathogens on crop plants. For example, *P. violae* can cause severe cavity spot of carrot crops (refs), although other *Pythium* species may also be involved. Most *Pythium* species are, however, facultative pathogens, causing disease when conditions are conducive to pathogen proliferation. *Pythium* infections are a common contributor to damping-off of seedlings of many different plants.

Other lesser known genera occurring in families of the Peronosporales include pathogens on other organisms.

- Peronosporaceae (*Peronospora* and sister genera; *Bremia*; *Plasmopara*; *Phytophthora*);
- Albuginaceae (*Albugo*; *Pustula*; *Wilsoniana*);
- Pythiaceae (*Pythium*; *Phytopythium*; *Lagenidium*).

Some authorities maintain placing of *Phytophthora* in the Pythiaceae. A new family, the Salisapiliaceae, was proposed within the Peronosporaceae in 2010 (Hulvey et al. 2010), associated with dead foliage of *Spartina alternifolia*.

Downy Mildews

There are many plant diseases known as downy mildews, though strictly, the causal agents should be Oomycota in the family Peronosporaceae. They are obligate parasites, unable to grow and reproduce in the absence of a host plant. Arguably the best known species is *Plasmopara viticoa*, cause of grape vine downy mildew, which is endemic in North America on, for example, *Vitis aestivalis*. The pathogen was inadvertently introduced from North America into Europe in the 19th century. In the absence of suitable control and management measures it causes major losses on wine and dessert grapes (add ref). The pathogen was also transported to other grape-producing regions of the world, including Australia and New Zealand (add ref).

Plasmopara species causing downy mildew on crops such as sunflower (and other Asteraceae), lettuce, carrot, parsley and parsnip (add ref). The most widespread pathogen in *Bremia*, a genus with few species, is *B. lactucae*, a damaging downy mildew in commercial lettuce production (add ref).

White rusts (white blister rusts)

The common name of these pathogens suggests that they are related to the Basidiomycota rust species, yet both groups have distinct and different taxonomies and biology. The most commonly encountered genus of white rusts is *Albugo*, which includes species causing diseases on several Brassicaceae, and less commonly on lettuce (and other Amaranthaceae), spinach and sweet potato (add ref). Two other species in the Albuginaceae, *Pustula* and *Wilsoniana*, are less well-known genera, but species can cause white rust-like symptoms on plants including sunflower and other Asteraceae, on *Portulaca* (Portulacaceae) and on Amaranthaceae (e.g. Ploch et al. 2011).

Other Pythiaceae

The genus *Lagenidium*, also placed in the Pythiaceae, includes species that are pathogenic on animals (mammals, insects). *L. gigateum* was used as a biological control agent for reducing mosquito populations (Teng et al 2005), but was subsequently withdrawn when pathogenicity to mammals (dogs, cats, humans) was demonstrated (Vilela et al. 2015).In the past 30+ years additional genera related to *Phytophthora* (and *Pythium*) have been described, including most notably:

- *Halophytophthora* (Ho & Jong 1990; Nakagiri 2000)
- *Nothophytophthora* (Jung et al. 2017)
- *Phytopythium* (Bala et al. 2010)

The genus *Halophytophthora* was proposed by Ho and Jong in 1990 to include *Phytophthora*-like species with an ecological preference for saline environments, with distinct zoospore morphology and the presence of a persistent vesicle. Species are commonly found in tropical and sub-tropical mangroves (Nakagiri 2000), although many species also occur in temperate regions. To date 14 species, plus two varieties, of *Halophytophthora* have been described. It is possible that *Halophytophthora* species are not truly confined to saline habitats. When grown in the laboratory isolates can tolerate a wide range of salinities (Nakagiri et al. 1994; 2001). At least one species, *H. mycoparasitica* is parasitic on true fungi (add ref).

The genus *Nothophytophthora* was first proposed by Jung et al. in 2017 to include many slow-growing isolates of Oomycetes. Morphological characteristics and molecular analyses showed isolates to be close to *Phytophthora*, but of sufficient distinctness to warrant a separate genus. Six species were fully described, and three further taxa noted. The life strategy of *Nothophytophthora* remains to be elucidated, but isolation of species from forests showing dieback and caducity of sporangia suggests they may be pathogens (Jung et al. 2017). The genome of an isolate of *N. valdiviana* obtained from diseased foliage of *Eucalyptus nitens* in Chile was published in 2018 (Studholme et al. 2018).

Phytopythium includes species originally placed in in *Pythium* clade K, but separated into the newly erected genus by Bala et al. in 2010). Their initial specification of the genus listed fifteen species, mostly those previously placed in *Pythium* clade K, but also including a newly described species, *Phytopythium sindhum*, isolated from the rhizosphere of banana plants in the Sindh District of Pakistan. The morphology features of the genus are intermediate between *Pythium* and *Phytophthora*. However, molecular analyses show that *Phytopythium* is distinct from both (de Cock et al. 2015).

Since 2010, several new species have been either moved from another genus into *Phytopythium* or newly described, including *P. kandeliae* (previously *Halophytophthora kandeliae*; Marano et al. 2014), *P. mirpurense* (de Cock et al. 2014), *P. fagopyri* (Baten et al. 2014) and *P. leanoi* and *P. domae* (Bennett et al. 2017).

Several *Phytopythium* species are known to cause plant disease; other species are known only as saprotrophs. Species in the genus can be carried in irrigation waters (Redekar et al. 2019) or in drainage waters from other environments (Afandi et al. 2018), emphasizing the need to use treatments to remove Oomycota if nursery irrigation water is recycled. It is important to note that both *P. vexans* and *P. helicoides* have been shown to cause root and collar rot of *Actinidia* species (Wang et al. 2015; Polat et al. 2017).

ANNEX 2 | Three case studies of *Phytophthora* diseases: apple, avocado and strawberry

Each case study is presented using the following headings:

- Introduction
- Biology
- Genetics
- Detection and diagnostics
- Host range
- Management and control
- Impact and economic losses

CASE STUDY 1: *Phytophthora cactorum* on apple

Introduction

P. cactorum was one of the earliest members of the genus to be identified, first described in 1870 as *Peronospora cactorum* causing crown and root rot of the ornamental cacti *Carnegiea gigantea* and *Melocactus nigro-tomentosus* in Prussia (Lebert and Cohn, 1870). Since then the known host list for this common and highly destructive species has expanded to include over 200 species of trees, ornamental plants and horticultural fruit crops (Nienhaus 1960; Erwin and Ribiero 1996; Hudler 2013). It is regarded as the 'typical' *Phytophthora* disease in apple orchards, where it causes trunk cankers producing dark red exudates, reduced foliage size, chlorosis, dieback and mortality. These symptoms are typical of a root-infecting *Phytophthora*, but *P. cactorum* also spreads in the atmosphere, when caducous sporangia are dispersed in rain splash (Darmono et al. 1991). Aerial spread from rain splash is probably responsible for foliar infections on certain herbaceous species, such as American ginseng (*Panax quinquefolius*; Darmono et al. 1991).

Phytophthora cactorum is present in temperate regions throughout the world, and in conditions conducive to pathogen growth and development causes major losses on many different plants hosts. The disease caused in apple is considered the most important affecting this crop in many parts of the temperate world (Jeffers and Aldwinckle 1988). It is surprising to note that, although widely known USA apple growing areas from the 1930s (e.g. Baines 1935; 1939), this pathogen only appeared to begin causing notable losses in apple orchards in Europe in the 1950s (e.g. Braun 1952; Smith 1953), suggesting that introduction and establishment of *P. cactorum* on that continent occurred in the 1940s. The first report of *P. cactorum* causing problems on apples in New Zealand were made in the late 1940s onwards (e.g. Smith 1950; Northcote 1954).

Biology

Reproductive organs are separated from the hyphae by septa, although septation may be observed more commonly in hyphae of older cultures (Hudler 2013). Asexual reproduction is via papillate, caducous sporangia, from which zoospores are released in suitable conditions; if these conditions are not present, the sporangium can germinate directly to form a germ tube, which can infect a host plant. Chlamydospores are also present, formation depending on moisture and temperature fluctuations. Sexual reproduction involves the production of uninucleate oospores, which divide and become multinucleate immediately before germination (Hudler 2013). Antheridia are paragynous. Being homothallic, genetic diversity in *P. cactorum* populations within a given locality can be high. Chlamydospores and oospores form in the soil or in colonized plant materials, and can remain dormant until conditions conducive to pathogen growth occur (Hudler 2013).

Growth in culture was described by Erwin and Ribeiro (1996) as a 'less defined petaloid colony'. Approximately 50% of the mycelium was submerged in the growth medium, the remaining

mycelium being aerial (Erwin and Ribeiro 1996). Growth in vitro occurs between 4 - 30°C, with an optimum at 25°C (Harris 1988).

As with other species in the genus *Phytophthora*, *P. cactorum* proliferates rapidly under conditions of water saturated soils. Oospores or chlamydospores germinate to produce sporangia, from which the life cycle is continued. Suitable host plants growing in wet soils are infected rapidly, once the conditions for spore germination are met (Hudler 2013).

The infection biology of *P. cactorum* is best known from research on apples, where the pathogen is known as a disease affecting the rootstock or as collar rot, where the symptoms are on the scion, usually near ground level (Jeffers and Wilcox 1990). Most initial infections arise through penetration of fine roots by germ tubes arising from encysted zoospores. In addition, the pathogen can enter plants through wounds, either above or below ground, colonizing phloem in the stem and roots (subsequently phloem) in the roots.

Visible symptoms of infection include the foliage in the crown turning a red colour (Utkhede 1984; Erwin and Ribeiro 1996), followed by necrosis and twig/shoot dieback. Once the pathogen girdles major roots and, ultimately, the stem, mortality occurs. Removal of the bark at the base of the stem reveals a brown, necrotic area, sometimes with the margin of the necrosis/healthy tissues visible (Van der Merwe and Matthee 1973).

Apple trees are most susceptible to infection during periods of high humidity and rainfall Bark tissues are resistant to infection during the dormant season, but become susceptible during spring, as growth begins in the new season (Sewell and Wilson 1973; Bielenin 1977). Once the first leaves of the season are fully open, however, overall susceptibility declines.

Phytophthora cactorum is also a well-known component in the complex syndrome 'Apple Replant Disease', which prevents vigorous growth of apple trees in soils which have been used for apple crops in the recent past (e.g. Sewell 1981; Moein et al. 2108).

Genetics

Phytophthora cactorum is placed in Clade 1a of the genus taxonomy, along with *P. pseudotsugae*, *P. heidraiandra* and *P. idaei* (Martin et al. 2014). Other fully described clade 1 species that attack woody plants include *P. quercina* and *P. nicotianae.* The potato blight pathogen, *P. infestans,* is in Clade 1c.

The true status of *P. cactorum* as a single taxon has been disputed for many years, and work in the past 20-30 years has clearly distinguished several species within the complex (e.g. Hantula et al. 1997; 2000; Bhat et a. 2006; Pánek et al. 2016), including *P. heidriaindra* and the hybrid *P. x serendipita.* A draft of the *P. cactorum* genome, a strain isolated from European beech, was announced in 2017 (Grenville-Briggs et al. 2017). The full genome of a *P. cactorum sensu stricto* isolate from *Panax notoginseng* (ginseng) in Yunnan, China, was published in 2018 (Yang et al. 2018); the genome was large compared with other *Phytophthora* species, including over 121 million base pairs encoding 27,981 genes. Yang et al. (2018) indicated that the genome contained greater numbers of genes encoding enzyme involved in the degradation of plant defence compounds compared with the *P. sojae* genome, consistent with *P. cactorum* being a wide-host range pathogen.

Detection and diagnostics

Morphological methods have been widely used in the past to diagnose *P. cactorum* infections. On apple plants, there is likely to be small, yellow foliage produced, along with initial dieback of the branch tips. Initial detection of the pathogen can be made using *Phytophthora*-specific lateral flow devices (add ref.); until the recent widespread use of molecular methods, an ELISA test was used to identify *P. cactorum* infections in plant materials (add ref.).

Cultures of *P. cactorum* are homothallic, with paragynous antheridia couple closely with the oogonial stalk. Oospores can be both plerotic or aplerotic. Sporangia are cauducous and papillate, formed on a short pedicel (add ref).

Host range

The first finding of *P. cactorum* affecting apples in orchards, reputedly in 1858, predated the isolation and description of the pathogen from cacti. The causal agent was determined some years later (see: Mason & Huber, 2002).

The host range of *P. cactorum sensu lato*, however, is very wide (Erwin and Ribiero 1996; Hudler 2013). The more recent recognition that *P. cactorum* represents a complex of species (e.g. Hantula et al. 1997; 2000; Pánek et al. 2016) suggests that the host range for each individual species will require careful testing to determine the actual damage caused. Apart from apple orchards, *P. cactorum* is sometimes a severe problem in forest nurseries, where many plant species can be infected (Hudler 2013). It also causes serious crown and root rot, plus leather rot of fruits, on strawberry crops (Rose 1924).

Amongst many ornamental woody plants infected, *Rhododendron* varieties and cultivars can be seriously damaged by *P. cactorum*, although this pathogen species is considered less of a threat to these ornamental woody plants than *P. ramorum* or *P. cinnamomi* (Benson and Hoitink 2014). *Phytophthora ramorum* and *P. cactorum* cause dieback of Rhododendron shoots, whereas *P. cinnamomi* causes severe root rot (Linderman and Benson 2014)

Management and Control

Management of problems caused by *P. cactorum* match those applied for other *Phytophthora* species (see below), and include:

- soil fumigation in nurseries where plants are raised for horticultural or forestry uses,
- avoiding any processes which might inflict wounds on the plants,
- applying proper sanitation management to irrigation waters
- growing plants in containers raised above ground level, and
- using good drainage in orchards.

Maintaining good soil drainage is certainly the most important of these management methods (Utkhede and Smith 1996), but ensuring the growing substrate is at a pH less than 4 can also inhibit development of Phytophthora propagules: application of fertilisers that reduce the pH is used to prevent infections (e.g. Utkhede and Smith 1995a). High levels of fertilizer, particularly excess nitrates or ammonium, however, can result in increased disease severity (Schmitthenner and Canaday 1983; Utkhede and Smith 1995a).

Current chemical applications are mainly based on fosetyl-Al, which can be highly effective in prevention of infections and treatment of ongoing infestations (Utkhede and Smith 1995c). The mechanism of action of fosetyl-Al is unclear, but activity against Phytophthora has long been maintained (e.g. Long et al. 1989). Metalaxyl has proven effective against *Phytophthora* diseases since it was marketed in the 1970s, but increasing numbers of *Phytophthora* species and isolates are showing resistance to this chemical, the first appearing within a few years of first introduction (Cooke 1981; Davidse et al. 1981).

Certain biological control agents, both bacteria and fungi (Utkhede 1983; 1987; Utkhede et al. 2001; Smith et al. 1990), have been proposed for use against development of *Phytophthora* diseases, but their efficacy depends greatly on edaphic and other environmental factors.

Host resistance has long been recognized as having potential to reduce the impacts of *P. cactorum* in apple orchards (e.g. McIntosh and Mellor 1954; Sewell & Wilson 1959), and provides the most reliable method of control for plant diseases in the medium to long-term. With apples and *P. cactorum*, it is the rootstock which should provide host resistance. Methods available for testing the susceptibility of apple rootstocks to *Phytophthora* are varied (Borecki and Millikan 1969; Sewell and Wilson 1973; Bielenin 1977a; Bielenin 1977b; Dakwa and Sewell 1981; Jeffers and Aldwinckle 1986; Utkhede and Quamme 1988; Browne and Mircetich 1993; Zondo 2001), suggesting that standardized protocols are required for this approach to disease control.

During aging, apple trees appear to become more susceptible to infection and mortality from *P. cactorum* (Sewell and Wilson 1973; Miller and Pollard 1976; Soteros et al. 1985). This type of early

resistance may be referred to as juvenile resistance, but it is unclear why the resistance is lost with increasing age. Nevertheless, loss increasing susceptibility with age must be taken into account when planning resistance screening of apple against *P. cactorum*. Both polygenic and single gene resistance to *P. cactorum* have been proposed, following artificial inoculations (e.g. Alston 1970; Brown 1975). A particularly useful rootstock, in terms of conferring resistance on offspring, is Malling Merton cultivar Northern Spy (Cummins and Aldwinkle 1992). It is also known that resistance of a given rootstock may vary between regions (Utkhede 1986), indicating the requirement for extra care in planning planting. It is also possible that the speciation with the *P. cactorum* complex (see above) contributed to the differential resistance effects observed, as different species within the complex will undoubtedly show varying aggressiveness to apple rootstocks. It is also of importance to consider resistance to other species of *Phytophthora* when proposing plants for establishing new orchards.

Impact and economic losses

In the past, *Phytophthora cactorum* infections were very damaging to apple yields in most regions of the world was extensive production occurs. In the UK, nurseries producing apples switched from the highly susceptible MM104 rootstock to MM106, which is more suited to local conditions (Harris 1988). Losses are more severe in the USA due to the use of more susceptible rootstocks (compared to those used in in Europe). The impact of *P. cactorum* on strawberry can be high when the plants are cultivated using older methods.

CASE STUDY 2: *Phytophthora cinnamomi* on avocado

Introduction

Arguably, *Phytophthora cinnamomi* is the most destructive of all known species in the genus. It could, overall, be the most damaging plant pathogen known, as it causes major losses in both plantation crops and in natural forest ecosystems (Zentmeyer 1980; Hardham 2005; Hardham and Blackman 2018). First isolated and described in the 1920s from dying cinnamon trees (*Cinnamomum burmanii*) planted in Sumatra and New Guinea (Rands 1922), *P. cinnamomi* is now recorded on all habitable continents. Some of this spread almost certainly occurred before the organism itself was first described (see Newhook & Podger 1972; Coffey, 1987; Santini et al. 2013), through human activities. Initial dispersals from the centre of evolution were most likely made with the extensive plant exploration expeditions between the late 18th and early 20th Centuries (Robin et al. 2012). The true origin of *P. cinnamomi* was a matter of considerable scientific debate for some time (e.g. Arentz & Simpson 1986; Zentmeyer 1987), but the early idea that the taxon evolved in the New Guinea-Sulawesi-Malaysia region, with populations also present in Taiwan (Ko et al. 1978), has persisted. Ko et al. (1978) suggested that Taiwan was within the centre of origin of *P. cinnamomi*, as the pathogen was found in native, healthy forest in the central region of the island, whilst at the same time severe damage on avocado was occurring in avocado groves on the island.

Phytophthora cinnamomi was first identified in Australasia before 1930 as the causal agent of pineapple top rot (Simmonds 1937). The disease caused epidemics in Queensland in the late 19th Century (Tryon 1913). The pathogen remains highly damaging to production of both avocado and pineapple in subtropical areas of New South Wales and Queensland and in other avocado growing regions of the world, including South Africa, California, Mexico and Colombia. The first report of *P. cinnamomi* in New Zealand was in approximately 1950 (cited from a personal communication in Newcombe and Podger 1972), although the host plants were not clear.

A survey of damage caused by *P. cinnamomi* to shelter belts of the exotic gymnosperms *Pinus radiata* and *Cupressus macrocarpa*, carried out in New Zealand in 1956 showed significant damage by the pathogen in 50% of shelter belts examined (Sutherland and Newhook 1959). Moreover, little leaf disease, a problem well known on pines in the former cotton-growing areas of the southern USA (Campbell 1948), is also known to affect *Pinus radiata* in plantations in New Zealand (Hepting and Newhook 1962; Newhook 1970). In general, however, the severity of forest diseases caused by *P. cinnamomi* in New Zealand is thought to be less than seen in parts of Australia, despite the hypothetically more conducive environmental conditions (Weste and Marks, 1987).

Biology

Compared with many *Phytophthora* species, *Phytophthora cinnamomi* is relatively easy to identify in culture. Growth can be vigorous on V8 agar (Smith 1988). Petalloid growth occurs on potato dextrose agar. Hyphae produce coralloid-like structures during growth, through the formation of swellings. The optimum temperature for mycelial growth in both soil and in culture is 24 – 28°C, with some growth occurring between 5°C and about 32–34°C (Smith 1988).

Sporangia are ovoid and non-papillate, approx. 57 x 33 µm, forming on simple sporangiophores and showing nested (internal) proliferation (Robin et al. 2012). Sporangia may produce 10 – 30 zoospores, or germinate directly to form hyphae, depending on temperature and soil matric potential and pH (Harris 1988).

Thin-walled chlamydospores are also formed in culture. Oogonia are not produced in single isolate cultures, as *P. cinnamomi* is heterothallic. The most common mating type found globally is A2; A1 isolates are uncommon, except in the presumed region of origin. Typically only one mating type is found in a region. Mating type A2 can be induced to produce oospores in a homothallic manner, if provided with the correct stimulus, such as volatile organic compounds from *Trichoderma viride* (Smith 1998).

Genetics

Molecular analyses place *Phytophthora cinnamomi* in clade 7, along with *P.* x *cambivora* (long considered a 'true' species, but recently recognized as a hybrid), *P. fragariae*, *P. pistaciae*, *P. sojae* and *P. neiderhauseriae* (Blair et al. 2008; Martin et al. 2014). The full genomes of three isolates of *P. cinnamomi* are available online:

http://fungidb.org/fungidb/

http://genome.jgi.doe.gov/Phyci1/Phyci1.home.html

www.ncbi.nlm.nih.gov/assembly/GCA_001314365.1

www.ncbi.nlm.nih.gov/assembly/GCA_001314505.1

Transcriptomes of the pathogen are also available (Meyer et al. 2016; Reitmann et al. 2016).

Detection and diagnostics

The pathogen is first observed from the detrimental impact it has on infected plants. Various further tests are available for identification of the pathogen causing the symptoms. Immunodiagnostic tests, often based on the use of Phytophthora-specific lateral flow devices (Lane et al. 2007) can demonstrate that a *Phytophthora* spp. is causing the symptoms, but these tools are not sufficiently discriminatory to determine the species involved. Molecular analyses are now the most common methods of identification of *Phytophthora* spp. causing disease (Vincelli and Tisserat 2008). These methods are rapid, sensitive and highly accurate. Quantitative PCR is now used in many diagnostics laboratories and, utilizing the correct primers, can detect *P. cinnamomi* very rapidly (Elliot et al., 2015; Eshraghi et al., 2011). Nested PCR is also useful for detecting the pathogen when quantities of DNA present are very low (Engelbrecht et al., 2013)

Host range

Zentmeyer (1980) listed approximately 950 woody plants susceptible to *P. cinnamomi* attack, each of which may be badly damaged or killed when growing in conditions conducive to pathogen development. Over 15 years later, Erwin and Ribeiro (1996) suggested the host range included over 1000 plant species, with both gymnosperms and angiosperms susceptible to the pathogen, under conducive conditions. The most recent estimate of the host range is that over 3000 plant species are infected by *P. cinnamomi* (Hardham 2005). The Kiwi fruit is known to be susceptible to *P. cinnamomi* (e.g. Stewart and McCarrison, 1991).

Management and Control

In general, control of *P. cinnamomi* is complicated by the very wide host range of the pathogen. The longevity of *P. cinnamomi* propagules and hyphae in soil and in plant root debris (Crone et al. 2013;

Jung et al. 2013) also complicates attempts to use control measures. Under these circumstances, it is necessary to manage edaphic conditions, as well as implement biological and chemical control options. In recent years, drastic attempts have been made to reduce the impacts of *P. cinnamomi* in wildlands in Western Australia, where the disease caused by this pathogen has spread at an alarming rate (Shearer et al. 2007) and threatens an estimated 3,000 species in this region known as a global biodiversity hotspot (Shearer et al. 2004). Attempts to eradicate the pathogen in this region have had mixed success. The use of trenching and chemical barriers, including fumigation, gave temporary reduction in *P. cinnamomi* inoculum in the soil (Weste et al. 1973), but the effect was reversed after high rainfall (Weste and Marks 1987). A later attempt, again using physical barriers to root growth and drenching the soil with formaldehyde and metalaxyl solutions, was also partially successful (Hill et al. 1995), although formaldehyde application did not eradicate the pathogen. More recent attempts to manage the *P. cinnamomi* problem in Australia have built on the earlier work, but recognised that highly destructive intervention was required, including removal of host materials (including root debris), the application of fungicides, soil fumigation and introducing physical barrier to root spread (Dunstan et al. 2010). Over a two years monitoring period, the methods applied reduced *P. cinnamomi* recoveries at the site in Western Australia, but appeared to eradicate the pathogen at another site (in Tasmania). Clearly, such methods are highly labour intensive and expensive to apply.

Various agrochemicals have been used in the management of avocado root rot caused by *P. cinnamomi*, although the use of metalaxyl in nursery situations has reduced due to increasing resistance in various *Phytophthora* species (Morton and Urech 1988). Phosphonate, applied as organic and inorganic salts of phosphite, however, is still widely used with good results, although the most effective – and expensive - method utilizes fosetyl-Al (alkyl phosphonate; Darvas et al. 1984). Trunk injections on avocado trees have been used widely for over 40 years (e.g. Darvas et al. 1983; Pegg et al. 1987) and remain very effective against root rot of avocado (McLeod et al. 2018). The beneficial activity of phosphites soon became evident as trees previously in serious decline from root and collar rot recovered and began to thrive (Whiley et al. 1995).

The process of trunk injection, however, is very costly, requiring considerable time for each tree, along with specialized training and equipment. Trunk injection also causes physical damage to the trees, potentially allowing decay fungi to enter and proliferate. More recently, the possibility of using foliar sprays of phosphite-based agrochemicals to treat *P. cinnamomi* on avocado has been explored, as this application method is far simpler and more cost effective than trunk injections (McLeod et al. 2018).

Given the importance of *P. cinnamomi* in avocado production globally, considerable efforts have gone into examining the relative resistance/susceptibility of different avocado genotypes to the pathogen (Zentmeyer and Thorn 1956; Zentmeyer 1980). In early work on resistance, it became clear that exploitation of the innate resistance in some avocado lines could help in managing the disease. Based on screening in the 1970s, Zentmeyer (1980) recommended two rootstocks, Duke 7 and G6, originating in Mexico, be used on badly affected sites. Selection and breeding programmes for resistance have also been ongoing in South Africa (Botha et al.1990) and Australia (Smith et al. 2011). Other resistant rootstocks have been released for field use in the intervening period, a recent one being 'Dusa', first marketed in 2004 following 15 years of exhaustive testing (cf. van den Berg et al. 2018).

Impact and economic losses

Phytophthora root rot affects approximately 60-75% of avocado groves in California. The disease first became important in the 1920s when a severe decline of avocado trees was noticed, especially in regions of San Diego County. Where the pathogen arrived from at that time is unknown: it may have been introduced on stock plants of avocados, although the disease probably did not occur in the regions of Mexico from where the majority of avocado introductions originated. It is also thought that *P. cinnamomi* may have been introduced into California on one of the many ornamental species brought into the state as it was colonized by European-descent settlers in the late 19th and early 20th centuries.

Phytophthora cinnamomi was described as '*the main biological constraint of avocado production throughout the world, especially in areas that are prone to flooding and hypoxia*' by van den Berg et al. (2018). It is the most important disease problem impacting on avocado production globally (Coffey 1987; Ploetz et al. 2002; Ramirez-Gil et al. 2017).

In infested soils, feeder roots of avocado are rapidly destroyed by *P. cinnamomi*, resulting in aerial symptoms including reduced foliage size, chlorosis and wilting, and dieback, with death occurring within two years of infection (Zentmeyer 1984).

Published losses of avocado production to this pathogen are over 20 years old, but in 1996, it was estimated that *P. cinnamomi* infections in avocado groves in California alone were some US$30 million annually (Erwin and Ribeiro, 1996). A later estimate suggested losses in California were over US$ 40 million annually (Ploetz 2013). Data used in calculating losses include reductions in fruit production, along with the costs of diagnostics, remedial treatments and research to improve management protocols.

CASE STUDY 3: *Phytophthora fragariae* on strawberry

Introduction

This problematic disease, now widespread on strawberries wherever they are grown commercially was first fully described following detection in 1934-35 on a crop in Kent, England (Hickman 1940). Affected plants were growing in a small area of the field where water gathered after heavy rain. Treatment with formalin in an attempt to eliminate supposed root parasites had no effect on newly planted strawberries, which also died. Inspection of the dead plants showed that the root systems had decayed from the root tips backwards towards the crown. Fibrous roots were almost entirely destroyed. Examination of roots from plants more recently infected revealed the typical symptom of red core (red stele), the response in the root cortex to the presence of *P. fragariae*. The disease itself had been noted prior to Hickman's report (e.g. Alcock and Howells 1936), and recognised as caused by a *Phytophthora,* but the causal agent had not been isolated with certainty not fully described. Subsequent work by Hickman and others (Hickman and English 1951; Hickman and Goode 1953; Goode 1956) firmly established the causal agent and demonstrated modes of infection.

Early work also suggested that different races of *P. fragariae* existed, with isolates from the USA and Canada showing varying virulence on a range of strawberry varieties (Converse and Scott, 1962; Hickman1962; Pepin and Daubeny 1964; Montgomerie 1967). By the 1960s, red core disease was known in all regions where strawberries are grown, including New Zealand (Montgomerie 1967), suggesting that the pathogen was probably transported between continents from its region of evolution with the movement of strawberry germplasm. The variety of the pathogen prevalent on strawberry is now named *P. fragariae* Hickman var. *fragariae* Wilcox & Duncan, to distinguish this variety from *P. fragariae* Hickman var. *rubi* Wilcox & Duncan, which attacks predominantly raspberry (Wilcox and Duncan 1993; Wilcox et al. 1993). In the remainder of this review, *P. fragariae* will be used to refer to the variety that predominates on strawberry crops.

Biology

In culture, *P. fragariae* is relatively slow growing compared with some other *Phytophthora* species (Duncan 1988, with a temperature optimum of approx. 22°C (min: 3°C; max 30°C). The large, non-papillate sporangia are on-caducous. Oospores are produced sparsely in culture, but can be abundant in infected roots of strawberry (Duncan 1977; 1988). Germination of oospores prepared from infected strawberry roots was rapid on distilled water agar, with mycelia or sporangia observed from 58 and 79% after incubation for 7 and 14 days, respectively (Duncan 1977). Optimum germination of oospores occurs at 10 – 15°C. Pre-incubation, before plating on distilled water agar markedly improved germination. There was no evidence of direct germination of oospores to produce mycelium in *P. fragariae* (Duncan 1977).

Non-papillate sporangia are approx. 20 – 30 μm in breadth, 25 – 45 μm long, on maturity releasing between 8 – 14 (possibly up to 16) motile zoospores into the substrate (Duncan 1975). Zoospores

can remain motile for several hours at temperatures up to 15°C, but in warmer conditions, motility is greatly reduced. Sporangia are produced and release zoospores throughout the autumn period, when conditions are suitable for production (Duncan 1988).

Infection is via the root tips, where zoospores encyst before forming germ tubes that penetrate the root cortex. The optimum temperature for infection, 10 – 17°C, is closely allied to that for zoospore release, although infections can occur at temperatures as low as 2°C; no infection occurred at 25°C (Duncan, unpublished, cited in EPPO 19??). The pathogen grows into the stele, the response of which results in the typical red core (red stele) symptoms of infection (add ref). At the same time as growth in the stele occurs, branching hyphae emerge through the root cortex, forming sporangia outside the host plant, from which further zoospores are released. This mode of infection, coupled with the tendency of zoospores to show negative geotropism, results in accumulation of infective propagules in the soil water near the surface. Later in the infection cycle, the roots begin to rot from the distal parts towards the crown of the plant. Oospores form in the stele of dead roots, and remain dormant through winter, until suitable edaphic conditions occur enabling germination (EPPO 19??).

Spread on plants occurs rapidly on sloping field sites. The pathogen overwinters as oospores in roots; strawberry root debris containing these sexual structures enables *P. fragariae* to persist for many years in the absence of living host plants (Duncan and Cowan 1980). Methods for cultivation of strawberry, with large numbers of clonal plants planted closely together, encourage the rapid spread of the pathogen in a crop.

Genetics

Phytophthora fragariae is placed in clade 7a of the most recent phylogenetic analyses of the genus (Martin et al. 2014). Clade 7a also includes: *P. fragariae* var. *rubi, P. x cambivora, P. europaea, P. uliginosa, P. alni* subsp. *alni* and *P. uniformis*. The sister clade 7b includes *P. vignae, P. cajani, P. melonis, P. pistaciae, P. sojae, P. cinnamomi, P. parvispora* and *P. neiderhauseri*. Despite being closely related to *P. x cambivora*, and to *P. cinnamomi*, *P. fragariae* is placed in Waterhouse Group V (Förster et al. 2000).

A partial genome of *P. fragariae* was published in (info to be added). The full genome of *P. fragariae* var. *fragariae* was published in 2014 (Gao et al. 2014).

Phytophthora fragariae var. *fragariae* occurs in a number of distinct races, which show differing virulence on varieties of strawberry (Converse and Scott, 1962; Hickman1962; Tweedy and Powell 1963; Pepin and Daubeny 1964; Gill and Powell 1965; Montgomerie 1967). By the early 1970s, at least eight races were thought to occur (Maas 1972), where? More recent data suggest that seven 'isolate clusters' (cf. races) occur in the UK, ten races in the USA and six in Canada (EPPO 19??), although there are overlaps between races on the two continents (Europe and North America; Kennedy and Duncan 1993). To date, there is no fixed definition of a race within *P. fragariae*.

The close relatedness but distinct identities of *P. fragariae* var. *fragariae* and *P. fragariae* var. *rubi* was confirmed on first application on molecular methods (restriction fragment length polymorphism) to understanding variation within the taxon (Stammler 1993).

Host range

The pathogen appears to be highly host specific (Hickman 1940; Bain and Demaree 1945), although in both field and inoculation tests, other species of Rosaceae closely related to *Fragaria* spp. have been infected (McKeen 1958; Converse and Moore 1966; Pepin 1967). Loganberry has also been found naturally infected by *P. fragariae* var. *fragariae* (McKeen 1958). Despite the host specificity, the pathogen is very persistent between strawberry crops, surviving for at least 15 years in the soil in the absence of strawberry plants (Montgomerie 1951). The second established variety, *P. fragariae* var. *rubi* appears to be highly host specific on raspberry, *Rubus idaeus*.

Detection and diagnostics

Given the importance of the disease in strawberry crops, many countries have protocols in place for the inspection of nursery production facilities (ref?). Initially, these inspections relied solely on the observation visible symptoms on propagation materials, but it is clear, given the continuing spread of the pathogen, that apparently health-looking plants can carry asymptomatic infections

(Duncan 1980); earlier work demonstrated that the pathogen was also vectored to new planting sites on resistant plants (Fulton 1959).

Early methods for detecting the pathogen in visually health stock plants used bait plants of susceptible cultivars planted into soil samples or planned field sites (e.g. Duncan 1976; 1979). Further confirmation of the presence of *P. fragariae* was through observation of red core in the stele, and confirmation of the presence of oospores in the stele of infected roots (EPPO 19??). In a more rapid method developed in the late 1970s, and suggested as a replacement for the lengthy bait plant methods, root tips from very susceptible plants were exposed to the pathogen in a growing substrate (Duncan 1980). These tests, however, could still take 3 – 5 weeks to detect the pathogen, sometimes precluding the timely planting of a crop.

Enzyme-linked immune absorbent assays (ELISA) were developed to detect *Phytophthora* spp. in the 1980s (Amouzou-Alladaye et al., 1988; Mohan, 1988; Werres 1988; Pscheidt et al., 1992), but are not specific for *P. fragariae*.

Since the introduction of molecular methods for detecting plant pathogens, methods developed for *P. fragariae* have been established and are used routinely in some diagnostic laboratories. Specific primers for the detection of *P. fragariae* by polymerase chain reaction (PCR) were developed in the early 1990s (e.g. Cooke et al 1995; Bonants et al. 1997) and proof of their wide-applicability demonstrated (Hughes et al. 2000). A nested PCR based on highly sensitive and selective internal transcriber sequence-based primers were shown to detect the pathogen in symptom-free root systems; the method was further confirmed by the Dutch General Inspection Service (Bonants et al. 1997). More recently, highly sensitive TaqMan PCR assays have been developed for the rapid detection of *P. fragariae* in soil and strawberry plant samples (e.g. Bonants et al. 2004). These state-of-the-art methods reduce the time to make a diagnosis of *P. fragariae* from the five weeks with bait methods (Duncan 1980) to a single day.

Management and Control

The planting of infected strawberry plants is forbidden under legislation in many countries. For example, measures were introduced in the UK in the early 1950s, making it an offence to sell strawberry runners that were not previously inspected for the disease by the relevant agriculture phytosanitary authorities (Duncan 1980). Plant that were inspected and approved for planting as a crop were certified by the relevant authority. Disease outbreaks on previously uncropped land suggested that the pathogen was still spreading via cryptic infections, however, including on resistant stock (Fulton 1959; Duncan 1980; see above). The European and Mediterranean Plant Protection Organisation (EPPO) has produced guidelines for instigating certification schemes for this pathogen (EPPO 1984).

Cultural methods designed to increase drainage, or remove strawberry plants from contact with the ground are now commonly used in production systems. Plants are grown on ridges (similar to potatoes), or grown in nutrient film culture, raised above the ground (EPPO 19??). These simple methods of management can be highly effective, particularly in areas with high disease incidence.

Fungicides active against *Phytophthora* spp. are used by many farmers. Several fungicides (captan, dichlofluanid, fentin HCl, streptomycin) reduced the impact of *P. fragariae* on inoculated strawberry plants in pots (Montgomerie and Kennedy 1975). Metalaxyl was used for several years, although resistant strains of *P. fragariae* are now common (Seemüller & Sun 1989; Nickerson and Maas 1991). As with other *Phytophthora* diseases, fosetyl-Al has been particularly useful for many years (ref?).

Difference in resistance to *P. fragariae* occur within commercial cultivars of strawberry, a phenomenon first reported by Reid (1949). Several varieties of strawberry with defined resistance to some of the races of *P. fragariae* were released to growers in the early 1970s (Gooding 1972); one of the reasons that the use of resistance has found less utility than other forms of management is that an individual variety may be resistant to one or more races of *P. fragariae* but susceptible to others (Kennedy and Duncan 1988). Race-specific resistant cultivars are used reasonably successfully in part of the USA (Scott et al. 1984).

More recent work on resistance of strawberry to *P. fragariae* suggested that the host and pathogen interact in a gene-for-gene manner, as first mooted by Flor (1956) for rust disease of flax (Van de

Weg 1989; 1997a). Van de Weg (1997b) demonstrated inheritance of single gene resistance to *P. fragariae* in offspring of 12 populations of strawberry. Field deployment of single-gene resistance, however, runs a great risk of the pathogen overcoming that resistance, leading to the new cultivars being withdrawn from commerce very quickly.

Impact and economic losses

The pathogen can lead to large losses in strawberry crops, wherever it occurs (EPPO date?). For example, Gourley and Delbridge (1972) reported a loss of 78% of strawberry plants in a 9 hectare field planting. The disease becomes particularly damaging after severe and wet winters (Reid 1949), resulting in very low yields of poor quality fruit.

ANNEX 3 | References

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