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Potential disease control tools most likely to be effective against *Austropuccinia psidii*

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Executive summary

Myrtle rust, caused by the pathogen *Austropuccinia psidii*, is one of the major threats to plants belonging to the Myrtaceae family worldwide and this pathogen was first detected in mainland New Zealand in May 2017. Since then the pathogen has been found on at least 23 host species (June 2019), including native species such as pōhutukawa (*Metrosideros excelsa*), ramarama (*Lophomyrtus bullata*), rātā (*Metrosideros* spp.) and mānuka (*Leptospermum scoparium*). Native Myrtaceae have significant cultural and ecological importance to New Zealand and, along with exotic Myrtaceae, also support many of the country's plant-based economies such as honey, essential oils, forestry, horticulture, plant propagation, floriculture and tourism industries.

Eradication of *A. psidii* was not possible. The response to this incursion closed in April 2018 and transitioned to a long-term management approach. To assist with future decisions on the best control options to investiagate and develop, a comprehensive **review of the literature was undertaken. The aims of this desktop review were to** explore the potential **cultural, chemical, and biological controls that have been used to manage biotrophic pathogens (including myrtle rust) in other pathosystems. The review also** identifies research gaps associated with the application and acceptability of particular tools to control myrtle rust in New Zealand. Breeding for resistance was out of scope for this review but is acknowledged as an important component for long-term management of myrtle rust and should be incorporated in any long-term intergrated disease management strategy.

This report comprehensively reviews a range of cultural, chemical and biological control options that could potentially be effective against *A. psidii.* Included are tables of agrichemicals that are currently registered for use in New Zealand and others that could be considered in the future, along with lists of biological control agents, elicitors, anti-microbial peptides and mcyoviruses that have been used against myrtle rust or other fungal diseases.

In summary the main findings **from this review are:**

- The broad host range of the pathogen and the wide types of scenarios (i.e. native or exotic plants in natural, commercial or urban areas) require a suite of different control options and need to include short-term options through to the development of medium- and long-term sustainable tools.
- Consultation with local councils, Māori iwi and hapū, and industry are essential to ensure social and cultural licences required to operate are in place.
- **A range of different cultural practices were identified, including removal of susceptible hosts, hygiene practices and deployment of resistant or alternative species. Some of the cultural practices can be implemented in the short term, but long term options have also been suggested.**
- Used correctly and as part of an integrated pest management plan, fungicides can play an important role in managing myrtle rust in the short term while longer term options are developed. This review identified that active ingredients from the strobilurin and triazole groups are effective in controlling myrtle rust.
    - Any spray regimes should alternate and mix active ingredients to minimise the likelihood of the rust developing resistance to them.
    - Any fungicide used needs to be managed in such a way that it protects both public health and New Zealand's natural resources.
- Biological control can be an important tool for long-term integrated disease management (IDM).
    - **There are currently no known commercial or registered biological control agents available specifically for the control of myrtle rust.**
    - **Numerous candidate or groups of biological control agents (i.e. endophytes, elicitors, anti-microbial peptides or mycoviruses) were identified and could be developed for long-term management of myrtle rust. Options that do not require importation of biological control agents are likely to have a shorter time to deployment.**
- Engagement with Māori to incorporate, or co-develop, control solutions with kaupapa Māori and mātauranga Māori is critical.

    - Māori views on the use of contemporary biological control agents need to be taken into account in the early stages of their development.
    - There is potential for mātauranga Māori to guide pre-screening and development of indigenous biocontrols for use against myrtle rust.
- Most of the different myrtle rust control options identified (cultural, biological and chemical practices) cannot be applied immediately as they require further research into acceptability as well as their specificity, efficacy and feasibility in controlling myrtle rust on trees under different environmental conditions in New Zealand, or product and research development (e.g. biological control agents production and breeding, and selection of resistant cultivars for deployment).

Contents

1 Project background

To better understand myrtle rust and limit its impact in New Zealand, the Ministry for Primary Industries commissioned a comprehensive research programme in 2017 with more than 20 projects valued at over $3.7 million. Projects in this programme were completed by June 2019.

The projects covered research in the following themes:

- Theme 1 - Understanding the pathogen, hosts, and environmental influence.
- Theme 2 – Building engagement and social licence: Improved understanding of public perceptions and behaviours to allow better decisions about investment, improved design of pathway control strategies and maintain social license for use of management tools.
- Theme 3 – Te Ao Māori: Greater understanding of Te Ao Māori implications of myrtle rust in order to support more effective investments, and improved use of Mātauranga, specific Māori knowledge, and kaupapa Māori approaches in management regimes.
- Theme 4 – Improving management tools and approaches: Improved diagnostic and surveillance speed, accuracy and cost-effectiveness, supporting eradication efforts and enabling scaling up of surveillance efforts for a given resource. More effective treatment toolkits to avoid emergences of MR resistance to treatments and to enable disease control over increasingly large scales that will lead to reduced or avoided impacts.
- Theme 5 - Evaluating impacts and responses: Improved understanding of environmental, economic, social and cultural, impacts to inform risk assessment and management and to communicate implications to decision/makers and stakeholders.

This report is part of the MPI commissioned research under contract MPI18607 which addressed research questions within Theme 2, 4 and 5.

Text in the report may refer to other research programmes carried out under the respective theme titles.

2 Introduction

Myrtle rust, caused by the pathogen *Austropuccinia psidii*, is one of the major threats to plants belonging to the Myrtaceae family worldwide. The pathogen likely originated from Central and South America (Coutinho, Wingfield, Alfenas, & Crous, 1998), but over the past decade it has spread globally. The pathogen is native to Uruguay and Brazil and is known to be present in the USA (California (Mellano, 2006), Florida (Rayachhetry, Elliott, & Van, 1997)), Jamaica (MacLachlan, 1938), Argentina, Cuba, Paraguay, Colombia, Venezuela, Ecuador, Mexico, Salvador, Guatemala, Puerto Rico, Dominican Republic (Coutinho et al., 1998; Ross-Davis et al., 2013). In Asia, the pathogen has been reported in China (Zhuang & Wei, 2011), Japan (Kawanishi et al., 2009), Indonesia (McTaggart, Roux, et al., 2016) and Singapore (Du Plessis et al., 2017), and in the Pacific in Hawaii (Uchida, Zhong, & Killgore, 2006), Australia (Carnegie & Cooper, 2011), New Caledonia (Giblin, 2013) and New Zealand (www.mpi.govt.nz). It is also present in South Africa (Jolanda Roux, Greyling, Coutinho, Verleur, & Wingfield, 2013). Since the early 2000s, *A. psidii* has become an important biosecurity challenge due to the emergence of new strains, which have impacted Myrtaceae species in several countries. As a result, the actual host range has expanded to around 500 known host species, with the highest impact in Australian and New Caledonian flora where the pandemic biotype (Stewart et al., 2018) has been causing severe outbreaks (Giblin & Carnegie, 2014; Soewarto et al., 2017). Given its unusually broad host range, this rust pathogen is expected to affect many new Myrtaceae species, especially in the Asia-Pacific area where climatic conditions are optimum for rust development (Kriticos, Morin, Leriche, Anderson, & Caley, 2013) and Myrtaceae hosts have not developed resistance through co-evolution with the pathogen.

New Zealand is home to at least 29 native Myrtaceae species (six genera) and has a large number of exotic Myrtaceae (Buys et al., 2016), many of which have commercial value (i.e. eucalypt species and feijoas). Myrtle rust was detected on mainland New Zealand on 3 May 2017 (Beresford et al., 2018) and since then has been found on 23 host species, including the iconic pōhutukawa (*Metrosideros excelsa*), mānuka (*Leptospermum scoparium*) and ramarama (*Lophomyrtus bullata*). As *A. psidii* spreads across New Zealand, the pathogen presents a substantial threat to New Zealand's indigenous ecosystems and plant industries, such as mānuka honey and oil, forestry, horticulture, plant propagation and cut flowers.

The Australian and New Caledonian experiences have shown that, once introduced in new areas, the persistent nature of myrtle rust in native environments makes it difficult, or even impossible, to eradicate. While removing infected trees may provide a short-term solution for reducing the spore load and slow the spread of the disease, a longer-term option is to establish an integrated pathogen management approach to minimise myrtle rust spread and its impact on New Zealand environment and economy sustainably and effectively.

During the incursion response initiated when the rust was first found in New Zealand, the Ministry for Primary Industries (MPI) surveyed Myrtaceae across the country for myrtle rust symptoms and removed infected trees to prevent spread of the pathogen. In December 2018 MPI announced the incursion response would transition to long-term management, and as a result, options to control or manage this disease across a large variety of plant species for a range of different purposes or uses (i.e. from the native estate, to urban environments through to commercial industries) are required. The objectives of this review were to:

- Explore potential disease control tools most likely to be applicable and effective against myrtle rust so as to help guide future decisions on the tools to be pursued for the control of the disease in New Zealand
- Discuss the value of controlling myrtle rust on iconic Myrtaceae species
- Discuss public acceptance and Māori views on the different control measures, and the social licences that may be required for operation
- Identify the research gaps necessary to apply these tools.

3 Methods

Literature searches relevant to cultural, biological and chemical control practices/options that have been used to manage myrtle rust and other biotrophic pathogens, both in other pathosystems outside and within New Zealand, were conducted across online scientific citation indexing platforms and search engines such as Web of Science, ProQuest Science & Technology, Google Scholar and worldwide web. Materials selected covered published books, journal articles, electronic articles, popular articles, newsletters, government and industry websites relevant to the subject of investigation conducted in the country of origin.

Some examples of specific search terms used in the process include: ("Austropuccinia psidii" OR "Puccinia psidii" OR rust OR myrtle OR Myrtaceae) AND (disease AND (biosecurity OR biocontrol* OR control* OR manage*)) AND (cultur* AND (practice* OR tradition* OR method* OR rules OR ritual*) OR indigenous OR ethnic or diversification OR hygiene OR scout* OR "resistan* cultivar*" OR fertili* or biosecurity or disease* or infest* or control* OR biocontrol OR manag* or fungicide).

Initial searches identified more than 1000 relevant published journal papers. Abstracts and full text of relevant papers, books and other publication sources were scanned and compiled into a shared Endnote library. In addition, 115 references were added from the citations of relevant papers and through personal communication with authors and other researchers known to be working in the relevant areas. There were 1436 references recorded in the library at the time of preparing this review.

For areas relating to public acceptability and the views/knowledge within the Te Ao Māori of iwi, hapū and whanau of the various control tools, contacts were made via individuals directly with the associated councils, iwi and hapū, depending on the context of whether the control is to be conducted in urban locations, nurseries or natural habitats.

4 Overview of *Austropuccinia psidii*

4.1 Background

In 1884, Winter described a rust fungus occurring on the leaves of *Psidium guajava* (common guava) in Brazil and named it *Puccinia psidii* (Ghabrial & Suzuki, 2009; Winter, 1884). Recent work using molecular data demonstrated that *P. psidii* is recovered in another family in Pucciniales, not Pucciniaceae (McTaggart, Shivas, et al., 2016; Van Der Merwe, Walker, Ericson, & Burdon, 2008) as originally thought. Subsequently, a new genus, *Austropuccinia*, was created for this species in Sphaerophragmiaceae (Beenken, 2017). *A. psidii* is now recognised as the causal agent of myrtle rust, which sometimes is referred to as guava, 'Ōhi' or eucalypt rust (Stewart et al., 2018). Synonyms for this species include *Uredo psidii* and *Caeoma eugeniarum* (Simpson, Thomas, & Grgurinovic, 2006). Another anamorphic species, *U. rangelii*, was described as a new species on *Myrtus communis* (Simpson et al., 2006), but is also considered a synonym of *A. psidii* (Glen, Alfenas, Zauza, Wingfield, and Mohammed (2007); the one DNA sequence of *U. rangelii* publicly available on GenBank (HM448900) has 99% sequence identity match with the epitype of *A. psidii* (KM282154).

4.2 Biology

A. psidii is a biotrophic pathogen that completes its life cycle on actively growing shoots and fruits of susceptible hosts (Stewart et al., 2018) in the Myrtaceae. It has recently been confirmed as autoecious (completing its life cycle on the same host) with basidiospores (Stage IV) that are capable of infecting the same hosts on which teliospores (Stage III) and urediniospores (Stage II) are formed (McTaggart et al., 2018). However, as of yet, spermogonia (pycnia) (Stage 0) or aeciospores (Stage I) have not been observed in the field (Morin, Talbot, & Glen, 2014). The life cycle of *A. psidii* (Figure 1) is hypothesised to begin with the anastomoses of hyphae produced from basidiospores, which is thought to form a dikaryotic hymenium that produces telia or uredinia (McTaggart, 2017; McTaggart et al., 2018). The McTaggart et al. study (2018) suggested that this could indicate that a uredinial stage need not be formed if environmental conditions suit the production of telia. Uredinia are presumed to be mitotic and telia are formed from uredinia; teliospores were found to be diploid and germinate to form basidia (McTaggart et al., 2018; Morin et al., 2014). Basidiospores were found with one or two nuclei with one polar germ tube (Morin et al., 2014).

The spores of *A. psidii* are spread by the action of wind (main dispersal mode), rain, insects and birds (Masson, Moraes, & Furtado, 2013). The pathogen attacks young, soft, actively growing leaves, shoot tips and young stems. Fruit and flower parts are also susceptible. The first signs of rust infection in susceptible genotypes are tiny spots or pustules that can appear 2-4 d after infection (Coutinho et al., 1998). However, this may differ due to environmental conditions present in New Zealand and/or the plant species infected. Symptoms can vary depending on the host species, susceptibility level within a host species, and age of the host leaf. After a few days, the pustules or uredinia erupt with the production of distinctive, yellow urediniospores. The infected area spreads radially outwards and multiple pustules eventually merge with age. Secondary infections can occur within days but are usually confined to new young tissue, shoots and expanding foliage. Left untreated, the disease can cause deformed leaves, heavy defoliation of branches, dieback, stunted growth and even plant death (CABI, 2018).

The environmental conditions for optimal rust development include periods of high relative humidity that are longer than eight hours and temperatures between 15–25˚C (Glen et al., 2007). The disease affects young leaves (Xavier et al., 2015), i.e. no leaf older than 45 days (in *Syzygium jambos*) becomes infected (P. Hunt, 1968).

Uredinia of *A. psidii* are formed at temperatures of 15–20°C. They range from 0.1–0.5 mm diam., amphigenous, yellowish (but fade to pale tan when old), more common and larger on the abaxial surface, subepidermal becoming erumpent and up to 500 µm. Urediniospores vary from globose, ellipsoidal to ovoid and obpyriform, are yellowish, 14–27 x 14–29 µm, finely echinulate, with or without a tonsure; germ pores have not been observed (McTaggart, Roux, et al., 2016).

Telia are produced at warmer temperatures of 21–25°C (McTaggart et al., 2018). They are 0.1–1.5 mm diam., sub-epidermal to erumpent, abaxial, pulvinate and yellowish-brown. Teliospores are 22–50 x 14–28 µm, cylindrical to ellipsoidal, with a rounded apex, yellowish brown, 2-celled, constricted at the septum and pediculate. Basidia are cylindrical, up to 110 µm long, 6–8 µm wide, hyaline, 4-celled, produced from each cell of the teliospores, apically in upper cell and laterally in lower cell.

Basidiospores are optimally produced at 21°C, with between 400–600 basidiospores per square mm of telia (McTaggart et al., 2018). The basidiospores are globose to pyriform, 8–11 µm, hyaline and smooth (CABI, 2018; Morin et al., 2014; Simpson et al., 2006). As spores germinate, an appressorium forms at the tip of the short germ-tube and is usually larger than the epidermal cells and so will overlap two or more cells. The appressorium develops into a narrow infection peg that penetrates between epidermal cells and then enlarges once in the leaf. Occasionally, the infection peg will penetrate through the substomatal chamber (P. Hunt, 1968).

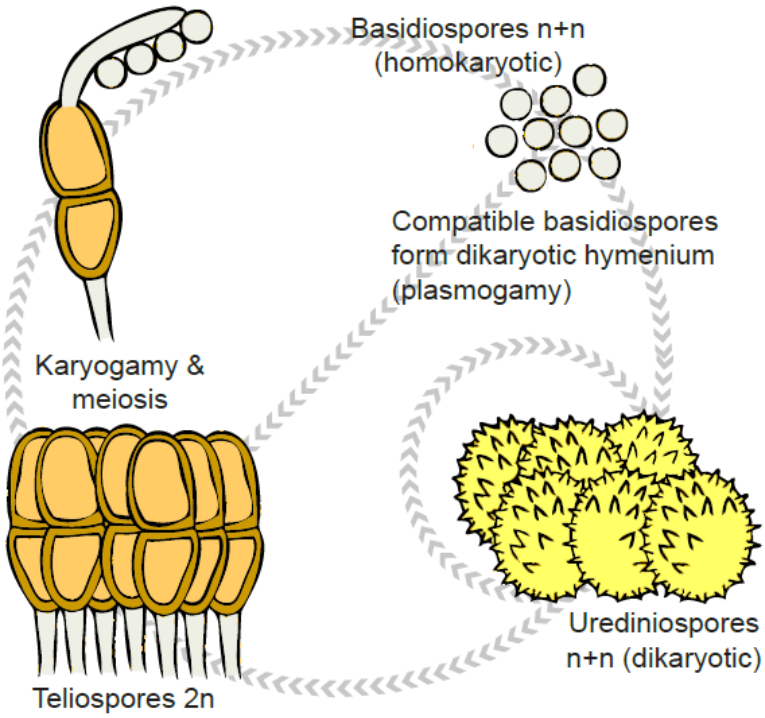

Figure 1. Diagrammatic life cycle of *Austropuccinia psidii* (McTaggart, 2017).

4.3 *Austropuccinia psidii* strains

Understanding the population structure of a pathogen population is important for forecasting its evolutionary potential and may prove useful to optimise disease control management (B. A. McDonald, 1997). A number of studies using Single Sequence Repeats (SSRs) show that *A. psidii* is genetically diverse and forms a complex (*A. psidii sensu lato*) composed of a several races/strains/biotypes/multilocus genotypes (Glen et al., 2007; Graça et al., 2011). Cross-inoculation studies further showed that physiological specialisation within *A. psidii* complex resulted in the inability of specific host-associated strains to infect different host species (Coelho, Alfenas, & Ferreira, 2001; Ferreira, 1983; Rayachhetry, Van, Center, & Elliott, 2001).

In Brazil, the putative centre of *A. psidii* diversity, high genetic variability has been demonstrated within *A. psidii* populations, apparently through adaptation to separate hosts. In their work, Graça et al. (2013) showed the existence of at least five strains specifically associated with different host species in Brazil: one strain was associated with *Eucalyptus* spp. and *S. jambos*, another with guavas (*P. guajava* and *P. guineense*), and three unique strains were associated with *Syzygium cumini*, *Eugenia uniflora* and *Myrciaria cauliflora*. Outside Brazil, one different strain occurred in Jamaica on *Pimenta dioica* (Ross-Davis et al., 2013) and three more strains were identified in Florida (Zhong, Yang, & Puri, 2011). More recently, analysis based on multilocus genotypes has been used to group isolates into related clusters (Stewart et al., 2018). This study identified two clusters (C1 and C4) which combined are referred to as the “pandemic biotype” and it is this biotype that is able to infect a wide host range (da S. Machado, Alfenas, Alfenas, Mohammed, & Glen, 2015; Graça, 2011; Granados et al., 2017; Ross-Davis et al., 2013; Sandhu, Karaoglu, Zhang, & Park, 2016; Stewart et al., 2018; Zhong et al., 2011). Another distinct strain which is also able to infect multiple host species occurs in South Africa (J. Roux et al., 2016).

4.4 Host range

Myrtaceae represents a large plant family of more than 5600 species (Grattapaglia et al., 2012). *A. psidii* has a wide host range within Myrtaceae, with more than 500 species in 74 genera being infected (Beenken, 2017; Giblin & Carnegie, 2014; 2018). These hosts include commercially important species of *Eucalyptus* for the forestry industry (Coutinho et al., 1998) and endangered species in genera such as *Eugenia*, *Rhodamnia*, *Cloezia*, *Metrosideros* and *Tristaniopsis* in Australia (Carnegie et al., 2016; G. Pegg et al., 2017; G. S. Pegg et al., 2014) and New Caledonia (Soewarto et al., 2017). In New Zealand, *A. psidii* has infected species within four native genera: *Leptospermum, Lophomyrtus, Metrosideros*, and *Syzygium* (www.mpi.govt.nz).

5 Management of other rust diseases and myrtle rust

Rust fungi are obligate biotrophs that are completely dependent on nutritional resources obtained from living host cells for growth and reproduction (Figueroa, Hammond-Kosack, & Solomon, 2018). To date, *A. psidii* is known to be autoecious with no alternate or aecial hosts reported. The management of myrtle rust, therefore, should take into consideration the pathogen's biology (polycyclic), mode of spread and should aim at interrupting the disease to delay the onset and duration of an epidemic or reduce the rate of disease spread.

Based on the climatic risk model of myrtle rust developed by Beresford et al. (2018), the conditions in most of the North Island of New Zealand, and localised areas of the west, north and east coastal regions of the northern half of the South Island, were favourable for myrtle rust development. The model indicated that most the South Island was "seasonally suitable" for the disease. Only 20% of the southern South Island (particularly central and southern Westland and Central Otago) was considered "seasonally marginal" or "unsuitable" for the disease.

With the above information in mind and taking into account the pathogen, host and environment, the three components of the disease triangle (Keane & Kerr, 1997), myrtle rust is expected to rapidly establish and develop as a common disease in much of New Zealand. Disease development is likely to be greatest, and occurrence widespread, in the North Island, and to be less in the South Island (although myrtle rust has been recorded on eucalypt hosts in northern Tasmania, at a latitude and climate similar to much of the South Island of New Zealand). At the time of preparing this review, the disease was detected from the most southern location so far, on a young pōhutukawa (*Metrosideros excelsa*) plant at a commercial property in Greymouth.

In this section, different cultural, biological and chemical control/management options that have been applied to *A. psidii* in other countries or have been used to manage other rust pathogens have been reviewed to determine potential control tools that may be suitable in a New Zealand context.

5.1 Cultural practices

Cultural control practices aimed at controlling diseases through the cultural manipulation of plants are widely applied in large areas and low-unit-value crops such as cereal and forestry (Ogle & Dale, 1997). The practices tend to be preventative and indirect in their actions against pathogens as success depends on understanding the biology of the pathogen (vulnerable stage of their life cycles) and the response of the host to infection (Ogle & Dale, 1997).

In cropping situations, cultural practices such as lowered seed rates, increased row widths, and proper row orientation to the sun to help minimise leaf wetness duration, are environmental modifications that create a microclimate less conducive to disease development (Robert J Cook & Yarhm, 2006). A comprehensive account by Ogle & Dale (1997) on practices applicable to cropping systems includes:

- Deployment of resistant cultivars into the field or by increasing the plant diversity by planting different plant species in the same field to create a spatial separation of the disease susceptible plants
- Protective fungicides (non-cultural)
- Biological control agents targeted at initial inoculum (non-cultural)
- Elimination of living plants that carry the pathogen by removing diseased plants or plant parts
- Destroying infested plant debris
- Removal of alternative hosts.

Although tolerance and resistance are critical aspects of an effective myrtle rust management strategy, these will not be discussed in depth in this review because resistance of different Myrtaceae species to myrtle rust is being investigated in Theme 1: Understanding the pathogen, hosts and environmental influences.

5.1.1 Practices which reduce the rate of spread of diseases in agricultural systems

In many cases, cultural practices are directed at improving the growing conditions of plants by providing proper nutrition, moisture, light and lack of competition from other plants (Ogle & Dale, 1997). They may also be aimed at creating conditions unfavourable for the development of pathogens. According to Keane and Kerr (1997), the epidemic development of any plant diseases is largely dependent on the following factors within the disease triangle:

- Pathogen (e.g. reproductive potential/fitness, virulence, adaptability and dispersal and survival efficiencies)
- Host (e.g. susceptibility, growth stage and form, population density and structure, general health)
- Conduciveness of the environment for disease development (e.g. temperature, rainfall, and leaf wetness).

Manipulation of the environment or climate conditions is somewhat limited or impossible unless the plants are grown under controlled conditions or produced in nurseries with controlled irrigation. Some common practices applied in agricultural systems (Ogle & Dale, 1997) to reduce rate of disease spread are:

- Manipulation of irrigation systems (i.e. avoiding overhead watering) to make conditions unfavourable for pathogen germination
- Removal of diseased plants/materials to prevent further spread and reduce inoculum source
- Implementation of good hygiene practice after removal and disposal of infected plants. Washing of clothing and cleaning of any equipment with water and detergent before starting other activities that may infect further plants
- Fertiliser applications or crop nutrition to induce plants' resilience to diseases or reduce yield impact caused by the disease
- Planting low-value trap and decoy crops (not feasible as no alternative hosts have been reported for myrtle rust)
- Adjusting the sowing time (annual crops) to avoid growth stages that are susceptible for infection
- Application of systemic fungicides
- Placement of barriers, as in the form of fences, hedges or windbreaks, around fields where susceptible hosts are present.

Other than application of chemicals, nearly all the above methods are not feasible for the management of myrtle rust in natural environments and may have limited application in urban environments. For instance, placement of barriers has attracted some attention in cropping situations (Ogle & Dale, 1997), but may not be feasible given that *A. psidii* spores are mainly dispersed via wind. In addition, manipulating sowing time will not work in an established plantation/forest or urban situations.

5.1.2 Plant species migration

The potential of facilitating plant species migration has been extensively debated within the ecological research community under current pressing climate change phenomena and the pressure from tree pests and diseases that affect ecosystem functions and services (Boyd, Freer-Smith, Gilligan, & Godfray, 2013; Dumroese, Williams, Stanturf, & Clair, 2015; Williams & Dumroese, 2013). Through modelling, only 20% of the southern South Island (particularly central and southern Westland and Central Otago) is predicted to be "seasonally marginal" or "unsuitable" for myrtle rust (Beresford et al., 2018). Besides seed banking, which is currently being implemented under a different myrtle rust programme, the potential of artificially (man-made) migrating valuable iconic New Zealand plant species to areas of New Zealand where myrtle rust epidemics are unlikely to occur or rapidly develop should be considered.

5.1.3 Nutrients

Application of commercial fertilisers is a common practice in farming to maximise crop productivity and yield. Although increasing nutrients when water and light conditions are sufficient may permit the plants to grow to the maximum of their ability, some research studies have shown that the situation may modify plant ability to resist pathogen infections. In the case of biotrophic fungal pathogens, such as rust, the effects have been variable. For instance, some studies have highlighted that disease severity caused by biotrophic fungal pathogens, including rust fungi, decrease with nitrogen (N) additions only when N availability limits plant growth, but favour rust development when the available N surpassed the requirement of the plants (Robert, Bancal, & Lannou, 2002; Walters & Bingham, 2007).

Tratch et al. (2010) investigated the effect of N applied in the form of urea and potassium (K) on peach leaf rust (*Tranzschelia discolour*) and reported reduced rust severity with increased N. Potassium on its own did not decrease peach leaf rust severity in their study. In contrast, when K was applied into soil as potassium chloride (KCl at 140 kg ha^{-1}) in conjunction with a fungicide application onto soybean to control soybean rust (*Phakopsora pachyrhizi*), disease severity was reduced (Fixen et al., 2008). Manganese and boron, which were the micronutrients applied as foliar sprays either on their own or in

combination (at 0.56 kg ha^{-1} and 0.28 kg ha^{-1}), also reduced rust incidence, especially in the upper canopy. Their impact on young growth is however, not known.

Nitrogen is absorbed by plants as either nitrate or ammonium ions. Some studies (Huber & Haneklaus, 2007; Huber & Watson, 1974) suggest that severity of disease caused by biotrophic fungi may be regulated by the form rather than the quantity of N fertilisers applied; nitrate fertilisers were found to increase the severity of disease whereas ammonium fertilisers decreased it. It seems that the form of N available to the host (not total soil N) has most influence on disease susceptibility, but the effects should be largely assessed in relation to specific host/pathogen relationships. Other factors including application rates, timing of application and methods will require consideration.

A study in Brazil had shown that when silicon (Si) was applied into the soil in which sugar cane was grown, the concentration of Si in the leaves increased, thereby reducing brown rust incidence substantially (de Camargo, Amorim, & Gomes Junior, 2013). The authors hypothesised that Si might help to form a physical barrier to prevent pathogen penetration or that Si might prime plant defence mechanisms. The absorption and deposition of Si (amorphous silica, SiO_2; nH_2O) in epidermal cell walls can strengthen plant tissues. This latter role of Si has been demonstrated in rice, which is also considered to be a Si-accumulator like sugar cane (Emanuel, 1999). The ability of different New Zealand myrtle rust susceptible species in accumulating Si will have to be investigated before Si application can be considered as a control option. As well, in situations where the soil nutrition is not limiting plant growth, addition of Si may not reduce myrtle rust infection effectively. Given the fact that *A. psidii* affects new growth and young plant parts, the application of Si may be an option to increase plant tissues' resilience to infection.

For the development of strategies to manage rust diseases, understanding the mobilisation, acquisition and metabolism of nutrients by the obligate biotrophic fungi within the host-pathogen interaction is fundamental. An early comprehensive account by Mendgen (1981) has described the uptake of different nutrients and/or metabolites by different rust fungi under axenic culture (uncommon but can be stimulated) and on hosts. Some examples include:

- Flax rust (*Melampsora lini*), sunflower rust (*Puccinia helianthi*) and wheat stem rust (*P. graminis* f. sp *tritici*) have some requirements for inorganic salts. Flax rust also requires carbohydrates in the form of hexoses
- Wheat stem rust and flax rust, in which sulphur amino acid as a source of N and S plus sugar resulted in urediniospore formation and subsequent teliospore formation in vitro
- Pine rust (*Cronartium fusiforme*), in which minor constituents such as cholesterol, ergosterol, sitosterol, oleic acid and ferulic acid allowed the culture of different spore forms
- Wheat stem rust, in which addition of adenosine triphosphate and ribose to the medium induced urediniospore and teliospore formation.

Nutrient requirements may be specific because different races of rust species may each have special nutritional requirements. While some urediniospores and teliospores obtained through axenic culture may retain their ability to re-infect host plants, many may not.

In addition, the potential in using some chemicals or metabolites to counteract the above-mentioned nutrient sources required by *A. psidii* for spore formation will have to be thoroughly investigated, which is not feasible. Given that *A. psidii* attacks the soft and young issues of hosts, it is crucial to ensure that application of fertiliser or nutrients will not further enhance new soft, lush growth that is easily colonised by myrtle rust under favourable weather conditions, which seems impossible. Unlike the wide range of Myrtaceae host species, many studies on nutrients were on pathogens that were host specific. For the use of nutrients to control myrtle rust, individual Myrtaceae host species for which treatment is being considered will have to be determined. This could be an expensive and time-consuming process. Moreover, the non-target ecological impacts of nutrients on evergreen plants in natural habitats could be detrimental and would require further investigation.

5.1.4 Oil and other remedies

Oils of various types, such as petroleum-based mineral oil, plant-based glyceride oil (e.g. neem oil), essential oil, and synthetic oil are capable of controlling plant diseases (Calpouzos, 1966). One good example is the large-scale use of petroleum oil together with fungicides to control a banana disease, Sigatoka leaf spot caused by *Pseudocercospora musicola* (Calpouzos, 1966; Marin, Romero, Guzmán, & Sutton, 2003; Pardeshi, Shaikh, & Chitodkar, 2015). Petroleum oil retards the development of initial stages of infection and, in combination with systemic fungicides, enhances the penetration of the systemic fungicide into the leaves (Carlier et al., 2000). The rates of oil used range

from 5 to15 L ha^{-1}. However, the accumulation of oil on the leaves reduces yield due to interference with gas exchange and therefore photosynthesis (Marin et al., 2003).

Pereira, Lucas, Perina, and Alves (2012) investigated the *in vitro* effect of medicinal plant essential oils of clove, citronella and thyme on the urediniospore germination of *Hemileia vastatrix*, their efficacy in the control of leaf rust on three coffee plant cultivars, and their effects on the urediniospore ultrastructure. They reported that all the essential oils inhibited the germination of urediniospores and gave partial control of the disease in the greenhouse.

The effect of some essential oils (chamomile, thyme, cumin, basil, eucalyptus and garlic oils) on wheat rust disease was tested at seedling and adult stages under greenhouse and field conditions by (Tohamey & El-Sharkawy, 2014). All concentrations of the six oils tested increased the latent period of the disease, decreased the number of pustules per cm^2 leaf area and leaf rust severity (%), and increased plant yield compared to the water control.

Other remedies, such as aspirin mixture, baking soda (sodium bicarbonate), Bordeaux mixture (copper sulphate mixed with lime and water sprayed on trees in winter) and sulphur mixture (as a preventative spray) are common home-made mixtures used by home gardeners to control rust diseases on plants (Lynn, 2018). Neem oil has also been recommended to be applied at the first signs of infection. It is suggested that any homemade mixtures should be tried on a couple of leaves and then wait for at least 24 hours to check for adverse reactions.

Some oil products and home remedies may potentially be used to control myrtle rust and are more acceptable by public. However, the control efficacy and phytotoxicity effects of individual oil products and remedies on treated and neighbouring plants would need to be determined. At the time of preparing this review, the efficacy of these products on controlling myrtle rust has not been reported.

5.1.5 Rust pathosystem using cultural control strategies – poplar leaf rust

The deployment of resistant varieties/hybrids to manage rust diseases is a common practice for many crops such as cereals, soybean and poplars. For some rust diseases, such as poplar leaf rusts e.g., *Melampsora larci-populina* (Europe), *M. medusa* and *M. occidentalis* (North America), the most effective methods of control involve sanitation and host resistance (Anonymous, 2017; Jacobi, 2013). Chemical treatments are sometimes not considered an effective form of management in forest or woodlot situations, but can be used to prevent the infection of high-value trees (Jacobi, 2013). Some of the potential measures for treating *Melampsora* rust include (Jacobi, 2013):

- Scouting of trees for signs of infection
- Removing the branches of infected aecial or telial hosts
- Removing of entire infected aecial or telial hosts
- Removing the fallen leaves of infected or susceptible trees from the plantation floor
- Planting trees further from infection centres and further from each other, if planting susceptible trees
- Planting clones of resistant or tolerant individuals
- Using preventative fungicides on high-value trees (Sharma, Sharma, & Gupta, 2005)
- Planting trees outside of the genus *Populus* and outside of the family Salicaceae (Pscheidt & Ocamb, 2018).

Interestingly, removal of infected plant parts at the telial stage may be a consideration as teliospores are thick walled and may be less likely to be dispersed by wind. However, the exact timing of telial stage of *A. psidii* under New Zealand conditions on each susceptible species would have to be determined.

5.2 Chemical control

Chemicals have long been used to control pests and diseases in agriculture (Conway & Pretty, 1991; W. Zhang, 2018) with fungicides being used since the early 1800s. The use of fungicides for disease control is still a significant component of any effective disease management programme, and this will most likely be the case for the management of myrtle rust in New Zealand.

Apart from what has been occurring operationally in the national response to the incursion of myrtle rust in New Zealand, there are currently no published reports evaluating fungicides known to be highly effective against this disease on susceptible, local/regional Myrtaceae species. Hence, there is a need to identify potential chemicals to support, and improve on, the already existing control and management practices.

This section discusses the different fungicide treatments that have been reported to be effective for the control of myrtle rust elsewhere and identifies fungicides that may potentially control the disease in New Zealand. The application techniques that could be considered for treating the plants under different scenarios are also described.

5.2.1 Fungicides

Fungicides have been made available and designed to control plant diseases based on their mode of action. The mode of action refers to the specific process in the metabolism of the fungus that is targeted, for example, arresting a key protein synthesis pathway or other relevant processes such as respiration or energy production. There has been extensive knowledge generated on the modes of action of fungicides impacting membranes, nucleic acids and protein synthesis, signal transduction, respiration, mitosis and cell division, and multi-site activity (Yang, Hamel, Vujanovic, & Gan, 2011).

Successful approaches for effective identification and use of fungicides to control diseases are highly dependent on understanding some key factors. These factors include the physiological, biochemical and molecular modes of action of the fungicides and the mechanisms required to avoid development of resistance. The Fungicide Resistance Action Committee (FRAC) has recently compiled a list of fungicides based on their target sites/modes of action and the chemical groups they belong to (Fungicide Resistance Action Committee, 2018). There are more than 40 target site of actions or groups of fungicides. The modes of action and potential non-target effects on soil microorganisms should also be considered in the selection of fungicide in order to protect the biological functions of soil and optimise the benefits derived from fungicide use.

Fungicides work by killing or inhibiting the growth of fungi or their spores that cause the diseases (Horst, 1990; McGrath, 2004). The trade/chemical name, active ingredient/s (a.i.) and the chemical groups (modes of action) are important information to consider before application of any fungicides to plants. In this review, only references to the a.i. have been used, where possible, as trade or product names can vary among countries.

Several reports have comprehensively elaborated on the names of fungicides as well as their classifications (McGrath, 2004; Mueller, Morel, & Hartman, 2006; Yang et al., 2011). Fungicides are classified in numerous ways. These include mobility of a.i. in the plant, role in protecting the plant, spectrum of activity, mode of action/target site and chemical group name.

In terms of mobility, fungicides can be subdivided into contact and systemic. Contact fungicides remain on the application surface with little or no capacity to penetrate the host tissue and no after-infection activity (Mueller et al., 2006; Ogle, 2016a). Because contact fungicides can be easily degraded by sunlight or washed off by rain or irrigation, application has to be repeated to protect new growth. Contact fungicides work best as protectants before infection occurs (Goes, Martins, & Reis, 2004; Martins, Silveira, Maffia, Rocabado, & Mussi-Dias, 2011). Systemic fungicides are absorbed into the plant tissues and translocated upward or locally from the site of penetration, redistributing to some degree, within the treated area of the plant and, as a result, may offer some after-infection activity (Ogle, 2016b).

Nearly all fungicides used in agriculture today show their best effect if applied before the infection occurs. When present on the surface of the plant organs, fungicides destroy fungal spores or suppress germination tubes, hyphae and other fungal structures (Dario, 2010). The preventative fungicides (mainly contact) are applied on the plants to act as a protective barrier before the pathogen arrives or begins to grow, to prevent infection from occurring.

For early-infection activity (i.e. before disease symptoms appear), ‘curative’ treatment with systemic fungicides is usually effective in controlling the pathogen when applied to the host-plant within 24 to 72 hours of infection (Mueller et al., 2006). Fungicides targeting early infection may stop the spread of disease after symptom expression. Such fungicides are extremely important in controlling plant diseases, however, there are very few such fungicides

Fungicides with anti-sporulation activity can potentially prevent germination, production and release of spores, but the disease continues to exist (and lesions continue to expand), attenuating the level of inoculum available to infect neighbouring plants. Most fungicides that have protective and curative properties with systemic action (such as tebuconazole, triadimenol, propiconazole, procymidone and flusilazole) serve as flexible windows for users when required and have become a mainstay for a variety of pathogens (McLaren, 1994).

The spectrum of activity of a fungicide can either be targeting single-site or multi-sites of the metabolic pathway of the pathogens, or against key enzymes or proteins that are needed by the pathogens for survival. Single-site refers to the ability of the fungicide to act against only one point in the metabolic

pathway or against a single key enzyme or protein that is needed by the pathogen. Such fungicides have been reported to be less toxic to plants and are systemic. In contrast, multi-site fungicides have activity affecting a number of different metabolic sites within the pathogen. To control multiple plant pathogens, multi-site fungicides are necessary (Hirooka & Ishii, 2013).

The chemical group or class refers to the name given to a group of chemicals that share a common biochemical mode of action, such as the strobilurins, triazoles, thiophanates and dicarboximides. The chemicals within a group may not necessarily share a similar chemical structure and could be organic or inorganic. The organic fungicides are those that contain carbon atoms as part of their structure but the inorganic do not. In the past, most of the chemicals produced were inorganic and based on the sulphur or metal ions such as copper, tin, cadmium and mercury. Most of the fungicides now used are organic (McGrath, 2004).

5.2.2 Chemical control used against different rust diseases

For most yield-driven crop species, such as soybean and cereal, fungicides are applied regularly to increase crop productivity. For instance, in soybean production, yield consistently increased (by 0.2–1.42 tonnes/ha) when fungicides were applied at the first appearance of rust on the crop (Hershman, Vincelli, & Kaiser, 2011). In many instances, fungicides are applied as protectants against rust diseases at regular timings that coincide with crucial crop growth stages, when susceptible varieties are grown under disease-favourable weather conditions or a local history of high disease pressure.

Cereal rusts

Cereal rusts, such as wheat stripe and leaf rusts (*Puccinia striiformis* var. *tritici* and *P. triticina*, respectively) and barley leaf rust (*P. hordei*) are managed by deploying rust resistant or tolerant cereal crop varieties into the field, coupled with fungicide applications that coincide with different plant developmental stages during the growing season. These fungicides are usually applied at key timings of the season to protect the crops against cereal diseases including rusts. For instance, fungicides are applied when the cereal crops are at pseudo stem erect stage (to reduce the initial inoculum), flag leaf to first awns emerging (to protect the top three leaves of the plant) and during ear emergence (N. Poole, 2016). An early 'holding' spray is sometimes applied before the pseudo stem erect stage if the crop is not irrigated (N. Poole, 2016).

Modern fungicide programmes for cereal crops are not specifically targeted for rust pathogens, but are generally quite effective for rust control. In the New Zealand context, the chemical groups of fungicides applied on cereals are strobilurins (quinone outside inhibitors, QoI), triazoles (demethylation inhibitors, DMI) and SDHIs (succinate dehydrogenase inhibitors e.g. bixafen and fluopyram) (FAR, 2016). Growers are recommended to tank-mix and apply fungicides with different modes of action to prevent fungicide resistance.

To date, resistance/insensitivity to the three fungicide groups has not been reported on any of the cereal rust pathogens (Fungicide Resistance Action Committee, 2018). However, insensitivity has been reported on other cereal pathogens, such as *Zymoseptoria tritici* to strobilurins and *Ramularia collo-cygni* to both strobilurin and SDHI fungicides, respectively, both internationally (Fungicide Resistance Action Committee, 2018) and in New Zealand (N. Poole, 2016).

Soybean rust

Soybean rust or Asian soybean rust caused by *Phakopsora pachyrhizi* is widespread in many soybean-producing countries such as Zimbabwe, Paraguay, Brazil, Africa, and USA (Sweets, Wrather, & Wright, 2004). Similar to managing cereal rusts, soybean rusts are controlled by combining deployment of resistant plant varieties (very limited in most countries) in conjunction with fungicide applications at key timings of crop developmental stages. In the US, management of soybean rust is through early detection and fungicide applications (Sweets et al., 2004).

The number of applications is very much dependent on how early the disease is detected and the weather conditions. However, growers are encouraged to wait until soybean rust is detected in the local region, the crop has reached reproductive stage (i.e. flowering) and weather is suitable for disease spread (Howle et al., 2008). Fungicide applications are recommended from flowering as fungicides applied prior to this stage have not been proven profitable. No fungicides are allowed after the start of full seed (Howle et al., 2008). Strobilurins and triazoles are the primary classes of fungicides applied, but occasionally, chlorothalonil (a nitrile fungicide) is used (Howle et al., 2008). Because of its acute toxicity, chlorothalonil is not recommended for controlling rusts in New Zealand. The Environmental Protection Authority (EPA) has banned any products containing chlorothalonil for

sale to the general public since April 2017. The triazole fungicides have curative and preventative activity, whereas strobilurin fungicides and chlorothalonil are preventative only. Both strobilurin and triazole fungicides will provide protection for 2 to 3 weeks depending on the rate at which they are applied. Coverage of the crop with fungicides is the key to optimal disease control from fungicides. Growers are recommended to use higher spray pressure and water volume (Howle et al., 2008).

Phakopsora pachyrhizi is currently considered as having low risk of developing resistance to fungicides by FRAC (2013). However, to ensure that these fungicides retain their activity against soybean rust, there are guidelines for the application of strobilurin and triazole mixed together and recommendations for the rate to be used on the labels (Phipps, Stromberg, Holshouser, & Bush, 2006). The latter allows more than a single mode of activity against the disease and decreases the likelihood of resistance development.

Poplar leaf rust

Poplar leaf rust caused by *Melampsora larici-populina*, *M. medusae* and *M.* × *medusae-populina* is common on poplars in New Zealand. Poplars are commonly grown as shelterbelts on farms and orchards. Disease infection ceases when all the leaves have fallen on susceptible deciduous poplars, but can persist and the fungus continues to produce spores all though winter and spring on the semi ever-green poplars. Although the pathogen overwinters on conifers, poplar leaf rust on conifers does not cause many issues (Spiers, 2009).

Control of poplar leaf rust is through planting of rust-resistant varieties (e.g., *P. alba*) and the application of fungicides, although in many cases this remains expensive, physically impractical and environmentally undesirable (Siamak & Soleiman, 2011). As with cereal rusts, substantial research has gone into fungicide application worldwide. Some examples are as follows:

- Copper (applied as copper oxychloride) and benodanil were shown to give significant control of poplar leaf rust (Fullerton & Menzies, 1974; Sheridan, 1978; Spiers, 1976)
- Benodanil and myclobutanil provided effective control of the rust, but only when applied as protectant at 14-day intervals, before the rust had an opportunity to establish itself (McCracken & Dawson, 1998)
- Successful control of leaf rust in nursery seedlings was achieved by spraying carbendazim and mancozeb (S. N. Khan, Rehill, Tiwari, Rawat, & Misra, 1988)
- Difenoconazole, captan and mancozeb were reported to be effective in preventing urediniospore germination under in vitro conditions (Ruaro & May, 1996)
- Post-symptom sprays of difenoconazole (0.02%), penconazole (0.06%) and carbendazim (0.05%) exhibited excellent eradicant activity and resulted in minimum production of urediniospores per uredinium and per unit leaf area when applied on nursery-grown poplar seedlings (Ruaro & May, 1996)
- When difenoconazole, penconazole and hexaconazole were applied separately as preventive and post-symptom sprays at fortnightly intervals, they resulted in the least disease incidence and uredinia pustules per leaf, and minimum rate of spread of disease and area under disease progress curve (Sharma & Sharma, 2000)
- Propiconazol was reported to reduce 80% of the proportion of pustules per leaf when applied as a foliage spray twice a year in recommended dose (Siamak & Soleiman, 2011).

In New Zealand, application of triadimefon (a systemic DMI fungicide, at 0.05%), copper oxychloride (0. 1%) or dodine (a guanidine, at 0.1 %) when the first rust pustules are seen is recommended (Spiers, 2009). Fungicide application is to be repeated at 3-weekly intervals as a new crop of spores is produced approximately every 2 weeks depending on weather conditions (Spiers, 2009). This intervening period can be longer during dry weather.

5.2.3 Chemical control options currently used against myrtle rust

There have been a relatively low number of trials testing fungicides against myrtle rust under field conditions over the past years (Ferrari, Nogueira, & dos Santos, 1997; Furtado & Moraes, 2011; Goes et al., 2004; Masson et al., 2013; Zauza, 2008) and none have been conducted in New Zealand. According to Masson et al. (2013), the most effective chemical groups against myrtle rust are the triazole fungicides (triadimenol, cyproconazole and tebuconazole) and the strobilurins (such as azoxystrobin and trifloxystrobin) mixed with triazole fungicides (such as azoxystrobin + cyproconazole + tiametoxam; azoxystrobin + difenoconazole and trifloxystrobin + tebuconazole). Trials have also shown that to prevent the development of pathogen resistance from occurring, the use of a protective

fungicide separately or in combination with a systemic active ingredient, or the alternation of a protective fungicide with an application of systemic fungicide must be considered (Tamra et al., 2016).

Earlier research testing the efficacy of fungicides for control of myrtle rust in Brazil on guava (*Psidium guajava*) by Ferrari et al. (1997) showed that application of chlorothalonil, mancozeb and copper oxychloride in the field post-infection did not significantly reduce disease levels, although chlorothalonil showed some efficacy. Chlorothalonil and mancozeb are protectant fungicides which remain on the surface of the leaf and are generally most effective when applied prior to infection (Miles et al., 2007). Goes et al. (2004) demonstrated that copper fungicides (oxychloride, hydroxide and oxide) applied pre-infection in the field for control of myrtle rust on *P. guajava* were equally effective as the systemic tebuconazole. These authors also found that copper fungicide or a combination of mancozeb and copper fungicide applied post-infection in the field reduced myrtle rust severity compared to mancozeb applied as a single treatment. Although mancozeb has been reported to be less effective when compared to the systemic fungicides (such as triadimenol, tebuconazole and azoxystrobin), the chemical has shown promising results in preventing myrtle rust in some field trials (Ferrari et al., 1997; Goes et al., 2004) and greenhouse studies (Ruiz, Alfenas, & Demuner, 1991). There is a need to consider and test copper and mancozeb fungicides along with other reported effective systemic fungicides as potential chemical control options for managing myrtle rust in New Zealand.

In Brazil, Masson, Moraes, Matos, Alves, and Furtado (2011) evaluated the efficacy and economic viability of three systemic fungicides (azoxystrobin, tebuconazole and trifloxystrobin), each applied at three doses via a ground application method (using a sprayer) on controlling myrtle rust on young sprouts of a susceptible commercial *Eucalyptus grandis* clone in the field. The treatments applied were: control, azoxystrobin (strobilurin), tebuconazole (triazole), combination of tebuconazole + trifloxystrobin (triazole + strobilurins) at respective rates of 0.5, 1.0 and 1.5 mL or g of a.i. L^{-1} of solution. Generally, higher fungicide levels led to a greater reduction of the disease in the host plants at 7 and 15 days after fungicide application. However, the combination of tebuconazole + trifloxystrobin in 1.5 mL L^{-1} was found to be the most effective against myrtle rust, reducing infection by 95% in the host plant. The authors concluded that tebuconazole was the most economically viable at the three tested levels, though costs were not shown in their study.

The effectiveness of the triazole fungicides, such as tebuconazole and triadimenol, can be explained by their uptake and systemic movement in plants, which facilitate early accumulation in the plant and, with sufficient amounts in plant tissue, act against fungal growth even at later stages of infection (Erincik, Daldal, & Özkul, 2016). It is due to these attributes that the importance and efficacy of these fungicides have been widely demonstrated (Martins et al., 2011; Masson et al., 2013; Zauza, 2008). For instance, Furtado and Marino (2003) carried out field trials to assess which active ingredient could be used as a preventive or curative fungicide against myrtle rust on *E. grandis* in Brazil. The fungicides tested were: propiconazole, triadimenol, tebuconazole and cyproconazole (triazoles); oxycarboxin (an anilide); chlorothalonil (a phthalonitrile); mancozeb (a dithiocarbamate) and cuprous products (copper oxychloride and cuprous oxide). Applications were performed every 14 days, with a total of six applications made. Plant materials used were: naturally infected 7-month-old *E. grandis* trees with more than 70% symptomatic shoots in the curative trial; uninfected 4-month-old *E. grandis* trees in the preventive trial. In the preventive trial, cyproconazole, triadimenol and tebuconazole showed the best results. In the curative trial, all treatments were effective, especially mancozeb (preventing the development of new lesions), difenoconazole, tebuconazole, propiconazole and triadimenol, which reduced the disease to less than 10% symptomatic shoots. Moreover, where plants were treated with propiconazole or triadimenol, the symptomatic condition remained close to zero.

In the Central-South region of São Paulo State, a field assay was carried out using naturally infected *E. grandis* aged six months (Masson et al., 2013). Different fungicide treatments were applied at 14-day intervals and the results showed that the most effective treatments in three applications were: azoxystrobin + cyproconazole + tiametoxam in 400 mL ha^{-1}, azoxystrobin + difenoconazole in 300 to 500 mL ha^{-1} with or without adjuvant, azoxystrobin + cyproconazole and trifloxystrobin + tebuconazole all in 750 mL ha^{-1}. These results confirmed previous work by Masson et al. (2011) that assessed the severity of rust disease after application of different fungicides on infected host plants in field. According to Masson et al. (2011), upon 7 or 15 days after application of fungicide solutions, the most efficient treatment was combination of tebuconazole + trifloxystrobin in 1.5 mL L^{-1}.

Martins et al. (2011) also evaluated systemic and protective fungicides under field conditions for their efficacy against myrtle rust on *P. guajava*. They tested five systemic fungicides namely: azoxystrobin, pyraclostrobin, cyproconazole, tebuconazole, triadimenol and a protectant, mancozeb. In their first trial, the application of fungicides was carried out at 2-weekly intervals, intercalated with bi-weekly sprays of copper oxychloride. In a second trial, copper oxychloride sprays were applied only when disease incidence was low (7%) on flower buds. They ensured that azoxystrobin, tebuconazole,

triadimenol and mancozeb treatments were started 9 days after a second application of copper oxychloride and maintained the same concentrations as the first trial. In this work, Martins et al. (2011) confirmed that triadimenol is one of the best fungicides against myrtle rust, a finding that supports earlier trials (Alfenas, Zauza, & Assis, 2003; Demuner & Alfenas, 1991). Zauza (2008) also showed that triadimenol can be effective when applied in later phases of the disease cycle, i.e., as a curative treatment that would reduce inoculum levels and slow the progress of the disease. In addition, the results gathered from various South American studies testing the efficacy of fungicides against myrtle rust on guava (Martins et al., 2011; Ruiz et al., 1991) and *Eucalyptus cloeziana* (Alfenas et al., 2003) affirmed the superiority of triadimenol. These findings were confirmed by Horwood, Carnegie, and Park (2013), who screened several fungicides (mostly triazoles and strobilurins) against myrtle rust infection on *S. jambos* and *Rhodamnia rubescens* plants in both field and greenhouse studies (Table 1). The authors applied the fungicides to both upper and lower leaf surfaces to the point-of-run-off with a hand-held atomiser. The controls were treated or sprayed with tap water. Spray residues were allowed to dry for 24 h before the plants were inoculated. The protectant activity of fungicides was tested by spraying the plants prior to inoculation and the eradicant activity tested by spraying 5 days after inoculation.

Table 1. List of fungicides tested by Horwood et al. (2013) for protective and eradicant activity.

Fungicides (a.i.)	Group	Full label rate (mg a.i./L)
Azoxystrobin	Strobilurin	300
Azoxystrobin+ Cyproconazole	Strobilurin+Triazole	200+80
Copper oxychloride	Protectant	2000
Triadimenol	Triazole	100
Difenoconazole	Triazole	125
Tebuconazole+Trifloxystrobin	Triazole+ Strobilurin	300+150
Triforine	Piperazine	285
Mancozeb	Dithiocarbamate	1500
Epoxiconazole	Triazole	63
Myclobutanil	Triazole	48
Oxycarboxin	Carboxamide	975
Prothioconazole+Tebuconazole	Triazoles	63+63
Propiconazole+Cyproconazole	Triazoles	80+26

In a greenhouse study, the chemicals were applied at quarter, half and full label rates to determine their protectant activity and, at full label rates for assessment of their eradicant activity. For the field study, diluted fungicides were mixed with a spray adjuvant (600 g L^{-1} nonylphenol-ethylene oxide condensate, a non-ionic organic surfactant) and applied at a rate of approximately 200 L ha^{-1} using a knapsack sprayer. Their results from the greenhouse study showed that all fungicides, with the exception of copper oxychloride, tested at full label rates for protectant activity, significantly reduced myrtle rust pustule formation on *S. jambos* compared to the controls. None or minimal rust development (0–3.33% leaf area covered by pustules) was observed on plants applied with: azoxystrobin + cyproconazole, triadimenol, tebuconazole, prothioconazole + tebuconazole, triforine, tebuconazole + trifloxystrobin, myclobutanil and propiconazole + cyproconazole, at any of the application rates tested. For eradicant activity, no rust development was observed with applications of azoxystrobin + cyproconazole, triadimenol, tebuconazole, epoxiconazole, prothioconazole + tebuconazole, triforine, tebuconazole + trifloxystrobin, myclobutanil, propiconazole or propiconazole+cyproconazole at all application rates. On *R. rubescens*, there was significantly more myrtle rust pustule formation on plants treated with mancozeb at the full label rate than on control plants. Horwood et al. (2013) continued to show that under greenhouse conditions, the single-active ingredient fungicides that consistently prevented rust development were the DMIs, namely: triadimenol, tebuconazole, triforine, myclobutanil, propiconazole, and the strobilurin, azoxystrobin. In a subsequent field study, the efficacy of azoxystrobin, azoxystrobin + cyproconazole, triadimenol and

tebuconazole + trifloxystrobin were relatively high as was the demethylation inhibitor, difenoconazole (Martins, Silveira, & Maffia, 2014).

During the myrtle response, MPI has identified some fungicides for the treatment or control of myrtle rust in New Zealand (Table 2) based on the Australian, Hawaiian and Brazilian published research. Among these identified fungicides, only mancozeb and copper oxychloride are used as protective/preventive measures (Furtado & Marino, 2003; Martins et al., 2011). None of these identified fungicides has been able to eradicate infection in New Zealand and the suggestion was for prospective users, such as nurseries or food-crop growers, to apply the active ingredients at the stipulated generic rates as indicated for similar types of pathogens on the individual product labels (www.nzppi.co.nz). There are no label recommendations for management of myrtle rust. A list of fungicides used against myrtle rust to date are shown in Appendix 1 and includes two management regimes (those referenced as either 'Falloon (2018) unpublished' or 'Keech (2018) personal communication') in use by commercial or research nurseries in New Zealand. A list of fungicides and their availability in New Zealand are summarised in Appendix 2.

Beside triazoles, the strobilurin fungicides have become valuable tools and are unique in that they are the first synthetic, site-specific compounds to provide significant control of plant diseases caused by the highly diverse phylum Basidiomycota (Heim et al., 2018), which includes the causal agent of myrtle rust disease, *A. psidii*.

Several of the QoI fungicides have been registered and considered by the Environmental Protection Agencies (EPAs) of both the United States and New Zealand. Currently, the most sought-after strobilurin is azoxystrobin. Azoxystrobin is a xylem-systemic compound with studies on cereal crops showing that 8% of the active ingredient enters the leaf above the point of uptake within eight days of application (Godwin, Bartlett, & Heaney, 1999). In broad-leaved crops, the movement of azoxystrobin to new growth areas occurred from initial spray deposition on the stem (Bartlett et al., 2002). However, further work showed that movement of azoxystrobin to new growth areas was insufficient to provide robust disease control on subsequently emerged leaves (Bartlett et al., 2002). The movement of azoxystrobin to new growths of Myrtaceae species requires investigation.

There are other active ingredients in the strobilurin group that require further research and these include, kresoxim-methyl, metominostrobin, pyraclostrobin and picoxystrobin (Bartlett et al., 2002). Among the known strobilurins, only azoxystrobin and trifloxystrobin are in the list of fungicides identified by MPI (Table 2). Kresoxim-methyl, metominostrobin, pyraclostrobin and picoxystrobin are commercial strobilurin fungicides (Bartlett et al., 2002) available for agricultural use and are extremely effective in controlling a wide range of fungal pathogens. However, their use against myrtle rust in New Zealand or overseas is unknown. Apart from metominostrobin, kresoxim-methyl, pyraclostrobin and picoxystrobin are available in New Zealand.

Table 2. Fungicides identified by the Ministry for Primary Industries (MPI) for myrtle rust treatment or control.

Fungicide active ingredient	Fungicide activity	Product available in NZ	Chemical group (Triazole/ Strobilurin)	Minimum re-treatment interval between consecutive applications
Triadimenol	Systemic, curative and protectant	Vandia 250 EC and Agpro Jupiter	3 (Triazole)	10-14 days
Triforine	Systemic, slightly curative and protectant	Saprol®	3 (None)	7-10 days
Mancozeb	Non-systemic protectant	Several available	M3 (None)	7-10 days
Azoxystrobin	Systemic, slightly curative and protectant	Amistar® SC	11 (Strobilurin)	14-21 days
Copper Oxychloride	Non-systemic protectant	Several available	M1 (None)	7-14 days
Propiconazole	Systemic, curative and protectant (Note: This has shown some phytotoxicity in Australian work)	Tilt® EC	3 (Triazole)	7-10 days
Tebuconazole	Systemic curative and protectant	Folicur®WG	3/11 (Triazole)	10-14 days
Trifloxystrobin	Systemic, curative and	Flint® and others	3/11 (Strobilurin)	10-14 days

	protectant			
Oxycarboxin	Systemic, curative and protectant	No NZ product (Australian product Plantvax750WP)	7 (None)	10-14 days

Studies with kresoxim-methyl, trifloxystrobin and pyraclostrobin have shown that fungal spores at germination stages are particularly sensitive to them (Bartlett et al., 2002). The biochemical mode of action of the active ingredients can disrupt the production of energy demanded by fungal development at various stages. This mechanism contrasts with that of the triazole fungicides, which inhibit ergosterol biosynthesis and therefore do not prevent spore germination and early germ-tube development because the pathogen obtains a supply of ergosterol or its precursors from reserves within the spore (Godwin, Young, & Hart, 1994). Therefore, strobilurins are best applied before infection or during early stages of disease development (Bartlett et al., 2002; Ypema & Gold, 1999). This information is important with respect to application timing if kresoxim-methyl, trifloxystrobin and pyraclostrobin are to be applied for the control of myrtle rust.

Kresoxim-methyl offers an effective resistance management tool because its efficacy against target pathogens is not affected by the occurrence of strains resistant to other fungicides (Ypema & Gold, 1999). Special physical and chemical properties of kresoxim-methyl result in its novel mode of action against plant pathogenic fungi, as well as unique uptake and diffusion properties (Ypema & Gold, 1999). In addition, under laboratory, greenhouse, and field research, kresoxim-methyl has demonstrated protective, post-infection, and anti-sporulation activity against economically important fungal diseases (Ypema & Gold, 1999). Reddy (2013) has also made some general suggestions that kresoxim-methyl is locally systemic with surface deposits ensuring a slow release into the plant over time and that washing off by rain is minimal. In addition, rainfall or dew wetting reactivates the spray residue on the leaf surface, allowing repeated uptake by plants over a longer period. Generally, trials using mist blowers and knapsack sprayers have shown that robust disease control can be achieved using low-volume (50–100 L ha^{-1}) and high-volume (>3000 L ha^{-1}) applications; however, the crop(s) on which such applications were made is not disclosed by Reddy (2013). Though application rates are still undergoing extensive trials on other ornamental crops, there is a need to explore the possibility of how effective this active ingredient may be on Myrtaceae spp. and myrtle rust in New Zealand.

Although fungicides have been identified by MPI (Table 2), there are other promising combinations of fungicides in addition to numerous fungicides (triazole or strobilurin) mentioned in this current review that should be incorporated into trials in New Zealand to ascertain if they are effective for controlling myrtle rust (Table 3). If successfully tested and their efficacy confirmed, these fungicides could be subsequently registered for application. Alternatively, a label change to current commercial chemicals may be possible, if supported by chemical companies. Once a combination of fungicides is determined, the type of adjuvant to use will need to be critically assessed. This is extremely pertinent as the presence of an adjuvant will improve coverage and also potentially enhance absorption and therefore efficacy of the fungicide (Gent, Schwartz, & Nissen, 2003). Adjuvants can also improve adhesion and retention of spray droplets, allowing a longer interval between sprays, provided the adjuvant is properly selected (Gent et al., 2003).

Chemical control of myrtle rust has undergone many changes from the earlier use of cuprous and dithiocarbamates to recent chemical products, which include triazoles and strobilurins. There is still much to be done to expand the scope of fungicides from which selection could be made for the control of myrtle rust in New Zealand, especially for trees of particular importance or which are highly susceptible. Understanding the detrimental effects of these fungicides on the beneficial activities of humans, the environment and non-target impact on other organisms, such as indigenous rust species is critical as we consider various chemical options to battle myrtle rust disease in New Zealand.

Table 3. Potential list of identified fungicides to consider for field or nursery trials against myrtle rust.

Active	Rate (a.i.)	Experimental site	Reference	Availability in New Zealand
Cuprous oxide	160-200 g/100L	Nursery	(Ferreira, 1989)	Yes
Cuprous oxide Difenoconazole Cyproconazole Difeniconazole+propiconazole	352 g/100L 100 mL/100L 50 mL/100L 80 mL/100L	Nursery and Field	(Furtado & Marino, 2003)	Yes Yes Yes Yes+Yes
Copper Oxychloride	160-200 g/100L	Nursery	(Alfenas, 2004)	Yes
Triadimenol+Azoxystrobin	Not described	Nursery	(Krugner & Auer, 2005)	Yes+Yes
Azoxystrobin+Tebuconazole	500-1500 mL/ha	Field	(Masson et al., 2011)	Yes+Yes
Azoxystrobin+Cyproconazole Azoxystrobin+Cyproconazole Azoxystrobin+Cyproconazole	0.3 L/ha 0.45 L/ha 0.45 L/ha+ (mineral oil 0.6 L/ha)	Field	(Moraes et al., 2011)	Yes+Yes Yes+Yes Yes+Yes
Azoxystrobin+Cyproconazole+ Tiametoxam Azoxystrobin+Difenoconazole Azoxystrobin+Cyproconazole Pyraclostrobin+Epoxiconazole Trifloxystrobin+Tebuconazole	250-400 mL/ha 300-500 mL/ha 300-450 mL/ha 500 mL/ha 750 mL/ha	Field	Furtado et al. (unpublished)	Yes+Yes+No Yes+Yes Yes+Yes Yes+Yes Yes+Yes
Azoxystrobin+Difenoconazole	300-500 mL/ha	Field	(Masson et al., 2013)	Yes+Yes
Azoxystrobin+Cyproconazole +Tiametoxam	400 mL/ha	Field	(Masson et al., 2013)	Yes+Yes+No
Tebuconazole+Trifloxystrobin	1.5 mL/L	Field	(Masson et al., 2013)	Yes+Yes

5.3 Fungicide application techniques for treatment of myrtle rust

5.3.1 General principles of fungicide application

The main purpose of the application technique or method used to apply a fungicide is to ensure optimal coverage of the target or host plant is achieved for pathogen control while, at the same time, minimising contamination of non-target organisms and spray drift (Ryley, 2003). Recommendations on the best method to apply the fungicides are important. This is because a systemic or curative fungicide has some room for applicator error, due to uptake and translocation throughout the vegetative material. However, this is not the case for non-systemic protectants, such as chlorothalonil, copper or mancozeb. For these products, a "protective" film covering the plant surface is required, meaning greater precision in the fungicide application or delivery technique on the plant of interest is necessary.

There are numerous different application techniques that can be considered for application of fungicides including: stem/bole injection, trunk implantation, trunk basal spraying; other ground rig application methods such as hand-held boom sprayers and tractor mounted-hydraulic booms and finally; aerial application methods using fixed-winged aircraft, helicopters or unmanned aerial vehicles (Baillie, Evanson, Unsworth, & Jeram, 2017; Carvalho, 2017; Durao & Boller, 2017; Gachomo, Dehne, & Steiner, 2009; Kanaskie, Hansen, Sutton, Reeser, & Choquette, 2009; Miles et al., 2007; Richardson et al., 2017; Strand et al., 2014). Regardless of the techniques chosen, for the application to be a success, factors including ease of access to the host plants, height above ground of the target, air temperature, relative humidity, wind speed, the presence of dew and occurrence of rainfall must be taken into consideration (Stefanello et al., 2016). In addition, for most plant species, transpiration rate is low at night and gradually increases during the day, hence the timing of the application is important as this can affect the absorption and translocation of the fungicide and ultimately, its performance (Stefanello et al., 2016). Climatic and environmental conditions thus play a critical role in choosing a particular application method (Nansen et al., 2015).

In New Zealand context, the application techniques (ground based and/or aerial) considered will have to be appropriate for the different situation. Situations such as, infected commercial crop in rural area or nursery (large-scale spraying), woodlot or smaller area of shrub-land vegetation (smaller area of medium to tall trees) or isolated tall trees, either in a native forest, forest patch, urban and sub-urban areas, all of which will require niche tools to ensure optimal fungicide delivery. Decision on which techniques of application to use will highly depend on finances, nature of the tree (hard bark, height and canopy foliage), its location and whether preventative or curative fungicides are applied. Techniques that do not harm the tree, especially if they are applied repeatedly, should be considered first.

According to N. F. Poole and Arnaudin (2014), combining the knowledge of fungicide effect on the crop canopy with soil water and nutrient availability enables better matching of fungicide product, dose and timing to a specific disease risk. In the field, securing effective disease control from fungicide applications is dependent upon the disease pressure and the effectiveness of the fungicide to control that disease (N. F. Poole & Arnaudin, 2014). The influence of biological and meteorological factors on spray efficacy are not always predictable, but must be considered in addition to the volume of fungicide (i.e. active ingredients) and the operational parameters (flow rate of a.i. or nozzle types) (Nansen et al., 2015). Furthermore, knowledge of the pathogen's life cycle or epidemiology is important to define the stage in the life cycle most vulnerable to the fungicide and to define the place on the host where it is most likely to be found (i.e. on foliage, under the leaves, on the shoots). The most susceptible stage of the pathogen for control measures, together with consideration of the host plant physiology, will determine the optimum time of application. The mode of action of the fungicide, its relative toxicity and other physico-chemical properties, together with the biology of the pathogen will help to determine the optimum droplet size and coverage required to maximise efficacy. For the control of myrtle rust, it is important to assess which fungicide is best used as a protectant, eradicant, or both, and how various application techniques could be implemented to provide the highest probability of success under different scenarios.

5.3.2 Ground-based application techniques

For most application trials from which fungicide efficacy data have been generated, the fungicides have been applied using ground application tools such as knapsack (Ferrari et al., 1997; McLaren, 1994) or hand sprayers (Horwood et al., 2013). J. McDonald (2012) suggested equipment used for the ground application of fungicides should be appropriate for the development of droplets that are within 150–250 µm in size. These droplet sizes were recommended for application of non-systemic

protectant fungicides (mancozeb, copper and chlorothalonil) and to ensure good leaf coverage. For ground application of such droplet sizes, the tools suggested were powered-hydraulic handguns/booms fitted with either solid or hollow cone nozzles, and three-point linkage/knacksack powered misters.

While fungicide application via knacksack sprayer technique has merit in some situations, particularly for ground vegetation and small patches of low-stature shrubbery, it will have major disadvantages for application of fungicide to trees, particularly the inability to target the part of the plant to be treated (i.e. tall foliage > 2m or large inaccessible canopy). Stem/trunk injection, on the other hand, provides a possible ground-based application technique for foliar pathogens if effective systemic fungicides are available. There are several types of stem injection techniques that may use either low pressure (i.e. using plastic capsules that are pressurised by depressing a plunger that locks in place) or higher pressure (i.e. using a syringe or tubing, tees, and a chemical reservoir designed to be under pressure) for injecting fungicides such as tebuconazole (in capsule form) or propiconazole (liquid form) respectively into the stem of a tree (www.arborjet.com) (Figure 2). Helson, Lyons, Wanner, and Scarr (2001) designed the injection system without drilling holes into the plants (Figure 2c), to overcome plants that block the drilled holes for fungicide application by releasing resins, such as pines and conifers.

There are currently no published reports on the use of stem injection for controlling myrtle rust. However, stem injection was used by Kanaskie et al. (2009) to apply phosphonate for control of *Phytophthora ramorum*, which causes sudden oak death in mature tanoak trees located in Oregon, USA. In New Zealand, injection of phosphite (Agrifos® 600) into the trunks of native kauri trees at Huia dam and Whatipu in the Waitakere ranges, Auckland, and Raetea and Omahuta Forest in the Mangamuka ranges, Northland, to control kauri dieback caused by *Phytophthora agathidicida*) was found to reduce disease lesions from 58.5% down to 0.8% (Horner, Hough, & Horner, 2015). In vineyard experiments conducted over 5 years in France, Darrieutort and Lecomte (2007) evaluated the effectiveness of the fungicides propiconazole and difenoconazole applied via trunk injections for control of eutypa dieback disease in grapevines (*Vitis vinifera*). The injection system delivered the fungicides under high hydraulic pressure in a few minutes into *V. vinifera* but could not control eutypa dieback. Düker and Kubiak (2011) also attempted to control powdery mildew in grapevines by injecting myclobutanil, penconazole and tebuconazole with a ChemJet® tree injector and all reduced infection by 20-30% when compared to the untreated control.

No literature on the use of basal bark application of fungicides for control of myrtle rust could be found at the time of preparing this review. However, the technique was applied via hand-held CO2-pressurised sprayers by Rosenberger and Cox (2009) to compare the efficacy of mancozeb with phosphite fungicides for control of apple scab disease. Extensive testing provided no evidence that phosphite fungicides with an adjuvant (Pentra-Bark®) applied via trunk basal bark spraying controlled apple scab; however, mancozeb applied to the bark provided 99% control.

Figure 2. Pictures showing: (a) pressurisd capsule injection system, (b) drilled hole injector, (c) injection system without drilled holes, and (d) pressurised reservoir and tubing system.

5.3.3 Aerial application techniques

Aerial application of pesticides via helicopters is widely used by the forestry sector in New Zealand to cover large areas of forest and enable targeted control of foliar pathogens/pests on the canopy. The use of specialised professionals and complete regulation and supervision of aircraft spraying activities make aerial application a safe and effective tool for fungicide application in most areas with low risk of environmental contamination if used appropriately (Furtado & Moraes, 2011). For this application method, droplet size is extremely crucial for accurate and efficient application with minimum off-target drift. A comprehensive report provided by the Ministry for the Environment, New Zealand, focused on a technical overview of the agricultural aviation industry to set standards for agrichemical application via aerial technique in 2013 (NZAAA, 2016). Droplets smaller than 200 µm are generally considered more prone to drift than larger droplets, which leads to the common “rule of thumb” that a spray quality no finer than coarse (droplets with size of 326–400 µm) will minimise spray drift in most situations.

Though aerial application of fungicides is widely used in New Zealand’s primary industries, there is no known or published report on the efficacy of this method for application of any fungicides to control myrtle rust in New Zealand. Moreover, aerial application of fungicides for control of myrtle rust on native New Zealand Myrtaceae tree species is likely to involve targeted or “spot spraying” rather than the more typical broadcast spraying operations (with an aerial boom) that are used in forestry. In New Zealand, several field trials testing the targeting efficiency of various aerial spot application methods have been carried out, though none of these specifically for application of a fungicide for control of myrtle rust (Richardson et al., 2017; Strand et al., 2014). Spot application methods applied via an aerial platform with helicopters (Figure 3) include use of a standard boom or partial boom below the craft (Strand et al., 2014), an extended wand operated by a person seated next to the pilot (Gous, Raal, & Watt, 2014; Strand et al., 2014) and a ring boom tethered below the craft (Richardson et al., 2017).

Spot application of herbicides using an extended wand is a commonly used technique to control isolated and difficult-to-reach wilding conifers where systemic herbicides are applied to the foliage and bark of the tree in an oil (Gous et al., 2014). However, spot application of pesticides using a ring boom, or partial boom, has only been trialled and not operationally deployed. Less is known about the efficacy and practicality of these methods for control of pests in different environments.

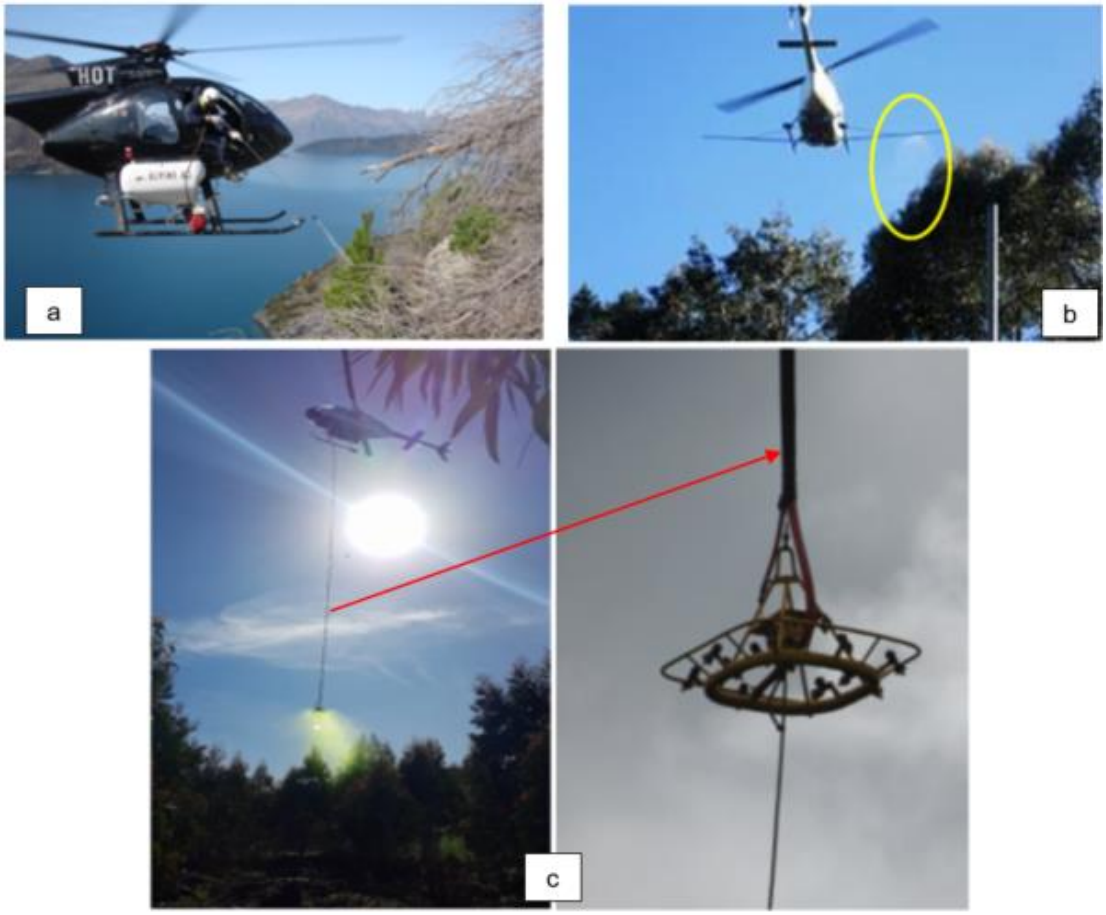

Figure 3. Targeted aerial spraying platforms with helicopter showing the (a) custom built spot gun (top), (b) use of a partial boom (yellow circled) and (c) underslung ring boom (red arrow pointing to clear view of ring boom).

Richardson et al. (2017) conducted a trial to validate the potential of the ring boom suspended on a tether for targeted spraying of individual trees or clumps of trees during pest eradication operations in an urban environment. This study was to evaluate the effectiveness of an approximately circular 'ring' boom suspended on a tether below the craft to apply spray mix on individual trees (Figure 3c). The technique could be tested for isolated cases of myrtle rust infected trees in the forest or in urban/suburban areas, depending on the context. Some concerns with this application method include:

- The helicopter moves slowly over the crown, until the pilot is convinced that adequate spray coverage through the canopy is achieved, which could be subjective;
- The technique of the helicopter hovering close to the canopy top increases the downwash velocities, a factor dependent on tether length. While high downwash velocities may improve spray penetration into lower canopy, potential negative consequences, such as reduced spray retention on leaf surfaces and increased likelihood of the helicopter wake encouraging dispersal of a pest organism, are something which could be of great concern for dispersal of pathogen spores.

When testing the potential of the manually operated custom-built spot-gun (or extended wand) for spot application of non-systemic pesticides to tree foliage from a helicopter, Strand et al. (2014) also raised concerns about the impact of the rotor downwash on pest dispersal. Further, these authors also identified potential issues with reduced leaf coverage in the lower crown when using this method, possibly also an effect of the downwash pushing droplets off or away from leaf surfaces. If aerial spot application methods, either with a ring boom or manually operated extended wand, were to be considered for the application of preventative or curative foliar fungicides to trees infected with myrtle rust, further work would need to be carried out to ensure adequate coverage was achieved and that downwash velocities did not pose a risk for spore dispersal. Some enquiries about the operational experience of commercial aerial pesticide applicators were made to clarify this point. The Heli Team, a company based in the USA, claimed that aerial application does not spread fungal spores and that this is one the advantages of helicopters for pesticide application (Heli Team, 2018). However, upon contacting them to ascertain the validity of this information, they failed to reply to our inquiries. Other

interviews conducted in New Zealand showed that similar assertions were not validated (Andrew Neal, personal communication, July 13, 2018). Generally, research on the use of aerial application techniques for fungicides (particularly spot application) effective against myrtle rust is lacking.

Success has been recorded in Australia with the evaluation of the efficacy of fungicide (tebuconazole and triadimenol) application by fixed-wing aircraft (Ryley, 2003) on other pathogens, but not on myrtle rust or Myrtaceae. Though success has been reported with fixed-winged aircraft, the use of helicopters for fungicide application, particularly for spot application, is preferred due to their ability to operate at lower speeds, manoeuvre in irregular areas, easily change direction and also land suitably in various locations (Miller, Manning, & Enloe, 2010) (www.nzaaa.co.nz, via request only). There may be several situations where of use of an aerial boom, either on a helicopter or fixed-wing aircraft, to broadcast fungicide (as opposed to spot control) will be advantageous. Broadcast aircraft applications would allow the treatment of large areas with a preventative fungicide within an appropriate and relatively short time and as a result, reduce inoculum loads and prevent the increase in areas with and/or new incidences of myrtle rust in the field (Furtado & Moraes, 2011). Further, applications using an aerial boom provide good application uniformity and allow treatment of canopy foliage for foliar treatment of trees not easily accessible from the ground (Furtado & Moraes, 2011). Most importantly, it should be noted that for an aerial application technique to be considered, it would depend on many conditions: disease intensity; inoculum load; time requirement of fungicide to be applied soon after infection starts; the distance of the targeted field from the runway. The spraying cost is directly related to the size of area to be treated, i.e. the larger the area, the lower the aerial spraying cost (Masson et al., 2013).

Unmanned aerial vehicles (UAVs), or drones, have been successfully used to detect and monitor myrtle rust infected areas in the forest. For targeted application of fungicides, UAVs may have advantages over helicopters or fixed-wing aircraft in certain situations. These include lower visibility and noise in urban and suburban areas, lower operating costs, and a more precise and controlled method of spray application, particularly in difficult-to-reach, sensitive, urban and suburban areas.

A main disadvantage is the low payload meaning they cannot carry large quantities of fungicides when compared to helicopters or winged aircraft. A main advantage is that UAVs could be used in urban and sub-urban environments to treat individual or isolated cases of myrtle rust where visibility and accessibility for the pilot are feasible. Research on the use of UAVs for fungicide application in New Zealand is generally lacking, but several pilot trials testing the use of UAVs for pesticide application are currently in progress at Scion (Richardson, personal communication, July 12, 2018). This research will help researchers and operators make an informed decision as to whether UAVs can play a role in the management of myrtle rust.

Moraes et al. (2011) compared three fungicide application techniques for control of myrtle rust in eucalyptus forests (natural field epidemic), namely: manual sprayer, tractor turbo atomiser and aerial application. They used the fungicides azoxystrobin and cyproconazole applied at different rates and application volumes. The spray volumes were 200 L ha^{-1} water for the sprayer, 350 L ha^{-1} water for the atomiser and 20 L ha^{-1} water for aerial application. The results showed that all methods of fungicide application and rates were effective in controlling myrtle rust in the field. They also reported no observation of anomalies regarding the effect of phytotoxicity of the fungicides via all the application techniques used in their study.

As much as we test different fungicides from various chemical groups with different modes of action, we will need to take a further step by considering the most appropriate application technique for the different situations. This is important, as some active ingredients may be more effective when applied via a certain application method and/or on a specific host when treating myrtle rust in New Zealand. There is no record of any research that has shown that application methods would support or enhance the effectiveness of a certain group of fungicides on a particular plant host. This calls for research to assess the efficacy of certain fungicides (a.i.) based on their application methods.

5.4 Biological control

5.4.1 A general overview of biological control

Biological control of plant disease is a non-chemical method, exploiting microbial antagonists to combat plant pathogens (Moricca, Ragazzi, & Assante, 2005). It relies on the inhibition of growth, infection or reproduction of one organism by a natural enemy and typically involves an active human management role (Baker, 1987; Robert J. Cook, 1993). The main aim of biological control is not eradication, but it represents a long-term and cost-effective pest management for reducing pathogen populations in a way that it becomes manageable. The microbial antagonists used to control

pathogens can be bacteria, fungi and viruses and they are referred as biological control agents (BCAs) (Ownley, Gwinn, & Vega, 2010). BCAs act to prevent infection or establishment of the pathogen in the plant. The basic biological control mechanisms may involve direct or indirect antagonistic interactions among microorganisms in nature. Direct antagonistic interactions result from the physical contact and/or high degree of selectivity for the pathogens by the mechanism(s) expressed by the BCA which includes parasitism (mycoparasitism and hyperparasitism), competition for nutrient and space, production of antibiotics (antibiosis), and secretion of lytic enzymes (El-Jaoual, 2008; Junaid, Dar, Bhat, Bhat, & Bhat, 2013). Indirect disease control is achieved by modulating the plant immune response, including the induction of systemic acquired resistance (SAR) and induced systemic resistance (ISR) (Busby, Ridout, & Newcombe, 2016; Robles, Ceriani-Nakamurakare, Slodowicz, González-Audino, & Carmarán, 2018). When selecting for a BCA candidate, the following general characteristics should be considered (Ulloa-Ogaz, Muñoz-Castellanos, & Nevarez-Moorillon, 2015; Upadhyay, Mukerji, & Chamola, 2001):

1. Target specific (narrow host range)
2. Not harmful to the environment
3. High reproductive potential
4. Easily disseminated
5. Self-sustaining population once established
6. Survive with a minimal requirement for nutrients
7. Survive under unfavourable environmental conditions.

During the past three decades, there has been a tremendous increase in interest and research on biological control, driven by a search for more environmental-friendly methods of plant protection (El-Jaoual, 2008). Cases of successful plant pathogen management through biological control were reported and resulted in reduction of pathogen densities and disease incidence (Baker, 1987; Robert J. Cook, 1993; Heydari & Pessarakli, 2010; Samavat, Heydari, Reza Zamanizadeh, Rezaee, & Alizadeh Aliabadi, 2014). Despite the research currently done and the successful examples, the application of microbiological control is still limited as outcomes of BCAs are often unpredictable. This is usually explained by the lack of consistency when BCAs are applied in the field or at large-scale and the lack of knowledge of the biological control system (Cory & Myers, 2000). In order to implement an effective biocontrol program, it is essential to understand the complex interaction between the plant, the pathogen, the BCA, and the environment to develop safe application processes and select new and efficient strains of BCAs. Biological control has far greater potential for success when used as part of an integrated disease management approach consisting of the deployment of several strategies that are collectively effective (e.g. breeding for resistance; chemical control strategies; cultural practices) (DiTomaso et al., 2017; Elad, Zimand, Zaqs, Zuriel, & Chet, 1993; Naranjo, Ellsworth, & Frisvold, 2015). For example, strategies combining BCAs and chemical products can overcome the lower efficacy of antagonists, while reducing the residues of chemicals in the environment.

Screening for ideal BCAs is also a critical step for the success of biological control. On average there are between 1 and 10% of the tested bacterial and fungal isolates from the environment that show effective capacity to inhibit the growth of pathogen in vitro (McSpadden Gardener & Fravel, 2002). From these, only a few isolates can suppress plant diseases under diverse growing conditions and fewer still have broad-spectrum activity against multiple pathogenic taxa (McSpadden Gardener & Fravel, 2002). Nonetheless, intensive screens have yielded numerous effective BCAs that are now commercialised, and many more candidate organisms have been identified for future commercial development (Sabaratnam & Traquair, 2002; Weller, 2007; Whipps & Lumsden, 2001).

5.4.2 Biological control agents of myrtle rust: state-of-art

Relatively few studies have focused on biological control of *A. psidii* so far. One has identified *Albonectria rigidiuscula* (synonym *Fusarium decemcellulare*) as a hyperparasite of *A. psidii* urediniospores on *Psidium guajava* (Amorim, Pio-Ribeiro, Menezes, & Coelho, 1993). Another study investigated the effect of *Bacillus subtilis* on *A. psidii* urediniospores germination and found all 24 isolates of *B. subtilis* tested in vitro had proven efficiency in reducing germination of *A. psidii* from an average of 34% (Santos, Castro, Bettiol, & Angeli Junior, 1998). Field experiments would be necessary to confirm these candidates for biological control of *A. psidii*, but these results are encouraging and deserve further consideration. Other fungal species have been found to co-occur in rust pustules and may have potential to antagonise *A. psidii* (Glen et al., 2007).

Given that little information is available in the literature, this section aims to review strategies of biological control of rust diseases with potential application to myrtle rust. A survey of BCAs effective against rust pathogen is given. Their control mechanisms and efficacies are also briefly described.

5.4.3 Biological control of rust diseases

Rust fungi are biotrophic (obligate) parasitic organisms that depend on living tissue to develop and propagate. Rust diseases are highly prolific and their spores have the tendency to disperse over long distances by wind. Because of their specific lifestyle and nature, the use of BCAs is a practical approach to control rust fungi. Biological control agents exploiting rust parasitism (mycoparasite, hyperparasites) can attack rust fungi in and on the host tissue (Moricca & Ragazzi, 2008a).

Plant endophytes represent one of the most important bioresources which have the potential for use as BCAs for rust disease management (Bamisile, Dash, Akutse, Keppanan, & Wang, 2018; Berg & Hallmann, 2006; Dutta, Puzari, Gogoi, & Dutta, 2014; H. Li, Zhao, Feng, Huang, & Kang, 2013; Melnick et al., 2008; Moricca & Ragazzi, 2008b). Endophytes are microorganisms (fungi, bacteria, actinomycetes and viruses) present in plant tissues during a part or all of their life cycle without causing any apparent symptoms of disease (Bao & Roossinck, 2013; Hirsch & Kapulnik, 1998; Stępniewska & Kuåniar, 2013). They are ubiquitous, colonise all plants and occur in all plant-growing regions in the world (Petrini, Sieber, Toti, & Viret, 1993; Strobel & Daisy, 2003). Endophyte association with the plants can be obligate or facultative, while they express a variety of lifestyles ranging from parasitism to mutualism depending on the plant host genotype and/or environmental conditions (Redman, Dunigan, & Rodriguez, 2001; Schulz & Boyle, 2005). They may be transmitted either vertically (from parents to offspring) or horizontally (from individual to unrelated individual). Based on recent work about taxonomy, functional diversity, biology and mode of transmission, endophytes can be classified into two main categories (Wani, Ashraf, Mohiuddin, & Riyaz-Ul-Hassan, 2015):

- Systemic/true endophytes: organisms that live within plant tissues for the entirety of their life cycle and share a symbiotic relationship with the host without causing visible symptoms of disease at any stage. Systemic endophytes concentrations and diversity do not change in a host with changing environmental conditions. They are furthermore transmitted vertically to next generation (i.e. by the means of seeds and/or vegetative propagules)
- Non-systemic/transient endophytes: organisms that spend at least a part of their life cycle living within plant tissues without producing any apparent disease symptoms in plants under normal conditions. However, they can turn pathogenic when the host plant is stressed or resource-limited. They vary both in diversity and in abundance with change of environment and are horizontally transmitted via spores.

It is now recognised that endophytes are involved in many important beneficial roles in the metabolism and physiology of host plants. These roles include fixing atmospheric nitrogen (Dalton et al., 2004), solubilising phosphates (Forchetti, Masciarelli, Alemano, Alvarez, & Abdala, 2007), synthesising plant-growth hormones (Hardoim, van Overbeek, & Elsas, 2008), degrading toxic compounds (Sheng, Chen, & He, 2008), inhibiting strong fungal activity (Brooks, Gonzalez, Appel, & Filer, 1994) and antagonising plant pathogens (Muthukumar, Udhayakumar, & Ramasamy, 2017). Included in this review are some examples of biological control (in vitro, in planta, or in the field) of rust diseases involving the use of endophytes. A list of BCAs effective against plant diseases, including rusts, is given in Appendix 3. Some examples of rust pathosystems controlled by endophytes are discussed below.

Coffee rust

The coffee leaf rust caused by *Hemileia vastatrix* is the most economically important coffee disease in the world, causing yield losses up to 35% (Talhinhas et al., 2017). In their work, Shiomi, Silva, De Melo, Nunes, and Bettiol (2006) tried to select endophytic bacteria from coffee leaves and branches with biocontrol potential against coffee leaf rust. Forty-three endophytic bacteria were isolated from *Coffea arabica* and *C. robusta* and were tested against leaf rust pathogen *H. vastatrix* by detached leaf and leaf disc assays. Of these endophytic bacteria tested, 23 inhibited germination of *H. vastatrix* in more than 40% of the spores after incubation for six hours from the time of inoculation. The endophytes bacterial isolates TG4-Ia (*Bacillus lentimorbus*), TF9-Ia (*B. cereus*), TF2-IIc (*Clavibacter michiganensis* subsp. *michiganensis*) and TF7-IIa (*Klebsiella pneumoniae*) exhibited highest growth inhibition against coffee rust pathogen. Another study (Haddad, Saraiva, Mizubuti, Romeiro, & Maffia, 2014) isolated 393 endophytes (154 bacteria and 239 fungi) from leaves, leaf residues (crop debris) and soil from coffee plants. Of these, 17 isolates were screened as potential antagonists to *H. vastatrix*. Thirteen of the isolates were shown to reduce rust infection frequency and sporulation

greater than 80% and 90%, respectively. The isolates included *Bacillus* sp., *Fusarium* sp., *Pseudomonas* spp., *Aspergillus* spp., *Penicillium* spp. and *Cladosporium* spp.

Poplar leaf rust

Poplar leaf rust caused by *Melampsora* spp. is one of the most important foliar diseases in poplar (*Populus* spp.) plantations in the world (Tabor, Kubisiak, Klopfenstein, Hall, & McNabb, 2000). Breeding for qualitative resistance to *Melampsora* rust has been the main control strategy, but the pathogen succeeded in overcoming all the major-resistance genes released in poplar plantations (Guinet et al., 2015). For this reason, breeders have focused more recently on quantitative resistance against *Melampsora* rust, which is supposed to be more durable. In their study, Raghavendra and Newcombe (2013) unravelled the importance of endophytic fungi from *P. trichocarpa* as major contributors to quantitative resistance to *Melampsora* rust. These fungi were identified as *Trichoderma atroviride* (anamorph of *Hypocrea atroviridis*), *Stachybotrys* sp., *Truncatella angustata* and *Ulocladium atrum*. Endophytic inoculation on infected leaves resulted in reduction of rust severity through local effects and direct interaction with *Melampsora*. However, the foliar endophytes did not induce resistance systemically. The authors hypothesised that foliar endophytes may constitute a second line of defence behind major genes for resistance to *Melampsora* rust.

White pine blister rust

The white pine blister rust causal pathogen, *Cronartium ribicola***,** is one of the most significant biotic stress agents impacting all five-needle pine species from the northern hemisphere. The disease has caused severe economic and ecological impacts. In North America where it was introduced, *C. ribicola* has decimated native white pines and significantly altered both forest ecosystems and the ability to manage the species for profitable timber production (Kinloch, 2003; J.-J. Liu, Sturrock, & Benton, 2013). Natural populations of *Pinus* are highly susceptible to this disease. Research on breeding for resistance and use of resistant germplasm has successfully identified major resistance loci (Geils, Hummer, & Hunt, 2010; K. Liu, McInroy, Hu, & Kloepper, 2017). However, the level of resistance in progeny was not constant in the field, and resulted in a wide variation in mortality (Kearns, Ferguson, & Schwandt, 2012).

In this context, foliar endophytes represent a potential new tool for white pine blister rust control. This is supported by the work of Ganley, Sniezko, and Newcombe (2008) who suggested that fungal endophytes on white pine needles could mediate or activate host resistance. They investigated the foliar fungal endophyte biodiversity from *Pinus monticola* (Western white pine) and showed that they were effective at increasing survival in host plants infected by *C. ribicola*. More specifically, seedlings previously inoculated with fungal endophytes lived longer and reduced in disease severity compared to endophyte-free seedlings.This ability to extend host survival was found to be effective over time, indicating persistence of the endophyte-mediated resistance.

Two-Needle pine stem rust

Some fungal endophytes species can colonise the uredinia, urediniospores and germ tubes of several rust-causing fungi. *Cladosporium tenuissimum* is known for being a hyperparasite of rust spores (*Puccinia, Cronartium, Uromyces, Hemileia, Melampsora*) and can be exploited as a BCA of rust fungi (Moricca et al., 2005). In their study, Moricca, Ragazzi, Mitchelson, and Assante (2001) demonstrated that *C. tenuissimum* provides in vitro and in planta control of *Cronartium flaccium* and *Peridermium pini*, the causal agents of the Scots pine blister impacting two-needle pines. Microscopic examinations showed that direct parasitism would explain the biocontrol activity of *C. tenuissimum*, although this fungus could also produce antifungal compounds.

Other known rust antagonists

Tuberculina spp. (Basidiomycota) are known for being mycoparasites of the spermagonial, aecial and uredinal stages of rusts (Moricca & Ragazzi, 2008a). In their study, (Bauer, Lutz, & Oberwinkler, 2004) showed that *Tuberculina persicina* parasitise the haploid stages of two rusts: *Puccinia sylvatica* and *Tranzschelia prunispinosae*. *Tuberculina persicina* is a contact parasite with a unique mode of action. It uses a direct cytoplasm-cytoplasm connection with their host rust that enables distinct interfungal interactions. As a result, the rust cells are dissolved at the point of contact with *T. persicina*.

The genus *Verticillium* (= *Lecanicillium*) comprises many parasites of rusts (Kranz & Brandenburger, 1981). For example, *V. lecanii* was reported as a hyperparasite of *Hemileia vastatrix* (Carrion & Rico-Gray, 2002; Shaw, 1988), *Puccinia recondita* (Spencer & Atkey, 1981), *Uromyces dianthi* (Spencer,

1980). Another species *V. psalliotae* was shown as an effective mycoparasite of the soybean rust fungus *P. pachyrhizi* (Saksirirat & Hoppe, 1990).

Sphaerellopsis filum (anamorph of *Eudarluca caricis*) is a known mycoparasite of at least 369 species of rust fungi worldwide (Kranz & Brandenburger, 1981). The mode of action of *S. filum* is based on its ability to degrade uredial sori, which result in stopping the propagation of uredospores and so prevents new rust infections (Gordon & Pfender, 2012).

Aphanocladium album is a hyperparasite of *Puccinia graminis* f. sp. *tritici*, the causal agent of wheat rust. *A. album* was shown to invade aeciospores and teliospores of *P. graminis* f. sp. *tritici* resulting in the collapse of the cells (Koĉl, Forrer, & Défago, 2008).

5.4.4 Potential of using natural endophytes from New Zealand Myrtaceae to control myrtle rust

Understanding leaf endophytes' diversity, taxonomic composition, influence on their host and sensitivity to environmental perturbation is crucial when exploring their potential as biological control tools against rust. In New Zealand, studies related to the community structure and diversity of leaf endophytes on Myrtaceae were mainly conducted on mānuka (*Leptospermum scoparium*) (Johnston, 1998; McKenzie, Buchanan, & Johnston, 1999; Wisnu Adi Wicaksono, Eirian Jones, Monk, & Ridgway, 2017; Wisnu Adi Wicaksono, Jones, Monk, & Ridgway, 2016) and kānuka (*Kunzea ericoides*) (Johnston, Sutherland, & Joshee, 2006; Joshee, Paulus, Park, & Johnston, 2009; McKenzie, Johnston, & Buchanan, 2006).

In kānuka, a high diversity of fungal endophytes has been recovered and identified from the leaves, with the most abundant taxa being *Mycosphaerella* spp. and *Torrendiella* sp. (Joshee et al., 2009). In mānuka, three major classes of endophytic bacteria have been identified so far from the stems and roots: Gammaproteobacteria (*Rahnella*, *Serratia*, *Erwinia*, *Pantoea* and *Pseudomonas*); Betaproteobacteria (*Burkholderia*) and Bacilli (*Paenibacillus*) (Wisnu Adi Wicaksono, Jones, et al., 2017). Some of these bacteria (*Erwinia* sp. T4MS11P and *Pseudomonas* sp. M3R43) have been shown to promote plant growth and modify metabolite profile when they are inoculated to mānuka seedlings (Wisnu Adi Wicaksono, Jones, et al., 2017). When tested against different kinds of plant pathogens (fungal pathogens *Ilyonectria lirioactinidiae* and *Neofusicoccum luteum,* and bacterial pathogen *Pseudomonas syringae* pv*. actinidiae* (Psa)), the mānuka endophytic bacteria showed in vitro antagonistic activity (Wisnu Adi Wicaksono et al., 2016). When transferred in a heterologous host, mānuka endophytic bacteria are still able to express their bioactivity. Among the endophytic bacteria recovered from mānuka, two isolates (*Pseudomonas* sp. I2R21 and *Pseudomonas* sp. W1R33) were transferred to grapevine (*Vitis vinifera*) and successfully antagonised *Neofusicoccum luteum* and *N. parvum* infections (Wisnu Adi Wicaksono, Eirian Jones, et al., 2017). When compared to untreated plants, the endophytic bacteria reduced lesion length caused by the pathogens by 32–52%. Similarly, three endophytic bacteria from mānuka (*Pseudomonas* sp. T1R21, T4MS32AP and T4MS33) were transferred to kiwifruit (*Actinidia deliciosa*) and demonstrated in vitro and in planta bioactivity against Psa, the causal agent of bacterial canker in kiwifruit (Wisnu Adi Wicaksono et al., 2018). The combination of these three bacteria reduced the Psa population 1000-fold compared with the positive control. Although the exact mechanism by which endophytic bacteria reduce Psa development and disease development has not yet been determined, the authors hypothesised that antibiosis through production of diffusible compounds is likely to be the main biocontrol mechanism. Therefore, the endomicrobiome of mānuka represents a source of antimicrobial agents and emphasises the potential of its use as a universal biological control agent in cross-species transfer.

5.4.5 Are endophytes good candidates for controlling myrtle rust

It is now well established that endophytes can mediate resistance against plant pathogens and could play a long-term role in the effective management of invasive pathogens. In New Zealand, endophytes recovered from representative native Myrtaceae species may provide good potential for selecting BCAs against myrtle rust. The potential of these BCAs establishing in the environments where they originate is likely to be greater and detrimental non-target impacts of such BCAs are likely to be less.

The endomicrobiomes of mānuka, pōhutukawa and kānuka and their potential for identifying BCAs to control myrtle rust is currently being investigated in New Zealand in a current MBIE programme (Beyond myrtle rust). The second approach would be to consider the endophytes isolated from other host species that have antagonistic effects on other rust pathogens (Section 5.4.3). Some of which are already present in New Zealand and could be tested against myrtle rust and possibly transferred to Myrtaceae seedlings as a preventive tool against the disease. A list of potential endophytes that could be used as BCAs against myrtle rust is provided in Appendix 3.

5.4.6 Other considerations when applying endophytes as BCAs

The practical implementation of BCAs on large scale can be constrained by many factors, such as application methods and BCAs' survival under adverse weather conditions. The transfer from controlled-environment to field trials is often complex since the BCAs face a wide range of environmental conditions in the field that cannot all be replicated in laboratory facilities. In addition, the non-target impact of the endophytes on other microorganisms, in particular those, which are native to New Zealand, must be considered. New Zealand has approximately 125 species of native or endemic rust fungi (McKenzie 1998); many are known from less than 10 collection localities (scd.landcareresearch.co.nz). There are also three rust fungi, *Puccinia embergeriae*, *P. freycinetiae*, and *Uredo salicorniae*, listed as nationally critical by the Department of Conservation. Therefore, any BCAs used against *A. psidii* must have a high degree of specificity to *A. psidii* and not spread or adversely affect endemic rust fungal species.

5.5 Other emerging biocontrol strategies

Enhancing pest management using the plant's own defences has been described as a promising way to improve the management of plant diseases (Llandres Ana et al., 2018). Plant immunity generally consists of several layers of defence to combat pathogens, which can be described as a combination of preformed and inducible components (Jones & Dangl, 2006). Using inducible mechanisms following recognition of appropriate stimuli, plants can widely enhance their defensive capacity against future attack of a broad spectrum of pathogens (Walters, Ratsep, & Havis, 2013). This protective effect has also been suggested to have long-lasting effect that would result in a generalised plant immunisation against subsequent infections (Durrant & Dong, 2004). The phenomenon is known as Systemic Acquired Resistance (SAR) and is associated with:

- Programmed Cell Death that is confined to the infected area
- Accumulation of pathogenesis-related (PR) proteins and salicylic acid1 in all plant parts distant from the original locus of stimuli (Angelova, Georgiev, & Roos, 2006; Durrant & Dong, 2004; Jayaraman, Rahman, Wan, & Punja, 2009)**.**

These features of SAR as a defence response have biotechnological applications to manage plant pathogens in crop plants growing under field conditions (Tamm et al., 2011; Yi, Yang, & Ryu, 2013). Immune-stimulated (or primed) plants are able to respond more rapidly and adequately to various biotic stresses, allowing them to efficiently combat an infection (Pastor, Balmer, Gamir, Flors, & Mauch-Mani, 2014). The protective effect of SAR can also be transferred to the progeny and can confer a fitness advantage under conditions of high disease pressure (Shah & Zeier, 2013).

It has been suggested that sustained activation of plant defence is associated with risk of low fitness costs for the plant. Such costs include a negative impact on growth, mostly resulting from metabolic competition: the plant resources are relocated away from growth towards defence (Walters & Heil, 2007). This phenomenon, also called the growth-defence trade-off, occurs in plants due to resource restrictions and demands prioritisation towards either growth or defence depending of external and internal factors (Huot, Yao, Montgomery, & He, 2014). Stimulation level of priming should also be considered as it might also induce direct resistance that compromises fitness. The cost of plant defence does not just include resource allocation, but also ecological costs. For example when the expression of a defence trait negatively interacts with one of the plant-environment interaction such as mycorrhizal associations (Heil & Baldwin, 2002). While the contribution of induced resistance by elicitors can be tested by comparing the obvious damages caused by the pathogens, it should also be combined with an assessment of the resulting cost-benefit balance.

5.5.1 Enhancing plant resistance using elicitors

The recognition of a range of molecular factors of plant or microbial origin called elicitors constitutes the basis of inducible plant defence mechanisms (Krzyzaniak et al., 2018; Walters et al., 2013). Elicitors are very stable molecules of low molecular weight that stimulate immune defence response in plants. They are classified in three major categories based on their function in the plant immune system: molecules that induce tissue damage (physical elicitors), molecules that control responses of the plant (phytohormones: salicylic acid, ethylene and jasmonic acid) to attack by a pest organism, and molecules that induce attack by a pest organism (chemical elicitors). Chemical elicitors can further be divided into:

[1] Salicylic acid (SA) is a plant hormone that plays an important role in induction of plant defence against a variety of biotic and abiotic stresses.

- Biotic origin: this includes substances of pathogen origin (exogenous elicitors), compounds released from plants by the action of the pathogen (endogenous elicitors) (Angelova et al., 2006)
- Abiotic origin: physical factors (radiation, temperature, ultrasounds), metal ions (CaCl2, AgNO3, CuSO4) and metals salts (Ca2+, Fe2+, Zn2+).

We will review here some of the various types of elicitors that can induce plant defence response and their potential use in crop protection and pest management. A summary of elicitors is provided in Appendix 4.

5.5.2 Fungal-derived elicitors

There have been several studies on the effectiveness of induced resistance for disease control using biotic and synthetic elicitors. Structural components of fungi, including breakdown of cell wall products such as chitin, mannoproteins and β-glucans, have proven capacity to increase resistance to disease in several plant species (Wiesel et al., 2014). In addition to the observed disease reduction, these studies also revealed how gene expression levels and defence responses are affected in plants following elicitor recognition. For instance, prior treatment of groundnut (*Arachis hypogaeae*) leaves with glucan isolated from *Acremonium obclavatum*, showed significant reduction in rust (*Puccinia arachidis*) disease development. This was also correlated with increased levels of chitinases, β-1,3-glucanase (both PR proteins) and salicylic acid. *A. obclavatum* excretes a soluble glucan that inhibits urediniospore germination of groundnut rust making it a prospective candidate for biological control (Gowdu & Balasubramanian, 1993). Shetty et al. (2009) further showed that prior application of β-1,3 glucan isolated from *Zymoseptoria tritici* (synonym *Septoria tritici*) cell walls can protect susceptible wheat cultivars from disease development. This protection against *Z. tritici* was also correlated with accumulation of PR-proteins and callose deposition. In *Arabidopsis thaliana* plants, disease resistance to botrytis was promoted by pre-treatment with the elicitor PebC1 isolated from *Botrytis cinerea*. The induced resistance involved the activation of defence response (i.e. ROS, NO generation, defence-related genes) and persisted for at least 21 days (Y. Zhang et al., 2014). An elicitor isolated from *Phytophthora colocasiae*, the causal agent of taro leaf blight, was shown to cause a local hypersensitive response and an induction of SAR in taro (*Colocasua esculenta*) plants (Mishra, Sharma, & Misra, 2009). In their study, N. U. Khan, Liu, Yang, and Qiu (2016) showed that rice seedlings pre-treated with the elicitor MoHrip2 derived from *Magnaporthe oryzae* induced resistance to rice blast disease. This was also correlated with an enhancement of basal defence responses such as ROS, plant cell death and defence-related proteins. Troncoso-Rojas et al. (2013) showed that a pre-treatment of tomato fruits with a fungal elicitor, B2-F, activated defence response. This was supported by a delayed development of fusarium rot, a reduction of lesion size (by 73%), and active synthesis of phenylpropanoid compounds. Other fungal components that showed elicitor activities may also include xylanase, sterols (ergosterol) and pectolytic enzymes (Hamid & Wong, 2017).

5.5.3 Phytohormone-induced resistance

Salicylic acid (SA) is a key signal for defence gene expression. This plant hormone, as well as its synthetic mimics, can be applied exogenously to plants to enhance resistance to many pathogens (Kouzai et al., 2017). For instance, SA pretreatment of rubber tree (*Hevea brasiliensis*) induced resistance against *Phytophthora palmivora* (Deenamo et al., 2018). In faba bean (*Vicia faba*), exogenous applications of salicylic acid and benzothiadiazole (BTH) induce SAR to various pathogens including rust (*Uromyces viciae-fabae*), ascochyta blight (*Ascochyta fabae*) and broomrape (*Orobranche crenata*). Pretreatment with SA was also shown to mediate induced disease resistance in pearl millet (*Pennisetum glaucum*) to the rust *Puccinia substrinata* (Crampton, Hein, & Berger, 2009).

5.5.4 Abiotic elicitors

Several studies have highlighted the potential of the synthetic elicitor, benzothiadiazole[2] (BTH, Acibenzolar-S-methyl, Bion®, Actigard™), to induce resistance to rust pathogens. In a study in *Eucalyptus* hybrids (*E. grandis x E. urophylla*), foliar application of BTH and *Saccharomyces cerevisiae* (yeast) extract appeared to be efficient at reducing myrtle rust (Boava, Kuhn, Pascholati, Piero, & Furtado, 2009). These two inducers were found to increase the activity of chitinase, peroxidase and phenylalanine ammonium lyase (PAL) enzymes together with the induction of a HR in both susceptible and resistant clones (Boava et al., 2009). Another study reported higher expression of genes encoding chitinase in the leaves of *Eucalyptus* pre-treated with BTH and challenged with *A. psidii*, suggesting the pre-conditioning effect was induced by exposure to BTH (Boava, Kuhn,

[2] Benzothiadiazole is a synthetic analogue for Salicylic Acid and the first SAR-inducing commercialised chemical that is effective against a broad spectrum of pathogens.

Pascholati, Di Piero, & Furtado, 2010). Han, Liu, Wei, Huang, and Kang (2012) demonstrated that disease resistance to *P. striiformis* f. sp. *tritici* was induced in mature wheat plants pre-treated with BTH and lasted for at least 60 days. Iriti and Faoro (2003) also highlighted the efficiency of a single application of BTH in preventing rust infection caused by *Uromyces appendiculatus* on French bean plants (*Phaseolus vulgaris*), and recent findings of Barilli, Rubiales, Amalfitano, Evidente, and Prats (2015) showed BTH reduced pre- and post-penetration of the rust pathogen *Uromyces pisi* through priming of phytoalexins accumulations in pea (*Pisum sativum*) leaves. Application of other abiotic agents such as oxalic acid, potassium oxalate, Fungastop, Photophor and salicylic acid have been shown significantly reduced powdery mildew disease, caused by *Sphaerotheca fuliginea* in cucumber (*Cucumis sativus*) (Alkahtani, Omer, El-Naggar, Abdel-Kareem, & Mahmoud, 2011).

5.5.5 Are elicitors good candidates for controlling myrtle rust?

Priming using elicitors is an effective strategy to combat biotic and abiotic stresses and therefore represents a potential approach to enhance plant protection in agricultural system. The exploitation of the natural capacity of the plant immune system, in combination with other strategies, may hold the potential to achieve more durable and effective plant protection. These inducible components of plant defences can be activated by spraying with compounds such as salicylic acid and are environmentally safer means of disease control. In the case of myrtle rust, some abiotic elicitors have already showed efficiency to control the pathogen, and other biotic ones have proven efficiency against other rust pathogens. However, a number of factors should be considered prior of the use of elicitors, such as the plant genetic background, the interactions with the environments and the trade-off costs for the plants. Despite a wide range of elicitors having been reported for their ability to induce defence responses, only few of them are able to trigger resistance against pathogens, especially under field conditions (Walters et al., 2013). Efficiency of the elicitors is unpredictable when transferred from the controlled laboratory conditions to the field because of the natural variations of the induced plant defense response caused by the plant genotype and the environmental conditions (Bruce, 2014). Plant genotype, environment and interaction between genotype and environment can also influence field performance and inducible defence traits.

5.5.6 Antimicrobial peptides (AMPs)

Antimicrobial peptides (AMPs) are endogenous polypeptides produced by multicellular organisms in order to protect a host from pathogenic microbes (Tam, Wang, Wong, & Tan, 2015). In plants, the majority of AMPs are cysteine-rich short amino-acid sequences, a feature that enables the formation of multiple disulphide bonds (usually two to six) that contribute to a compact structure and resistance to chemical and proteolytic degradation (Hammami, Hamida, Vergoten, & Fliss, 2009). Plant AMPs share several common characteristics with those from microbes, insects and animals including their molecular forms, positive charge and amphipathic nature (Tam et al., 2015). The repertoire of AMPs synthesised by plants is extremely large with hundreds of different AMPs in some plant species. The main families of AMPs comprise plant defensins, thionins, lipid transfer proteins, cyclotides, snakins, and hevein-like proteins, differing in structure, size and cysteine content (Montesinos, 2007). A detailed classification of plant AMPs based on cystein motifs and disulphide bond patterns can be found in previous reviews (Hammami et al., 2009; Tam et al., 2015). They are often tissue-specific and can be found in all plants organs, including seeds, bulbs, leaves, tubers, fruits, shoots, and roots (Yan et al., 2015).

As components of the plant induced systemic resistance (ISR) or systemic acquired resistance (SAR), AMPs can be responding to local infection and be accumulating in more distant (yet uninfected) parts of the plants (Lay & Anderson, 2005). The majority of AMPs in plants are located in the outer cell layer lining the organ, which is consistent with their role in constitutive host defence against pathogens attacks from the outside. Induction in expression of plant AMPs can also occur in response to pathogen attack, injury and some abiotic stresses (Lacerda, Vasconcelos, Pelegrini, & Grossi-de-Sa, 2014). For example, a strong induction of genes expressing either thionins, plant defensins, or lipid transfer proteins has been observed on infection of the leaves by microbial pathogens (Broekaert et al., 1997).

AMPs are of particular interest for protection against plant pathogens because their mechanism of action targets fundamental features of microbial cell membranes, which is thought to reduce the risk of resistance development in microbial populations (Yan et al., 2015). Most AMPs are cationic. They bind to the surface of microorganisms through receptor-mediated interaction and insert into the cytoplasmic membrane. Other AMPs, that are not membrane-disruptive, cross the cell membrane to interact with intracellular targets and inhibit nucleic acid or protein synthesis procedures (Bhima & Mohammed,

2016). Plants AMPs can also act against a broad spectrum of microorganisms and are low cytotoxicity to animals, which is viewed as an environmentally friendly potential antimicrobial (Games et al., 2016).

Antifungal peptides have been isolated from numerous plants (H. Wang & Ng, 2001; Wel & Loeve, 1972; Ye, Ng, & Rao, 2001). We will review here some examples of the use of plant AMPs in disease control, with emphasis on fungal pathogens. A list of known AMPs and their antifungal effects is provided in Appendix 5.

5.5.7 AMPs from plants

Plant defensins

Plant defensins have a widespread distribution throughout the plant kingdom, and are likely present in most plants (Lay & Anderson, 2005). They are encoded by small multigene families and exhibit a wide range of biological activities including growth inhibitory effects on a broad range of fungi and bacteria. Several plant defensins have been isolated and show in vitro inhibitory activity against filamentous fungi (Thomma, Cammue, & Thevissen, 2002; van der Weerden, Lay, & Anderson, 2008). Based on their antifungal effect, two groups of plant defensins can be distinguished. On one hand the morphogenic plant defensins cause reduced hyphal elongation with a concomitant increase in hyphal branching. These include for instance Rs-AFP1, Rs-AFP2 from *Raphanus sativus* (radish) and Hs-AFP1 from Alumroot (*Heuchera sanguinea*) (Carvalho Ade & Gomes, 2009; Terras et al., 1995). On the other hand, the non-morphogenic plant defensins only slow down hyphal elongation without inducing marked morphological distortions (Broekaert et al., 1997). These include Dm-AMP1, Dm-AMP2 from dahlia (*Dahlia merckii*), Ah-AMP1 from horse chestnut (*Aesculus hippocastanum*) and Ct-AMP1 from blue pea (*Clitoria ternatea*) (Fant, Vranken, & Borremans, 1999; K. Thevissen et al., 2003; Karin Thevissen, Osborn, Acland, & Broekaert, 2000). Interaction of certain plant defensins with specific cell wall/plasma membrane resident sphingolipids results in the induction of cell wall stress, accumulation of ceramides and reactive oxygen species (ROS), and ultimately cell death (Islam, Velivelli, Berg, Oakley, & Shah, 2017). Application of plant defensins in plant protection has been widely undertaken by transgenesis of important crop species, resulting in an enhanced protection against pathogen attacks (Carvalho Ade & Gomes, 2009; Lay & Anderson, 2005; Portieles, Ayra-Pardo, & Borrás, 2006; Sagaram, Pandurangi, Kaur, Smith, & Shah, 2011; Stotz, Thomson, & Wang, 2009; Thomma et al., 2002). For instance, Gao et al. (2000) characterised an antimicrobial plant defensin (alfAFP) isolated from seeds of alfalfa (*Medicago sativa*) that displays strong in vitro activity against the fungal pathogens *Verticillium dahlia*, *Alternaria solani*, and *Fusarium culmorum*. Expression of the corresponding gene in transgenic potato plants resulted in accumulation of high levels of alfAFP and provided robust resistance to *V. dahlia* both in greenhouse and field conditions. Constitutive expression of a plant defensin from *Brassica oleracea* and *B. campestris* in transgenic rice conferred effective resistance to Fungal Rice Blast (*Magnaporthe grisea*) and Bacterial Leaf Blight (*Xanthomonas oryzae*) (Kawata et al., 2003). The pea (*Pisum sativum*) defensins Drr230a and Drr230c expressed in transgenic tobacco have been shown to present antimicrobial activity against various phytopathogenic fungi, including *Fusarium solanii*, *F. oxysporum*, *Aschochyta pisi*, *Aschochyta pinodes*, *Aschochyta lentis*, *Alternaria alternata* and *Leptosphaeria maculans* (Lai, DeLong, Mei, Wignes, & Fobert, 2002).

Lipid transfer proteins (LTPs)

Lipid transfer proteins (LTPs) are small proteins (9–10 kDa, ~ 90 amino acids) preferentially located in plant epidermal cell wall, which can bind and transfer a variety of different lipids between membranes in vitro (Segura, Moreno, & Garcia-Olmedo, 1993; S. Y. Wang, Wu, Ng, Ye, & Rao, 2004). They were shown to play a role in plant defence, such as retarding the growth of fungal pathogens (Yan et al., 2015). A non-specific LTP was isolated from mung bean (*Phaseolus mungo*) seeds and exerted antifungal action toward *Fusarium solani*, *F. oxysporum*, *Pythium aphanidermatum*, and *Sclerotium rolfsii* (S. Y. Wang et al., 2004). Transgenic Chinese white poplars (*Populus tomentosa*) over-expressing *Leonurus japonicas* nonspecific lipid transfer protein LJAMP2 were resistant to the fungal pathogens Poplar Leaf Blight (*Alternaria alternata*) and anthracnose (*Colletotrichum gloeosporioides*) (Jia et al., 2010).

Hevein-like antimicrobial peptides

Hevein peptide was first isolated from the latex of the rubber tree (*Hevea brasiliensis*). Hevein-like peptides are now recovered from many different plant species. They consist of short basic peptides (29–45 amino acids) enriched with cysteine and glycine residues. These cysteine residues form a typical motif that is able to specifically bind to chitin and possesses antifungal activity in vitro against

several phytopathogenic fungi. Many chitin-binding proteins contain either a hevein domain or a homologous sequence including chitinases[3]. The general mode of action of hevein-like peptides consists of hyphal penetration leading to cell burst (Koo et al., 1998). For instance, Pn-AMP1 and Pn-AMP2 are two hevein-like peptides isolated from seeds of *Pharbitis nil* that showed potent antifungal acitivity. These peptides penetrate the fungal hyphae and localise at the septa and hyphal tips, causing the hyphae to burst (Koo et al., 1998). An hevein-like peptide isolated from *Capsicum annuum* (hot pepper), and named CaAFP, showed in vitro inhibition spore germination and appressoria formation in *F. oxysporum* and *Nectria radicicola* (Y. M. Lee, Wee, Ahn, Lee, & An, 2004). The expression pattern of this peptide showed that it may play a defensive role in protecting leaves and flower buds against a pathogen attack (Y. M. Lee et al., 2004).

Thionins

Thionins have been mainly identified from monocotyledonous but also in various dicotyledonous plants (Apel, Bohlmann, & Reimann-Philipp, 1990). They are small basic peptides (44–47 amino acids) that possess a conserved cysteine-rich domain and antimicrobial activities (Asano, Miwa, Maeda, Kimura, & Nishiuchi, 2013). Their mode of action is presumably to attack the cell membrane by inducing the opening of pores on the cell membranes of the pathogen, allowing escape of potassium and calcium ions from their cells (Pelegrini & Franco, 2005). In *Arabidopsis thaliana*, the Thi2.4 protein, mainly expressed in flower and flower buds, was shown to act both as an antifungal peptide and as a suppressor of the toxicity of a fungal effector fungal fruit body lectin (FFBL) from *Fusarium graminearum* (Asano et al., 2013). Overexpression of Thi2.1 from *A. thaliana* in roots and leaves of transgenic tomato resulted in significant resistance against *F. oxysporum* f. sp. *lycopersici* and bacterial wilt (Chan et al., 2005). Similarly, overexpression of α-hordothionin from barley endosperm in roots and leaves of transgenic sweet potato (*Ipomoea batatas*) induced resistance to the fungal pathogen *Ceratocytis fimbriata* (black rot) (Muramoto et al., 2012).

5.5.8 AMPs from microorganisms

Microorganisms can be considered as valuable sources for the production of antifungal compounds. Antimicrobial peptides produced by microorganisms include fungal defensins, peptaibols and cyclopeptides (Montesinos et al., 2012).

Fungal defensins

Several filamentous fungi can secrete AMPs that are similar to defensins from plants. The best-studied examples are the peptides AFP from *Aspergillus giganteus* (Theis, Wedde, Meyer, & Stahl, 2003), PAF from *Penicillium chrysogenum (Oberparleiter et al., 2003)*, Anafp from *Aspergillus niger* (Gun Lee et al., 1999) that exhibit antifungal activity.

Peptaibols

Peptaibols are a large family of antibiotic peptides from soil fungi including *Trichoderma* and related genera such as *Emericelopsis* and *Gliocladium*, which exhibit antibacterial and antifungal properties (Shi et al., 2012). To date, 309 peptaibols have been sequenced, among them more than 180 are synthesised by *Trichoderma* spp. (Shi et al., 2012). These peptaibols can act synergistically in antagonism together with the cell wall degrading enzymes arsenal of biocontrol-fungi. For example, a synergistic effect of the peptaibols Trichorzianine A1 and B1 from *T. harzianum* with chitinases and β-1,3-glucanases was showed to inhibit in vitro spore germination and hyphal elongation of *Botrytis cinerea* (Schirmbock et al., 1994).

Cyclopeptides

Cyclopeptides are secondary metabolites produced by bacteria, fungi, and cyanobacteria having antifungal and antibacterial properties (Montesinos et al., 2012). For instance, the tyrocidines, a complex of analogous cyclic decapeptides produced by *Bacillus aneurinolyticus*, exhibit noteworthy activity against a range of phytopathogenic fungi, including *Fusarium verticillioides*, *Fusarium solani* and *Botrytis cinerea*.

Recently, cyclopeptides isolated from two mangrove fungi *Phomopsis* sp. K38 and *Alternaria* sp. E33 were shown to exhibit moderate to high inhibitory effect against plant pathogenic fungi including

[3] Chitinases are hydrolytic enzymes that break down glycosidic bonds in chitin.

Gaeumannomyces graminis, *Rhizoctonia cerealis*, *Helminthosporium sativum* and *Fusarium graminearum* (C. Li, Wang, Luo, Ding, & Cox, 2014).

5.5.9 Are AMPs good candidates for controlling myrtle rust?

Antimicrobial peptides have proven effective activity against a broad spectrum of phytopathogens, including fungi. However, their use as tools in plant protection to date has been confined to model systems and crop improvement through the generation of genetically modified organisms (GMOs). Transgenic plants expressing high levels of AMPs from other plants could increase the pathogenic resistance reducing crop losses and chemical use (Yan et al., 2015) and they can inhibit the growth of a broad range of fungi and bacteria at micro-molecular concentrations. However, the use of transgenic technologies on native species including Myrtaceae is unlikely in New Zealand for a range of cultural, ethical and practical reasons.

A practical use of AMPs in plant protection could be through spraying on plant surfaces. Once again, this could be challenging because natural AMPs are produced in low amounts, some are toxic for plants and animals, some have low activity or are unstable, and procedures to extract and purify from the producing organism can be complex and costly (Montesinos, 2007). To overcome these problems, an alternative could be to design synthetic, non-toxic, more effective and more stable AMPs. An example of such approach is the de novo design of AMPs from plants to fight human pathogens. For instance, starting with Pg-AMP1, a peptide from the Myrtaceae guava, computer-aided design techniques were used to engineer synthetic AMPs with a stronger antimicrobial action than the original. One of these de novo peptides called Guavanin 2 is toxic to many human pathogenic bacteria (Porto et al., 2018). D. W. Lee and Kim (2015) indicated that synthetic cyclic peptides with antibacterial properties against *Erwinia amylovora* showed comparable activity to commercially available antibiotics. Even if antifungal synthetic cyclic peptide has not yet beent studied, the application of such approach has much appeal for consideration as a biological control tool against plant fungal pathogens.

As AMPs are key components of a plant's innate system (especially SAR), they could be used as diagnostic molecular markers of defence signalling pathways, and a marker-assisted selection process could be used to detect resistance traits in plants. Resistant genotype selection is regarded as one of the most economic forms of reducing the effects caused by disease in forest species (Sobrosa and Martins–Corder, 2001). In the case of myrtle rust, research is ongoing on several Australian species to detect candidate genes involved in resistance to *A. psidii* that could be implemented in breeding programme (Hsieh et al., 2018; Tobias, Guest, Külheim, & Park, 2017). Many TIR-NBS-LRR-type receptors, glycosyl hydrolase, chitinase, pathogenesis-related proteins and thaumatin-like genes have been detected with higher gene expression in resistant genotypes. Interestingly, no or very few antimicrobial peptide genes were detected in these studies but that may reflect the limited representation of the spectrum of defence mechanisms that can currently be identified. The molecular bases of Myrtaceae resistance to *A. psidii* are not completely unravelled and the potential of antimicrobial peptides should be investigated.

5.5.10 Mycoviruses

Mycoviruses (syn. mycophage) are viruses that cause infection in fungi. They are widespread in all major groups of plant pathogenic fungi (Ghabrial & Suzuki, 2009). A major part of the mycovirus consists of double-stranded RNA (dsRNA) but some of them are composed of single-stranded RNA (e.g. ss(+)RNA genome and ss(-)RNA genome) (Owens et al., 2012). Mycoviruses are transmitted intracellularly during cell division, sporogenesis, and cell fusion (Ghabrial & Suzuki, 2009), and were recently shown to perform extracellular transfer (Yu et al., 2013). They usually replicate in the cytoplasm, although some (e.g. *Mitovirus* genus) replicate in mitochondria of the host species (Muñoz-Adalia, Fernández, & Diez, 2016). Although the majority of mycoviruses have been reported to be associated with symptomless infections (cryptic), there are cases of mycoviruses that can induce hypovirulence[4], slow spore development, reduced growth rates and abnormal pigmentation of their host. Hypovirulence is regarded as an attractive trait of mycovirus that can be developed for biological control of plant pathogenic fungi (Ghabrial & Suzuki, 2009). The virus families Hypoviridae, Megabirnaviridae, Narnaviridae, Partiviridae, Reoviridae, as well as many unassigned – ssRNA and ssDNA mycoviruses were primarily responsible for hypovirulence in fungal hosts (Chiba et al., 2009; Nuss, 2005; Pearson, Beever, Boine, & Arthur, 2009). Nevertheless, mycoviruses effects on their host depend on host and environmental factors. For instance a single mycovirus strain may cause different

[4] According to Boland (2004), "Hypovirulence in fungal plant pathogens refers to the reduced ability of selected isolates within a population of a pathogen to infect, colonize, kill, and (or) reproduce on susceptible host tissues and is often associated with fungal viruses and associated double-stranded RNA elements".

effects on different host strains, and it also may have contrasting effects on the fitness of a single host isolate, ranging from no effect to harmful or beneficial depending on environmental and ecological conditions (Hyder et al., 2013).

5.5.11 Virocontrol of fungal pathogens

Virocontrol or virological control refers to one form of biological control utilising viruses that infect pathogens (Ghabrial & Suzuki, 2009). Among the biological control strategies that have been investigated by research, relatively few investigations of the use of mycovirus-mediated hypovirulence have been done. We will review here some of the best-studied examples of mycoviruses, including those that are currently used as BCAs of fungal diseases and those that have potential to be used as BCAs. A list of these mycoviruses is provided in the Appendix 6.

Hypovirulence against Chestnut blight disease

The best studied case of interaction between a fungal host and its mycoviruses, and the latter used as BCAs is for the pathogen *Cryphonectria parasitica*. Four ss(+)RNA mycovirus species have been identified from *C. parasitica*, the causal agent of the chestnut blight in chestnut (*Castanea* spp.) (Milgroom & Cortesi, 2004). These four mycovirus species all belong to the genus *Hypovirus* and are named *Cryphonectria hypovirus 1-4* (CHV-1, CHV-2, CHV-3 and CHV-4). The CHV-1, CHV-2 and CHV3 are particularly interesting as they cause hypovirulence, reducing mycelial growth and sporulation of its *C. parasitica* host. CHV-1 has been employed as a BCA in Europe since the 1960s and since then it has been credited with reducing the severity and extent of chestnut blight epidemic resulting from the natural spread through European chestnut coppice forest (Nuss, 2005; Rigling & Prospero, 2018). Other identified mycoviruses inducing hypovirulence of *C. parasitica* include the *Mycoreovirus 1* (MyrRV-1), *Mycoreovirus 2* (MyrRV-2) (Suzuki, Supyani, Maruyama, & Hillman, 2004) and *Cryphonectria mitovirus 1* (CpMV1) (Feau, Dutech, Brusini, Rigling, & Robin, 2014).

Hypovirulence against white root rot

Rosellinia necatrix is a fungal soilborne pathogen that causes white root rot disease on many perennial crops worldwide. Control of this pathogen is particularly challenging because of it wide host range of more than 197 species from 50 different families. Biological control of *R. necatrix* using mycoviruses has been suggested since several mycoviruses were shown to reduce the virulence and colony growth rate of the fungal host (Arakawa, Nakamura, Uetake, & Matsumoto, 2002; Kanematsu et al., 2004; Sasaki, Miyanishi, Ozaki, Onoue, & Yoshida, 2005). Among them, the *Reovirus Rosellinia* anti-rot virus (RarV) (Zhao Wei, Osaki, Iwanami, Matsumoto, & Ohtsu, 2003), *Rosellinia necatrix Mycoreovirus 3* (MyRV3) (Kanematsu et al., 2004), the partivirus RnPV1-W8 (Osaki et al., 2002) and *Rosellinia necatrix megabirnavirus 1* strain W779 (RnMBV1/W779) (Chiba et al., 2009) have been proposed as potential biocontrol agents of white root rot disease.

Hypovirulence against Dutch elm disease

Ophiostoma ulmi and *Ophiostoma novo-ulmi* are the causal agents of Dutch elm disease, the most devastating disease affecting elms (*Ulmus* spp.). Virocontrol of Dutch elm disease has been proposed since many mycoviruses have been identified under artificial conditions. Hong, Dover, Cole, Brasier, and Buck (1999) identified four different mitoviruses of *O. novo-ulmi* associated with hypovirulence: *O. novo-ulmi* mitovirus 3a-Ld, 4-Ld, 5-Ld and 6-Ld. Brasier (2000) described an extranuclear virus-like factor referred as the "d (devirulence) factor" in *O. ulmi*. Infected isolates of *O. ulmi* showed an unstable amoeboid colony morphology and severe reduction in its growth rate and aggressiveness. This work opened new opportunities for biocontrol of the pathogen through the release of d-factors. In their review, Ganley and Bulman (2016) suggested the use of d-factor viruses as biocontrol agents against *O. novo-ulmi* in New Zealand. Prior importation of some of these viruses and testing against the New Zealand *O. novo-ulmi* strain had shown promising results for reducing pathogen's virulence (unpublished data). However, field trials have not been conducted yet and would be required before the release of d-factors. Ganley and Bulman (2016) have also suggested that the use of d-factors virus on the *O. novo-ulmi* strain in New Zealand would be effective given the occurring low genetic diversity of the pathogen. Therefore, a uniform population of a pathogen would be more susceptible to BCAs than a genetically diverse population.

Limits and future prospects of using mycoviruses as biocontrol agents

The identification of suitable viral candidates is a critical step for the implementation of a mycovirus-based biological control system. Because of their high diversity and variable effects on the host

(ranging from hypovirulence to not causing discernible changes), detection of mycoviruses suitable for biological control can be difficult. Furthermore, the biotrophic nature of some fungi present additional difficulty in studying mycoviruses, as they cannot be grown on artificial medium to produce adequate mycelium for mycovirus purification (Pandey, Naidu, & Grove, 2018). Recent Next-Generation Sequencing technologies make it more feasible to screen fungi for the presence of potential viruses. For instance, S. L. Marzano et al. (2016) used a metatranscriptomic approach to characterise the fungal viromes of five prevalent plant fungal pathogens: *Colletotrichum truncatum, Diaporthe longicollam, Macrophomina phaseolina, Rhizoctonia solani* and *Sclerotinia sclerotiorum*. This resulted in the identification of 66 new mycoviruses that showed affinity with 15 distinct lineages Barnaviridae, Benyviridae, Chrysoviridae, Endornaviridae, Fusariviridae, Hypoviridae, Mononegavirales, Narnaviridae, Ophioviridae, Ourmiavirus, Partitiviridae, Tombusviridae, Totiviridae, Tymoviridae, and Virgaviridae. Pandey et al. (2018) used Illumina Hi Seq 2000 platform to sequence the dsRNAs extracted from *Podoshpaera prunicola* (powdery mildew fungus). The results indicated the presence of eight new mycoviruses (PPVS1-8), the majority of them showing affinity to the Partitiviridae family. Using a deep mRNA sequencing, J.-J. Liu et al. (2016) identified five new mycovirus species specifically infecting the basidiomycete fungi *Cronartium ribicola* (causal agent of white pine blister rust). These species were named *C. ribicola* mitoviruses 1,2,3,4 and 5 (CrMV1 to CrMV5).

Fungal vegetative incompatibility

The potential of using hypovirulent isolates of a fungal pathogen as a biocontrol strategy resides in the ability to transfer hypovirulence from individual hypovirulent isolates to virulent isolates within a population of the target pathogen (Boland, 2004).

Horizontal transmission during asexual reproduction is the primary mean of mycovirus spread, yet the process can be prevented by fungal vegetative incompatibility. Fungal vegetative incompatibility is likely to be the major barrier that limits the dissemination of mycoviruses and their further use as BCAs of fungal diseases (Heiniger & Rigling, 1994). This phenomenon of self-recognition occurs in many fungi to prevent incompatible strains from fusing. Basically, cell death occurs at point-of-contact of incompatible hyphal filaments, restricting the fusion necessary for mycovirus transmission (MacDonald & Double, 2005). Vegetative compatibility would occur when the fungal strains share the same genotypes. Therefore, virocontrol would be more successful in a less genetically diverse fungal host population (Ganley & Bulman, 2016; Milgroom & Cortesi, 2004). One strategy that has been proposed to solve this problem would be to screen for mycoviruses capable of overcoming hyphal incompatibility in transmission. For instance, SsHADV-1 (*Sclerotinia sclerotiorum* hypovirulence-associated DNA virus 1) was shown to transmit easily from one strain to another vegetatively incompatible one (Yu et al., 2013). To increase the chance of establishment of the mycovirus, direct manipulation of the fungal host genetics to create a “super donor strain” has been suggested. For instance, a transgenic *Cryphonectria parasitica* strain was obtained by disrupting four vegetative incompatibility loci and resulted with superior virus transmission capabilities (D.-X. Zhang & Nuss, 2016). The success of these transgenic hypovirulent fungal strains in the field would still need to be demonstrated.

Is mycovirus associated hypovirulence a good candidate for biocontrol of myrtle rust?

Studies conducted in many plant-pathogen systems have demonstrated that hypovirulence caused by mycoviruses occurs naturally. The use of hypovirulence to control fungal diseases represents a potentially effective and ecologically friendly method to incorporate in a long-term strategy. The successful biological control of *C. parasitica* (chestnut blight disease) in Europe, using the mycovirus CHV-1, has stimulated the search for other hypovirulence-associated mycoviruses in other plant fungal pathogens. Mycoviruses have been isolated from various fungal pathogens of important crops and to date, more than 250 mycoviruses have been sequenced and registered in the National Center for Biotechnology Information (NCBI). Therefore, the possibility that mycoviruses can be used against fungal pathogens such as myrtle rust is appealing from both the scientific and disease-management perspective. Several prerequisites should be considered before starting a hypovirulence-based biological control programme. First is the identification of mycovirus candidates. To date, no previous research has been conducted to identify mycoviruses from *A. psidii*. The ongoing work regarding the high-throughput sequencing of the whole pathogen genome would help to check for the presence of mycovirus. Secondly, as previously shown in other pathosystems, the fungal host genotype plays a major role in the transmission of mycoviruses. An investigation on the population structure of *A. psidii* in New Zealand and elsewhere in the world should be conducted to check the level of vegetative incompatibility and the potential of using virocontrol against myrtle rust.

6 The value of controlling myrtle rust on iconic Myrtaceae species

In Brazil, the cost involved in controlling myrtle rust on guava trees with triadimenol (a DMI fungicide) had the greatest economy of scale, increasing the net income by US$3,906.47/ha per season compared to the untreated trees, which had decreased net income by US$601.62/ha/season (Martins et al., 2011). There was a return on the proposed investment in control because guava is an edible marketable fruit. However, for the iconic New Zealand native Myrtaceae, it will be more difficult to evaluate the costs and economic benefits associated with chemical control of myrtle rust. Ultimately, the cultural, social and ecological values of these species will need to be evaluated against the cost and type of control method developed or used, versus the risk of their loss through infection with myrtle rust.

Myrtaceae is represented by some of the best-known New Zealand native plants such as the iconic pōhutukawa, rātā, *kānuka* and mānuka, as well as lesser-known species such as swamp maire, rōhutu, ramarama and the rare *Neomyrtus* (Clark et al., 2011). Species that are considered nationally critical in New Zealand, such as *Metrosideros bartlettii*, has only 29 individuals left in the wild (De Lange et al., 2004).

The WAI 262 claim 'Ko Aotearoa Tēnei' (This is Aotearoa/This is New Zealand) reports that, "iwi have relationships with species which are emblematic and have a spiritual element to them and their connection to the wider ecosystem, particularly, with regard to native plants such as harakeke, koromiko, pōhutukawa, kōwhai, puawānanga, poroporo, kawakawa, mānuka and kūmara". Though a number of New Zealand's Myrtaceae species are extensively used by Māori for medicine, construction, food and also have significant cultural value (S. Scheele, 2018), it is extremely difficult to attach a monetary value to most of them as these benefits are considered intangible. Information on the current use of these plants by Māori is likely to be iwi- and hapū-specific and difficult to obtain and catalogue according to Scheele (2014). Furthermore, Teulon et al. (2015) have shown that a number of Myrtaceae species, including pōhutukawa and mānuka, have been explicitly identified and confirmed as taonga species to Māori (Waitangi Tribunal, 2011).

Apart from the intangible values, some taonga species may contribute to the New Zealand economy. For instance, other than the many uses and medicinal properties of mānuka, New Zealand mānuka honey has contributed substantially to the total honey exported (total value of $NZ186.6M, Fresh Facts ("Fresh Facts ", 2014)), mostly due to its premium price, which is approximately three times higher than that of other table honey (Teulon, Alipia, Cromey, Marsh, & Viljanen-Rollinson, 2014).

Since 2014, prior to the arrival of myrtle rust in Aotearoa, Māori had already prioritised research into the potential impacts and management solutions should the fungus arrive and establish (Waipara & Black, 2014). As part of this preparedness approach, Māori also identified the need for Mātauranga Māori led solutions to be explored and prioritised as part of any government response and research programme (Waipara & Black, 2014). Māori have developed practices and methods, such as the use of ritenga (customs, laws, and protocols) and whakapapa (species assemblages, within a holistic ecosystem paradigm) to mitigate risks and threats to both endemic biodiversity and primary production systems from pests, weeds and pathogens. The 21st century has seen a rapid increase in species introductions to New Zealand with dramatic consequences for both Māori livelihoods and cultural integrity. The incorporation of Mātauranga Māori into the response to myrtle rust's arrival has been limited to date. The approach has mainly been one of engagement and the development of cultural health indicators is still at an early stage. However, kaitiaki (guardians) are already developing indicators to underpin surveillance and monitoring, as well as ideas on how to mitigate the effects of the disease. For example, they have expressed a desire to plant susceptible cultivars of ramarama either near sites of significance to take the brunt of the infection, or close by as sentinels. Essentially more time is needed to find other indicators and resource to develop kaupapa Māori led solutions (Lambert, Waipara, Black, Mark-Shadbolt, & Wood, 2018). However, engagement with Māori to date has already initiated interests within iwi, *hapū and whanau for the inclusion* of Te Ao Māori into all future assessments of the potential management options to control the disease in New Zealand, as well as including options that incorporate, or co-develop, control solutions with kaupapa Māori and Mātauranga Māori**.**

This review has identified a number of potential options to control myrtle rust under different scenarios, but future considerations of these scenarios must take into account the social and cultural licences (e.g. acceptability to Māori communities as well as the views/knowledges within the Te Ao Māori of iwi,

hapū and whānau). Ongoing engagement and research working closely with Māori iwi and hapū is being conducted to elaborate this information for each control scenario.

Although the many issues mentioned above make it challenging to perform an economy cost-benefit-analysis on the different control applications used to treat myrtle rust on iconic New Zealand Myrtaceae species, control of myrtle rust is essential in protecting/conserving these species, especially Māori taonga species.

7 Social and cultural acceptability on controlling Myrtle rust

In addition to technological feasibility and effectiveness, social, cultural and political acceptability will determine whether control options are available for use. Research into specific social and cultural acceptability of various control methods for myrtle rust will be addressed in Themes 1 and 2 within the current programme.

Existing literature on social acceptability of different control methods has largely focused on the control of vertebrate and insect pests (see e.g. Fraser, 2006; Kannemeyer, 2017) with less research related to public perceptions of plant pathogens and related control measures either in New Zealand or internationally. While some New Zealand research has considered public responses to kauri dieback control methods (e.g. phytosanitary cleaning stations and track closures), the review found no New Zealand research directly related to attitudes towards the plant pathogen control measures discussed in this report. Thus, likely public acceptability must be inferred from related forms of pest control and from international literature.

7.1 Social and cultural contexts

7.1.1 Perceived threat from the disease and management measures

People's attitudes towards control measures are based on how they perceive the relative benefits, risks and impacts of both the invasive species and the controls in context (Gobster, 2010a; Jay & Morad, 2006; Niemiec, Pech, Norbury, & Byrom, 2017; Shackleton, Richardson, et al., 2018). Because people have different values, priorities and pre-existing beliefs, they interpret the threat of invasive species and their impacts on ecosystems differently (Estévez, Anderson, Pizarro, & Burgman, 2015; Flint, McFarlane, & Muller, 2009; García-Llorente, Martín-López, González, Alcorlo, & Montes, 2008; Sharp, Larson, & Green, 2011). These assessments are made in reference to the specific context, so may vary across different times and places (Niemiec et al., 2017; Qin & Flint, 2017; Wyatt, Rousseau, Nadeau, Thiffault, & Guay, 2011). Importantly, differences in view cannot be neatly categorised according to demographic categories such as place of residence, occupation or ethnic group. It is therefore, essential to understand the values and attitudes people have within the specific situation and context to ensure proper response and engagement (Crowley, Hinchliffe, McDonald, & Lee, 2017; M. Marzano, Dandy, Bayliss, Porth, & Potter, 2015; Vanclay, 2017).

Individual perceptions about the seriousness of a threat are strongly affected by the visibility of impacts and the value that people place on affected host species, ecosystems and landscapes (Simberloff et al., 2013). Increasing public awareness of the negative impacts of a threat is broadly associated with higher support for management action. In particular, New Zealand research suggests the degree to which a control method is perceived as effective is an important factor in acceptability judgements (Gamble, Payne, & Small, 2010; Niemiec et al., 2017). Even control measures that are viewed as harsh or harmful may be considered acceptable in certain circumstances if they are perceived as necessary and likely to be effective, but such tolerance is likely to erode over time without evidence of success (Gobster, 2010a).

Surveys conducted for Biosecurity 2025 indicate around half of New Zealanders support biosecurity control actions overall and a third are neutral (Colmar Brunton, 2018). Even during a controversial painted apple moth response with vocal opposition and widespread negative media coverage, surveys consistently showed majority support for the eradication efforts and most people considered the government's actions justified (Office of the Ombusdman, 2007). However, minority opposition can jeopardise management success by shifting opinions within a weakly supportive majority, polarising debates or blocking management action (Crowley, Hinchliffe, & McDonald, 2017; Gobster, 2010b).

7.1.2 Quality of engagement and trust

The importance of early and meaningful engagement with stakeholders is well documented both in New Zealand (e.g. Allen et al., 2018; Allen & Horn, 2009; McEntee, 2007) and globally (e.g. Crowley, Hinchliffe, & McDonald, 2017; Mills et al., 2011; Novoa et al., 2018; Shackleton, Adriaens, et al., 2018). Early community engagement increases the likelihood of incorporating community concerns in decision-making, ideally building trust and reducing the likelihood of widespread opposition (Allen et al., 2018; Gamble et al., 2010; McEntee, 2007). The level of engagement and public involvement necessary varies depending on the level of perceived potential personal, social or environmental harm caused by the threat or its management. Trust plays an essential role in this as management often

requires the public accepting a level of perceived or real risk to health, economy or other valued assets (Estévez et al., 2015; Stern & Coleman, 2014). Particularly where perceived risks are higher and trade-offs must be made, people need to believe that they have been heard, that they have some influence in management and that they have some control over any perceived personal risks (Estévez et al., 2015; Gamble et al., 2010).

7.1.3 Location and setting

Responses to management are influenced by where management actions take place. Concern about management methods is higher when people feel they will be directly affected and those who support a control method in principle or for use in non-residential areas may oppose it in their own neighbourhood (Gamble et al., 2010; Gobster, 2010a). For example, public support for aerial spraying during the Auckland painted apple moth response was significantly lower in those neighbourhoods where spraying was most concentrated (60% versus 51%, respectively) (Office of the Ombusdman, 2007). In contrast, aerial spraying to eradicate the southern saltmarsh mosquito, conducted in less populated areas, received more positive response and little media attention (Office of the Auditor General, 2013), also more likely due to the human health impacts of the mosquito.

Acceptability is also affected by land use type: controls accepted in agricultural or industrial use may not be accepted in residential, wilderness or recreational areas and vice versa (Fuller, Marzano, Peace, Quine, & Dandy, 2016; Gamble et al., 2010; Poudyal, Bowker, & Moore, 2016). However, international evidence also suggests the mode of control application is a stronger influence on acceptability than the setting (Fuller et al., 2016).

7.2 Type of control

7.2.1 Cultural practices

The review found no existing New Zealand research into the social acceptability of cultural practices to control plant pathogens.

Several international case studies have highlighted the social disruption and intense public opposition caused by the removal of valued host plants and trees (e.g. Mackenzie & Larson, 2010; Porth, Dandy, & Marzano, 2015). However, these case studies have focused on those directly affected by removals and the wider public may be more accepting. Several other international surveys have found public support for the removal of infected hosts is significantly higher than for the use of chemical treatments (Eriksson, Bjorkman, & Klapwijk, 2018; Fuller et al., 2016; Schlueter & Schneider, 2016). Support for preventative removal of healthy trees was lower than that for infected hosts but still preferred over chemical treatment in all three studies.

Two international studies show long-term silviculture management options, including planting of resistant varieties or non-host species and increasing forest diversity, were preferred by the general public over the use of chemical controls, but preferences between silvicultural options and tree removals were mixed (Chang, Lantz, & MacLean, 2009; Eriksson et al., 2018). However, a Spanish study of forest owners faced with chestnut blight (*Cryphonectria parasitica*) found that most opted to abandon forest management—particularly if they valued their forests for non-monetary reasons—over biological controls or substitution for other species (Oliva et al., 2016).

7.2.2 Chemical control options

Although the use of chemical pesticides has caused public concern in recent decades (McEntee, 2007), New Zealanders support the use of chemicals agents for biosecurity in at least some circumstances. Notably, the use of chemical pesticides remains normal practice in plantation forests (Rolando, Garrett, Baille, & Watt, 2013) and agriculture (Chapman, 2010; Gabzdylova, Raffensperger, & Castka, 2009; Manketolow et al., 2005) without widespread public opposition. However, levels of support vary considerably depending on the specific setting and method of application (see discussion below).

7.2.3 Biological control options

Biological control options may be perceived by the public as more natural and less harmful than chemical controls and, therefore, more socially acceptable (Bailey, Boyetchko, & Längle, 2010; Chang et al., 2009; Fraser, 2006; Gamble et al., 2010; Glare et al., 2012; McFarlane & Watson, 2008). For example, a Canadian study by McNeil, Cotnoir, Leroux, Laprade, and Schwartz (2010) found that

surveyed members of the public were more than twice as likely to support the use of microbes to control pests, weeds or plant diseases (61%) than the use of synthetic chemicals (25%). Though their use is less than synthetic chemical pesticides, biopesticides have become common tools in New Zealand agriculture (Glare et al., 2012; Glare & O'Callaghan, 2017) and most biological control agents in New Zealand have avoided significant public opposition (Hayes et al., 2013). However, their use in pest eradication campaigns has been controversial when applied through aerial spraying (see discussion below). Additionally, if the development of biological controls involves genetic modification, acceptability may be reduced (R. Wilkinson & Fitzgerald, 2006).

The use and proposed introductions of BCAs to control introduced pest species is highly controversial among Māori; many oppose the importation and release of BCAs, even though this may be the last option for long-term management of an invasive species such as myrtle rust (Black, Tylianakis, Wood, Malcom, & Waipara, 2018). Furthermore, the process for approving the registration or importation and use of BCAs requires consultation with affected mana whenua. While Māori do support exploring their own biocontrol agents, concerns remain about the lack of supporting information regarding taonga species and an absence of the inclusion of Mātauranga Māori and tikanga in the development and use of introduced biocontrol agents (Black et al., 2018).

In general, Māori can be more supportive of the development of endemic biocontrols as an alternative to introduced exotic biocontrols and chemical solutions. However, this has yet to be fully realised, as has the inclusion of Mātauranga Māori that could contribute significantly to biological or natural solutions.

7.3 Control contexts

7.3.1 Mode of application

People are generally more concerned about aerial rather than ground application of controls and view blanket application less favourably than targeted uses. Varying degrees of public backlash and negative media attention followed widespread aerial spraying to control the white-spotted tussock moth (*Orgyia thyellina*; 1996-1999), painted apple moth (*Teia anartoides*; 1999-2006), and Asian gypsy moth (*Lymantria dispar*; 2003) (McEntee, 2007; Office of the Ombusdman, 2007). However, no research reported backlash following aerial spraying to control southern saltmarsh mosquito (*Aedes camptorhynchus*) a carrier of Ross River fever virus, which occurred primarily in less populated areas.

The Department of Conservation 2016 Survey of New Zealanders found that 73% of participants support the use of ground-based herbicide spraying but only 35% support the use of aerial herbicide spraying (Ipsos, 2016). Moreover, 25% believe that aerial spraying should never be used in any circumstances and 34% believe it should be used only as a last resort. A similar pattern is evident for ground-based versus aerial vertebrate poisons (receiving 78% and 34% support respectively).

A 2018 survey found 55% of people support targeted aerial spraying via drones of chemicals for biosecurity control and only 15% oppose with the remainder neutral or undecided (Colmar Brunton, 2018). Unfortunately, this survey did not ask about other means of spraying, did not specify the type of chemicals in question (i.e. whether fungicide, herbicides, pheromones or other chemicals) and used different scale descriptors to measure support from previous surveys, so it is not possible to identify which factors affected acceptability or to compare levels of acceptability directly across surveys.

7.3.2 Novelty

Several New Zealand studies have emphasised the role of perceived scientific uncertainty or risk of long-term harm in shaping how people respond to new biotechnologies, particularly where the potential for harm extends beyond consenting individuals to the wider community or environment (A. J. Cook, Fairweather, Satterfield, & Hunt, 2004; Fraser, 2006; Gamble et al., 2010; L. M. Hunt, Fairweather, & Coyle, 2003; Richardson-Harman, Phelps, Mooney, & Ball, 1998; Roger Wilkinson & Fitzgerald, 1997, 2014). Stakeholders who are already familiar and comfortable with the use of chemical fungicides may prefer these over novel biocontrol methods if they are seen as more complicated, less effective or requiring further development (Charudattan, 2005). The time required to develop and test BCAs also risks creating perception of inaction.

8 Conclusion and recommendations

This review has outlined the current response to myrtle rust in New Zealand, the efficacy and application of different cultural, biological and chemical control practices/options that have been used to manage biotrophic pathogens in other pathosystems and on myrtle rust. Any successful method for control of myrtle rust must take into account the disease triangle – pathogen, host and the environment. Control of myrtle rust under different scenarios must also take into consideration the different social licences, public acceptability (Section 7) and the views/knowledges within the Te Ao Māori of iwi, hapū and whanau. This can be achieved by working closely with the local councils and Māori iwi and hapū depending on the context of whether the control is to be conducted in urban, nursery or natural habitats.

Not all the myrtle rust control options covered in the review are suitable, nor can they be applied immediately as some (e.g. endophytes, mycoviruses and specific chemicals) will require investigations on their specificity, efficacy and feasibility in controlling myrtle rust on trees under different environments in New Zealand or research development (e.g. breeding and selection of resistance cultivars for deployment).

To ensure the perspectives of Te Ao Māori are included within the current response to myrtle rust, Māori will need to be engaged and have access to information of the proposed methods and strategies, costs, benefits and risks, which will then ensure they can contribute, collaborate and make decisions about the future management and protection of their taonga plants. Work is currently underway in other programmes to review the current position and Mātauranga of Myrtaceae in Aotearoa as well as evaluate what Mātauranga-based solutions and practices are in place, or available, for the the control of *A. psidii* as well as the bioprotection and management of taonga Myrtaceae. To understand the costs, benefits and risks posed by the different control methods and strategies will require input from an economist and assessment of ecological risk and merits, which are outside the scope of this review.

With the aim to impose minimal ecological, environmental, human and animal health impacts, integrated disease management, combining cultural, chemical and biological practices, is the most sensible and ideal approach for controlling myrtle rust. Considering the biology of the pathogen, host range and environmental conditions (or scenarios), control of myrtle rust can be split into short-, medium- and long-term measures. Table 4 summarises the targets, control options and considerations required for controlling the disease under the conditions that all control products (fungicides and biological agents) are commercially available. This is not the case for the biological option at this stage. Of note, many of the control measures, such as facilitated migration of iconic native plants and application of chemicals to plants in urban areas, will require social licences and consultation with local councils and Te Ao Māori Iwi or hapū to operate.

As myrtle rust impacts a large range of Myrtaceae that are present in natural ecosystems or grown for commercial (i.e. nurseries or plantations) or asthetic purposes (private and public urban land), there are no control methods that can be selected that will be suitable for all scenarios. For example, the use of the chemical control has different levels of acceptability and applicability depending on the plant species in question and the reason for use. Widespread application of chemicals over native forests may be unacceptable but use on particular trees of importance may be acceptable to some mana whenua, and alternatively may be part of a suite of control methods commercial growers would be interested in for short-term use. Selection of what control options should be developed or used will depend on the objectives or outcomes for long-term management of myrtle rust in New Zealand and is beyond the scope of this project. All biological control would fall into long-term implementation as there are no products available to immediate use. Comprehensive lists of BCAs, elicitors, AMPs and mycoviruses that have been used against myrtle rust or other fungal diseases are presented in Appendices 3–6).

Table 4. The disease triangle, its implications, control targets, options and considerations required to manage myrtle rust summarised from the review.

Disease triangle	Implications	Control targets	Control options	Technical, social and environmental considerations
Biology of *Austropuccinia psidii* • Biotrophic • Autoecious and polycyclic • Dispersal by wind, movements of people, infected plant materials and insects • Optimal temperature range 15-25°C • Affects young plant parts (in particular during spring when flushes of new growth and flowering are happening) Host • Myrtacea plant species Environment • Local climatic conditions (temperature, rainfall and leaf wetness).	• *A psidii* requires a living host for survival and multiplication • *A. psidii* can complete its life cycle on the same host • Fast epidemic, strong reproductive potential and fitness under suitable weather conditions • Many native, iconic and introduced Myrtaceae plant species in New Zealand can be susceptible to myrtle rust. • Conduciveness of the environment (i.e. temperature, rainfall, and leaf wetness) suitable for *A. psidii* germination, infection, multiplication and disease development • Can survive in many regions in New Zealand where hosts are present • Disease will be prominent during spring to summer.	• Make the host unavailable or not suitable for myrtle rust infection • Reduce pathogen's reproductive potential and fitness so as to reduce inoculum load and slow down disease spread • Make the environment not suitable for disease development - limited or impossible unless under controlled/semi-controlled environment (e.g. nursery production).	Cultural • Disease forecasting as a warning system for control decisions. • Removal of susceptible hosts (may or may not be feasible) • Scouting for infection and removal of infected telial plants/plant parts • Hygiene implementation after removing and disposing of infected plants/plant parts. • Artificial migration of susceptible hosts to region not conducive to myrtle rust • Dilute susceptible host population by planting non-susceptible species in close proximity • Deployment of myrtle rust resistant/tolerant cultivars Chemical • Curative fungicide application (strobilurins and triazoles) • Sequential preventive application of strobilurin and triazole fungicides during 'off-season' (e.g. winter) in areas where susceptible hosts are grown • Application of natural oil products Biological (need further work to test efficacy, production and application) • Biological control agents (BCAs) such as endophytes, antimicrobial peptides, mycoviruses and elicitors.	• Ecological impact on ecosystem services in natural forest/vegetation • Major, minor or durable resistance and the resistance longevity • The concept of using some chemical control options must be determined and proven to work in New Zealand • Chemical application methods, rates, spray drift, non-target and environmental impacts, fungicide resistance monitoring and careful stewardship to avoid resistance of pathogen to the chemicals • Efficacy, ease of production, application methods, fitness and adaptability of biological control agents on different hosts and under varying weather conditions have to be determined. •Non-target impact on endemic native microorganisms (e.g. other rust species) and ecosystems • Social licences required for control measures must be communicated with public, local councils and Māori iwi.

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Appendix 1. Fungicides used against myrtle rust to date

Active ingredient (a.i.)	Application rate of a.i.	Application method	Host species in field conditions	Host species in glasshouse/ controlled conditions	Host species in nursery	Comments/ success recorded	Research location	References
Propiconazole	0.63 g/L [2.5 ml /L	Knapsack Sprayer	N	N	Mānuka	Effective - 0, First application (mid Oct)	New Zealand	Falloon (2018) unpublished
Azoxystrobin	0.2 g/L [0.8 g/L]	Knapsack Sprayer	N	N	Mānuka	Effective - 2 weeks (1 Nov)	New Zealand	Falloon (2018) unpublished
Copper Oxychloride	2.4 g/L [3 g/L]	Knapsack Sprayer	N	N	Mānuka	Effective - 5 weeks (22 Nov)	New Zealand	Falloon (2018) unpublished
Propiconazole	0.63 g/L [2.5 ml /L]	Knapsack Sprayer	N	N	Mānuka	Effective - 7 weeks (6 Dec)	New Zealand	Falloon (2018) unpublished
Azoxystrobin	0.2 g/L [0.8 g/L]	Knapsack Sprayer	N	N	Mānuka	Effective - 10 weeks (27 Dec)	New Zealand	Falloon (2018) unpublished
Mancozeb	1.5 g/L [2 g/L]	Knapsack Sprayer	N	N	Mānuka	Effective - 13 weeks (17 Jan)	New Zealand	Falloon (2018) unpublished
Copper Oxychloride	2.4 g/L [3 g/L]	Knapsack Sprayer	N	N	Mānuka	Effective - 15 weeks (31 Jan)	New Zealand	Falloon (2018) unpublished
Mancozeb	1.5 g/L [2 g/L]	Knapsack Sprayer	N	N	Mānuka	Effective - 17 weeks (14 Feb)	New Zealand	Falloon (2018) unpublished
Propiconazole + Mancozeb	0.63 + 1.5 g/L [2.5 ml + 2 g/L]	Knapsack Sprayer	N	N	Mānuka	Effective - 19 weeks (28 Feb)	New Zealand	Falloon (2018) unpublished
Azoxystrobin	0.2 g/L [0.8 g/L]	Knapsack Sprayer	N	N	Mānuka	Effective - 23 weeks (28 Mar)	New Zealand	Falloon (2018) unpublished
Mancozeb	1.5 g/L [2 g/L]	Knapsack Sprayer	N	N	Mānuka	Effective - 27 weeks (25 April)	New Zealand	Falloon (2018) unpublished
Copper Oxychloride Or Mancozeb	2.4 g/L [3 g/L] or 1.5 g/L [2 g/L]	Knapsack Sprayer	N	N	Mānuka	Effective -(During Winter Season-If disease appears)	New Zealand	Falloon (2018) unpublished
Mancozeb	210 g/100L	Knapsack	N	N	All Myrtaceae in scion	Protectant	New Zealand	Keech (2018) personal communication
Triforine	100 ml/100L	Knapsack	N	N	All Myrtaceae in scion	Protectant	New Zealand	Keech (2018) personal communication
Tebuconazole	40 g/100L	Knapsack	N	N	All Myrtaceae in scion	Protectant	New Zealand	Keech (2018) personal communication
Chlorothalonil	300 ml/100L	Knapsack	N	N	All Myrtaceae in scion	Protectant	New Zealand	Keech (2018) personal communication
Copper Oxide	300-500 g/100L	Knapsack	N	N	All Myrtaceae in scion	Protectant	New Zealand	Keech (2018) personal communication
Triadimenol	250 g/L	NM	All Myrtaceae	N	All Myrtaceae	Protectant and/or curative	New Caledonia	(Giblin, 2013)
Triforine	190 g/L	NM	All Myrtaceae	N	All Myrtaceae	Protectant and/or curative	New Caledonia	(Giblin, 2013)
Mancozeb	750-800 g/kg	NM	All Myrtaceae	N	All Myrtaceae	Protectant and/or curative	New Caledonia	(Giblin, 2013)

Active ingredient (a.i.)	Application rate of a.i.	Application method	Host species in field conditions	Host species in glasshouse/ controlled conditions	Host species in nursery	Comments/ success recorded	Research location	References
Azoxystrobin	250 g/L	NM	All Myrtaceae	N	All Myrtaceae	Protectant and/or curative	New Caledonia	(Giblin, 2013)
Copper Oxychloride	500 g/kg	NM	All Myrtaceae	N	All Myrtaceae	Protectant and/or curative	New Caledonia	(Giblin, 2013)
Propiconazole	250 g/L	NM	All Myrtaceae	N	All Myrtaceae	Protectant and/or curative	New Caledonia	(Giblin, 2013)
Azoxystrobin	300 mg/L	Hand-Held Atomiser	*B. citriodor*a	*S. jambos, R. rubescens, B. citriodora, G. inophloia & M. alternifolia*	N	Good protectant	Australia	Horwood *et al.* (2013) unpublished
Azoxystrobin+ Cyproconazole	200+80 mg/L	Hand-Held Atomiser	*B. citriodor*a	*S. jambos, R. rubescens, B. citriodora, G. inophloia & M. alternifolia*	N	Good protectant	Australia	Horwood *et al.* (2013) unpublished
Triadimenol	100 mg/L	Hand-Held Atomiser	*B. citriodor*a	*S. jambos, R. rubescens, B. citriodora, G. inophloia & M. alternifolia*	N	Good protectant & Best eradicant	Australia	Horwood *et al.* (2013) unpublished
Difenoconazole	125 mg/L	Hand-Held Atomiser	*B. citriodor*a	NM	N	Effective eradicant	Australia	Horwood *et al.* (2013) unpublished
Tebuconazole+ Trifloxystrobin	300+150 mg/L	Hand-Held Atomiser	*B. citriodor*a	*S. jambos, R. rubescens, B. citriodora, G. inophloia & M. alternifolia*	N	Good protectant	Australia	Horwood *et al.* (2013) unpublished
Triforine	285 mg/L	Hand-Held Atomiser	N	*S. jambos, R. rubescens, B. citriodora, G. inophloia & M. alternifolia*	N	Good protectant & Least effective eradicant	Australia	Horwood *et al.* (2013) unpublished
Mancozeb	1500 mg/L	Hand-Held Atomiser	*B. citriodor*a	*S. jambos & R. rubescens*	N	Least effective eradicant	Australia	Horwood *et al.* (2013) unpublished
Epoxiconazole	63 mg/L	Hand-Held Atomiser	N	*S. jambos & R. rubescens*	N	Best eradicant	Australia	Horwood *et al.* (2013) unpublished
Oxycarboxin	975 mg/L	Hand-Held Atomiser	N	*S. jambos & R. rubescens*	N	Least effective eradicant	Australia	Horwood *et al.* (2013) unpublished
Prothioconazole+ Tebuconazole	63+63 mg/L	Hand-Held Atomiser	N	*S. jambos & R. rubescens*	N	Best eradicant	Australia	Horwood *et al.* (2013) unpublished
Propiconazole+ Cyproconazole	80+26 mg/L	Hand-Held Atomiser	N	*S. jambos & R. rubescens*	N	Best eradicant	Australia	Horwood *et al.* (2013) unpublished
Azoxystrobin + Difenoconazole	300 to 500 mL/ha	Coastal Sprayer	*Eucalyptus* sp.	N	N	Most effective	Brazil	(Masson et al., 2013)
Azoxystrobin + Cyproconazole +Tiametoxam	400 mL/ha	Coastal Sprayer	*Eucalyptus* sp.	N	N	Most effective	Brazil	(Masson et al., 2013)
Azoxystrobin + Ciproconazole+ Trifloxystrobin + Tebuconazole	750 mL/ha	Coastal Sprayer	*Eucalyptus* sp.	N	N	Most effective	Brazil	(Masson et al., 2013)

Active ingredient (a.i.)	Application rate of a.i.	Application method	Host species in field conditions	Host species in glasshouse/ controlled conditions	Host species in nursery	Comments/ success recorded	Research location	References
Azoxystrobin	0.5 mL/L	Coastal Sprayer	*Eucalyptus* sp. *Grandis*	N	N	Most effective	Brazil	(Masson et al., 2013)
Tebuconazole	1.0 mL/L	Coastal Sprayer	*Eucalyptus* sp. *Grandis*	N	N	Effective	Brazil	(Masson et al., 2013)
Azoxystrobin+ Tebuconazole	500-1500 ml/ha	Coastal Sprayer	*Eucalyptus* sp.	N	N	Effective	Brazil	(Masson et al., 2013)
Tebuconazole + trifloxystrobin	1.5 mL/L	Coastal Sprayer	*Eucalyptus* sp. *grandis*	N	N	Effective	Brazil	(Masson et al., 2013)
Azoxystrobin+ Cyproconazole	0.45 L/ha	Coastal Sprayer	*Eucalyptus* sp.	N	N	Effective	Brazil	(Moraes et al., 2011)
Azoxystrobin+ Cyproconazole	0.3 L/ha+(0.6 L/ha mineral oil)	Coastal Sprayer	*Eucalyptus* sp.	N	N	Effective	Brazil	(Moraes et al., 2011)
Azoxystrobin+ Cyproconazole	0.3 L/ha+(0.6 L/ha of mineral oil),	Atomizer	*Eucalyptus* sp.	N	N	Effective control	Brazil	(Moraes et al., 2011)
Azoxystrobin+ Cyproconazole	0.45 L/ha	Atomizer	*Eucalyptus* sp.	N	N	Effective control	Brazil	(Moraes et al., 2011)
Azoxystrobin+ Cyproconazole	0.3 L/ha+(0.6 L/ha of mineral oil),	Aerial	*Eucalyptus* sp.	N	N	Effective control	Brazil	(Moraes et al., 2011)
Azoxystrobin+ Cyproconazole	0.45 L/ha	Aerial	*Eucalyptus* sp.	N	N	Effective control	Brazil	(Moraes et al., 2011)
Mancozeb	1600 mg/L	Tractor-Mounted Sprayer & Backpack Sprayer	*Psidium guajava*	N	N	Least efficient	Brazil	(Martins et al., 2011)
Azoxystrobin	100 mg/L	Tractor-Mounted Sprayer & Backpack Sprayer	*Psidium guajava*	N	N	Best control	Brazil	(Martins et al., 2011)
Tebuconazole	150 mg/L	Tractor-Mounted Sprayer & Backpack Sprayer	*Psidium guajava*	N	N	Best control	Brazil	(Martins et al., 2011)
Triadimenol	310 mg/L	Tractor-Mounted Sprayer & Backpack Sprayer	*Psidium guajava*	N	N	Best control	Brazil	(Martins et al., 2011)
Pyraclostrobin	100 mg/L	Tractor-Mounted Sprayer	*Psidium guajava*	N	N	Best control	Brazil	(Martins et al., 2011)
Cyproconazole	150 mg/L	Tractor-Mounted Sprayer	*Psidium guajava*	N	N	Best control	Brazil	(Martins et al., 2011)
Copper Oxychloride	2400 mg/L	Tractor-Mounted Sprayer	*Psidium guajava*	N	N	Good when rotated with other systemic fungicides	Brazil	(Martins et al., 2011)
Triadimenol+ Azoxystrobin	NM	ND	NM	NM	Nursery trial	NM	NM	(Krugner & Auer, 2005)
Copper Oxychloride	160-200 g/100L	ND	*Eucalyptus* clones	N	N	Effective protectant	Brazil	(Alfenas, 2004)
Azoxystrobin	0.1 g/L	ND	*Eucalyptus* clones	N	N	Most Effective protectant	Brazil	(Alfenas, 2004)
Mancozeb	1.6-2.0 g/L	ND	*Eucalyptus* clones	N	N	Effective protectant	Brazil	(Alfenas, 2004)

Active ingredient (a.i.)	Application rate of a.i.	Application method	Host species in field conditions	Host species in glasshouse/ controlled conditions	Host species in nursery	Comments/ success recorded	Research location	References
Triadimenol	0.125 g/L	ND	*Eucalyptus* clones	N	N	Most Effective protectant	Brazil	(Alfenas, 2004)
Tetraconazole	NM	ND	*Eucalyptus* clones	N	N	Curative	Brazil	(Alfenas, 2004)
Tebuconazole	NM	ND	*Eucalyptus* clones	N	N	Effective protectant	Brazil	(Alfenas, 2004)
Epoxiconazole +Pyraclostrobin	NM	ND	*Eucalyptus* clones	N	N	Effective protectant	Brazil	(Alfenas, 2004)
Copper Oxychloride	NM	ND	*Psidium guajava*	N	N	Effective	Brazil	(Goes et al., 2004)
Copper Hydroxide	NM	ND	*Psidium guajava*	N	N	Effective	Brazil	(Goes et al., 2004)
Copper Oxide	NM	ND	*Psidium guajava*	N	N	Effective	Brazil	(Goes et al., 2004)
Cyproconazole	50 ml/100L	ND	*Eucalyptus* sp.	N	N	Effective protectant	Brazil	(Furtado & Marino, 2003)
Triadimenol	NM	ND	*Eucalyptus* sp.	N	N	Effective protectant	Brazil	(Furtado & Marino, 2003)
Tebuconazole	NM	ND	*Eucalyptus* sp.	N	N	Effective protectant	Brazil	(Furtado & Marino, 2003)
Mancozeb	NM	ND	*Eucalyptus* sp.	N	N	Curative effect	Brazil	(Furtado & Marino, 2003)
Difenoconazole	100 ml/100L	ND	*Eucalyptus* sp.	N	*Eucalyptus* sp.	Curative effect	Brazil	(Furtado & Marino, 2003)
Tebuconazole	NM	ND	*Eucalyptus* sp.	N	N	Curative effect	Brazil	(Furtado & Marino, 2003)
Propiconazole	NM	ND	*Eucalyptus* sp.	N	N	Curative effect	Brazil	(Furtado & Marino, 2003)
Triadimenol	NM	ND	*Eucalyptus* sp.	N	N	Curative effect	Brazil	(Furtado & Marino, 2003)
Difenoconazole+Propiconazole	80 ml/100L	ND	*Eucalyptus* sp.	*Eucalyptus* sp.	*Eucalyptus* sp.	Curative effect	Brazil	(Furtado & Marino, 2003)
Cuprous oxide	352 g/100L	ND	*Eucalyptus* sp.	N	*Eucalyptus* sp.	Effective	Brazil	(Furtado & Marino, 2003)
Chlorothalonil	150 g/100L	Back Power Sprayer	*Psidium guajava*	N	N	Efficacy (<10%)	Brazil	(Ferrari et al., 1997)
Copper Oxychloride	100 g/100L	Back Power Sprayer	*Psidium guajava*	N	N	Efficacy (10-20%)	Brazil	(Ferrari et al., 1997)
Mancozeb	160 g/100L	Back Power Sprayer	*Psidium guajava*	N	N	Efficacy (10-20%)	Brazil	(Ferrari et al., 1997)
Triadimenol	200 L/ha	Manual Coastal Sprayer	*E. cloeziana coppice*	N	N	Protective and Curative effect	Brazil	(Alfenas, Maffia, Macabeu, & Sartorio, 1993)
Diniconazole	30 g/L	Manual Coastal Sprayer	*E. cloeziana coppice*	N	N	Efficacy (65%)	Brazil	(Alfenas et al., 1993)
Oxycarboxin	210 g/L	Manual Coastal Sprayer	*E. cloeziana coppice*	N	N	Efficacy (90%)	Brazil	(Alfenas et al., 1993)
Triadimenol	100 g/L	Manual Coastal Sprayer	*E. cloeziana coppice*	N	N	Efficacy (40%)	Brazil	(Alfenas et al., 1993)
Chlorothalonil	NM	Atomizer Regulated Electric Compressor	*Eucalyptus cloeziana*	N	N	Not effective	Brazil	(Demuner & Alfenas, 1991)

Active ingredient (a.i.)	Application rate of a.i.	Application method	Host species in field conditions	Host species in glasshouse/ controlled conditions	Host species in nursery	Comments/ success recorded	Research location	References
Copper oxychloride	NM	Atomiser Regulated Electric Compressor	*Eucalyptus cloeziana*	N	N	Not effective	Brazil	(Demuner & Alfenas, 1991)
Diniconazole	0.075 g/L	Atomiser Regulated Electric Compressor	*Eucalyptus cloeziana*	N	N	Effective for only 14 days	Brazil	(Demuner & Alfenas, 1991)
Mancozeb	NM	Atomiser Regulated Electric Compressor	*Eucalyptus cloeziana*	N	N	Not effective	Brazil	(Demuner & Alfenas, 1991)
Oxycarboxin	1.125 g/L	Atomiser Regulated Electric Compressor	*Eucalyptus cloeziana*	N	N	Effective for only 7 days	Brazil	(Demuner & Alfenas, 1991)
Triadimenol	0.4 g/L	Atomiser Regulated Electric Compressor	*Eucalyptus cloeziana*	N	N	Effective for only 28 days	Brazil	(Demuner & Alfenas, 1991)
Triforine	NM	Atomiser Regulated Electric Compressor	*Eucalyptus cloeziana*	N	N	Not effective	Brazil	(Demuner & Alfenas, 1991)
Triadimenol	0.5 g/L	Atomiser Regulated Electric Compressor	N	*Psidium guajava*	N	Most Protective and Curative effect	Brazil	(Ruiz et al., 1991)
Triadimenol	0.75 g/L	Atomiser Regulated Electric Compressor	N	*Psidium guajava*	N	Protective and Curative effect	Brazil	(Ruiz et al., 1991)
Triforine	0.28 mL/L	Atomiser Regulated Electric Compressor	N	*Psidium guajava*	N	Protective and Curative effect	Brazil	(Ruiz et al., 1991)
Oxycarboxin	0.75 g/L	Atomiser Regulated Electric Compressor	N	*Psidium guajava*	N	Protective and Curative effect	Brazil	(Ruiz et al., 1991)
Chlorothalonil	150 g/100L	Back Power Sprayer	*Psidium guajava*	N	N	Efficient	Brazil	(Ferreira, 1989)
Mancozeb	160 g/100L	Back Power Sprayer	*Psidium guajava*	N	N	Good	Brazil	(Ferreira, 1989)
Copper Oxychloride	100 g/100L	Back Power Sprayer	*Psidium guajava*	N	N	Good	Brazil	(Ferreira, 1989)
Cuprous oxide	160-200 g/100L	Back Power Sprayer	*Psidium guajava*	N	N	Good	Brazil	(Ferreira, 1989)
Azoxystrobin+Cyproconazole+ Tiametoxam	250-400 mL/ha	ND	*Eucalyptus* sp.	N	N	Effective	Brazil	Furtado et al. (unpublished)
Azoxystrobin+Difenoconazole	300-500 mL/ha	ND	*Eucalyptus* sp.	N	N	Effective	Brazil	Furtado et al. (unpublished)
Azoxystrobin +Cyproconazole	300-450 mL/ha	ND	*Eucalyptus* sp.	N	N	Effective	Brazil	Furtado et al. (unpublished)
Pyraclostrobin+Epoxiconazole	500 mL/ha	ND	*Eucalyptus* sp.	N	N	Effective	Brazil	Furtado et al. (unpublished)
Trifloxystrobin+Tebuconazole	750 mL/ha	ND	*Eucalyptus* sp.	N	N	Effective	Brazil	Furtado et al. (unpublished)

*N=None; NM=Not Mentioned; *ND=Not Described

NOTE: Some publications stated efficacy levels in percentage (%). For such reports, the efficacy is stated in the table above or otherwise.

Appendix 2. List of fungicides and their availability in New Zealand

Active Ingredient (a.i.)		Availability Status In New Zealand	Chemical Group	Products Names	Rate
1	Mancozeb*	YES	Dithiocarbamate	Adama® Mancozeb contains mancozeb Defensor® contains mancozeb Dithane® Rainshield Neotec contains mancozeb Manco™ 75WG contains mancozeb Manzate® Evolution contains mancozeb Penncozeb® DF contains mancozeb Promanz® contains mancozeb Unizeb® contains mancozeb Penncozeb and Unizeb contain Hexamine	750 g/kg 750 g/kg 750 g/kg 750 g/kg 750 g/kg 750 g/kg 750 g/kg 25 g/kg
2	**Triforine***	YES	Amide	SA-N	NA
3	Azoxystrobin*	YES	Strobilurin	Amistar® WG Mirado 500 WG	500 g/kg 500 g/kg
4	Triadimenol*	YES	Triazole	Triadimenol+plus N-methyl-2-pyrrolidinone (except cereous). AGPRO Jupiter also contains ethoxylated dodecyl alcohol.	250 g/litre 250 g/litre
5	**Trifloxystrobin***	YES	Strobilurin	SA-N	NA
6	Oxycarboxin	YES	Organic fungicide	SA	NA
7	Copper Oxychloride*	YES	Inorganic copper	Fruitfed copper oxychloride contains copper as copper oxychloride Oxi-Cup® 50WG contains copper as copper oxychloride in the form of water dispersible granules. AGPRO copper oxychloride 800 WP contains copper oxychloride in the form of a wettable powder.	500 g/kg 500 g/kg 800 g/kg
8	Tebuconazole*	YES	Triazole	AGPRO tebuconazole 430 SC contains tebuconazole Compass® contains tebuconazole Folicur® SC contains tebuconazole Hornet® 430SC contains tebuconazole Rebuke 430 contains tebuconazole AGPRO Envy contains tebuconazole AGPRO Envy contains 2-pyrolidone, 1-methyl Orius® 250 EW contains tebuconazole	430 g/litre 430 g/litre 430 g/litre 430 g/litre 430 g/litre 250 g/litre 50 g/litre 250 g/litre
9	**Epoxiconazole+Azoxystrobin**	YES	Triazole+Azoxystrobin	NSA	NA
10	**Propiconazole***	YES	Triazole	SA-N	NA
11	**Thiametoxam***	YES	Neonicotinoid	SA-N	NA
12	Prothiconazole+Fluoxystrobin	YES	Triazole+Strobilurin	NSA	NA
13	Prothiconazole+Trifloxystrobin	YES	Triazole+Strobilurin	NSA	NA

Active Ingredient (a.i.)		Availability Status In New Zealand	Chemical Group	Products Names	Rate
14	Azoxystrobin+Chlorothalonil	YES	Strobilurin+Nitrile	NSA	NA
15	**Copper (I) Oxide/Cuprous oxide***	YES	Inorganic copper	SA-N	NA
16	Difenoconazole*	YES	Triazole	Glacier also contains N-methyl-2-pyrrolidone and xylene. Divino® also contains hydrocarbon liquids. Score also contains hydrocarbon liquids and 2-pyrolidinone, 1-methyl.	30 g/litre + 610 g/litre 617 g/litre 508 g/litre+120 g/litre
17	Epoxiconazole*	YES	Triazole	Epoxiconazole	125 g/litre
18	**Prothioconazole***	YES	Triazole	SA-N	NA
19	**Cyproconazole***	YES	Triazole	SA-N	NA
20	**Pyraclostrobin***	YES	Strobilurin	SA-N	NA
21	Tetraconazole	YES	Triazole	SA	NA
22	Kresoxim-Methyl	YES	Stobilurin	SA	NA
23	Copper Hydroxide*	YES	Inorganic copper	AGPRO Cupric hydroxide 350 SC contains copper Champ Flo contains copper as copper hydroxide Champ WG contains copper Kocide® Opti™ contains copper Champ DP contains coopper as copper hydroxide Hortcare Copper Hydroxide 300 contains copper hydroxide	350 g/litre 334.5 g/kg 500 g/kg 300 g/kg 375 g/kg 300 g/kg
24	Paclobutrazol	YES	Triazole	SA	NA
25	Flutriafol	YES	Strobilurin	SA	NA
26	**Myclobutanil***	YES	Triazole	SA-N	NA
27	Diniconazole	NO	Triazole	SA	NA
28	Metconazole	NO	Triazole	SA	NA
29	**Flusilazole***	NO	Triazole	SA-N	NA
30	Uniconazole	NO	Triazole	SA	NA
31	**Boscalid***	NO	Carboximide	SA-N	NA

1-9 = fungicides identified by MPI, New Zealand
10-31 = Potential fungicides against myrtle rust
23-31= Potential fungicides against myrtle rust and are not available in New Zealand
***on** a.i. information was retrieved from NZ Novachem Agrichemical Manual 2016/2017
Active ingredients in **bold** are stand-alone products.
NA = Not Applicable since it is stand-alone product. Our interest is focused on product mixes
SA = Stand-alone product not in Novachem Agrichemical Manual 2016/2017
SA-N= Stand-alone product in Novachem Agrichemical Manual 2016/2017
NSA= Not Stand-alone product.

Appendix 3. List of plant endophytes with biological control activity against plant pathogens

Kingdom	Division	Order	BCA-species	Host plant	Substrate	Targeted plant pathogens	Common disease name	Reference
Bacteria	-	Pseudomonales	*Pseudomonas* sp. *R4R21AP*	*Actinidia deliciosa*	leaves	*Pseudomonas syringae* pv. *actinidiae*	bacterial canker	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Pseudomonales	*Pseudomonas* sp. *T4MS32AP*	*Actinidia deliciosa*	leaves	*Pseudomonas syringae* pv. *actinidiae*	bacterial canker	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Pseudomonales	*Pseudomonas* sp. *T4MS33*	*Actinidia deliciosa*	leaves	*Pseudomonas syringae* pv. *actinidiae*	bacterial canker	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Burkholderiales	*Burkholderia* sp. *W4R11*	*Leptospermum scoparium*	leaves	*Neofusicoccum luteum, Neofusicoccum ribis, Neofusicoccum parvum, Neofusicoccum australe, Diplodia mutila, Diplodia seriata*	grapevine trunk disease	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Burkholderiales	*Burkholderia* sp. *W6RA*	*Leptospermum scoparium*	leaves	*Neofusicoccum luteum, Neofusicoccum ribis, Neofusicoccum parvum, Neofusicoccum australe, Diplodia mutila, Diplodia seriata*	grapevine trunk disease	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Pseudomonales	*Pseudomonas* sp. *I2R21*	*Leptospermum scoparium*	leaves	*Neofusicoccum luteum, Neofusicoccum ribis, Neofusicoccum parvum, Neofusicoccum australe, Diplodia mutila, Diplodia seriata*	grapevine trunk disease)	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Pseudomonales	*Pseudomonas* sp. *W1R33*	*Leptospermum scoparium*	leaves	*Neofusicoccum luteum, Neofusicoccum ribis, Neofusicoccum parvum, Neofusicoccum australe, Diplodia mutila, Diplodia seriata*	grapevine trunk disease	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Pseudomonales	*Pseudomonas* sp. *W7R11*	*Leptospermum scoparium*	leaves	*Neofusicoccum luteum, Neofusicoccum ribis, Neofusicoccum parvum, Neofusicoccum australe, Diplodia mutila, Diplodia seriata*	grapevine trunk disease	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Pseudomonales	*Pseudomonas* sp. *W7R13*	*Leptospermum scoparium*	leaves	*Neofusicoccum luteum, Neofusicoccum ribis, Neofusicoccum parvum, Neofusicoccum australe, Diplodia mutila, Diplodia seriata*	grapevine trunk disease	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Pseudomonales	*Pseudomonas* sp. *W7R21*	*Leptospermum scoparium*	leaves	*Neofusicoccum luteum, Neofusicoccum ribis, Neofusicoccum parvum, Neofusicoccum australe, Diplodia mutila, Diplodia seriata*	grapevine trunk disease	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Pseudomonales	*Pseudomonas* sp. *W7R22*	*Leptospermum scoparium*	leaves	*Neofusicoccum luteum, Neofusicoccum ribis, Neofusicoccum parvum, Neofusicoccum australe, Diplodia mutila, Diplodia seriata*	grapevine trunk disease	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Pseudomonales	*Pseudomonas* sp. *W7R31*	*Leptospermum scoparium*	leaves	*Neofusicoccum luteum, Neofusicoccum ribis, Neofusicoccum*	grapevine trunk disease	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)

Kingdom	Division	Order	BCA-species	Host plant	Substrate	Targeted plant pathogens	Common disease name	Reference
						parvum, Neofusicoccum australe, Diplodia mutila, Diplodia seriata		
Bacteria	-	Burkholderiales	*Serratia* sp. *W1R33*	*Leptospermum scoparium*	leaves	*Neofusicoccum luteum, Neofusicoccum ribis, Neofusicoccum parvum, Neofusicoccum australe, Diplodia mutila, Diplodia seriata*	grapevine trunk disease	(Wisnu Adi Wicaksono, Eirian Jones, et al., 2017)
Bacteria	-	Bacillales	*Bacillus cereus*	*Coffea arabica*	leaves	*Hemileia vastatrix*	Coffee rust	(Shiomi et al., 2006)
Bacteria	-	Bacillales	*Bacillus lentimorbus*	*Coffea arabica*	leaves	*Hemileia vastatrix*	Coffee rust	(Shiomi et al., 2006)
Bacteria	-	Pseudomonales	*Pseudomonas* sp.	*Leptospermum scoparium*	leaves, stem, roots	*Pseudomonas syringae* pv. *actinidiae*	bacterial canker of kiwifruit	(Wisnu Adi Wicaksono, 2016)
Bacteria	-	Bacillales	*Bacillus subtilis*		leaves	*Austropuccinia psidii*	Myrtle rust	(Santos et al., 1998)
Fungi	Ascomycota	Eurotiales	*Aspergillus brasiliensis*	*Olea europaea*	fruit	*Colletotrichum acutatum*	Anthracnose	(Preto, Martins, Pereira, & Baptista, 2017)
Fungi	Ascomycota	Eurotiales	*Aspergillus* sp. *1*	*Olea europaea*	fruit	*Colletotrichum acutatum*	Anthracnose	(Preto et al., 2017)
Fungi	Ascomycota	Eurotiales	*Aspergillus westerdijkiae*	*Olea europaea*	fruit	*Colletotrichum acutatum*	Anthracnose	(Preto et al., 2017)
Fungi	Ascomycota	Sordariales	*Chaetomium globosum*	*Olea europaea*	fruit	*Colletotrichum acutatum*	Anthracnose	(Preto et al., 2017)
Fungi	Ascomycota	Pleosporales	*Epicoccum nigrum*	*Olea europaea*	fruit	*Colletotrichum acutatum*	Anthracnose	(Preto et al., 2017)
Fungi	Ascomycota	Hypocreales	*Trichoderma virens*	*Zea mays*	leaves	*Colletotrichum graminicola*	anthracnose	(Djonović et al., 2007)
Fungi	Ascomycota	Pleosporales	*Epicoccum nigrum*	*Fraxinus excelsior*	leaves	*Hymenoscyphus fraxineus*	Ash dieback	(Kosawang et al., 2018)
Fungi	Ascomycota	Hypocreales	*Fusarium* sp.	*Fraxinus excelsior*	leaves	*Hymenoscyphus fraxineus*	Ash dieback	(Kosawang et al., 2018)
Fungi	Ascomycota	Pleosporales	*Sclerostagonospora* sp.	*Fraxinus excelsior*	leaves	*Hymenoscyphus fraxineus*	Ash dieback	(Kosawang et al., 2018)
Fungi	Ascomycota	Pleosporales	*Setomelanomma holmii*	*Fraxinus excelsior*	leaves	*Hymenoscyphus fraxineus*	Ash dieback	(Kosawang et al., 2018)
Fungi	Ascomycota	Eurotiales	*Byssochlamys nivea BN 1-1-1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad, Javan-Nikkhah, & Shier, 2017)
Fungi	Ascomycota	Sordariales	*Chaetomium globosum CG 6-2-1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Sordariales	*Chaetomium interruptum CI 8-1-1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Clonostachys rosea CR 2-3-1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Pleosporales	*Coniothyrium* sp. *Cs1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Pleosporales	*Epicoccum nigrum EN1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Fusarium acuminatum FA 7-2-1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Fusarium incarnatum-equiseti species complex Fi 13-2-1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)

Kingdom	Division	Order	BCA-species	Host plant	Substrate	Targeted plant pathogens	Common disease name	Reference
Fungi	Ascomycota	Hypocreales	*Fusarium tricinctum FT 6-3-1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Lecanicillium lecanii LL1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Trichoderma atroviride TA 2-2-1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Trichoderma harzianum TH 10-2-2*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Trichoderma harzianum TH 4-1-2*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Trichoderma longibrachiatum TL 10-3-1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Trichoderma longibrachiatum TL 11-2-1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Trichothecium roseum TR 1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Xylariales	*Truncatella angustata TA 1*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi	Ascomycota	Hypocreales	*Trichorderma asperellum*	*Cucumis sativus*	leaves	*Pseudomonas syringae* pv. *lachrymans*	bacteria	(Segarra et al., 2007)
Fungi	Ascomycota	Hypocreales	*Trichoderma harzianum strain T39*	*Vitis vinifera*	leaves	*Plasmopara viticola*	grapevine downy mildew	(Perazzolli, Dagostin, Ferrari, Elad, & Pertot, 2008)
Fungi	Ascomycota	Hypocreales	*Strachybotrys (S. cholorohalonata;S. chartarum)*	*Populus* sp.	leaves	*Melampsora* sp.	Melampsora rust	(Raghavendra & Newcombe, 2013)
Fungi	Ascomycota	Hypocreales	*Trichorderma atroviride (Hypocrea atroviridis)*	*Populus* sp.	leaves	*Melampsora* sp.	Melampsora rust	(Raghavendra & Newcombe, 2013)
Fungi	Ascomycota		*Truncatella angustata*	*Populus* sp.	leaves	*Melampsora* sp.	Melampsora rust	(Raghavendra & Newcombe, 2013)
Fungi	Ascomycota	Pleosporales	*Ulocladium atrum*	*Populus* sp.	leaves	*Melampsora* sp.	Melampsora rust	(Raghavendra & Newcombe, 2013)
Fungi	Ascomycota	Hypocreales	*Fusarium decemcellulare (Albonectria rigidiuscula)*	*Psidium guajava*	leaves	*Austropuccinia psidii*	Myrtle rust	(Amorim et al., 1993)
Fungi	Ascomycota	Hypocreales	*Trichorderma harzianum Rifai strain T39*	*Arabidopsis thaliana*	leaves	*Botrytis cinerea*	necrotrophic fungus	(Korolev, Rav David, & Elad, 2008)
Fungi	Ascomycota	Hypocreales	*Acremonium byssoides*	*Hevea brasiliensis*	leaves	*Oidium heveae*	powdery mildew	(Kiss, 2003)
Fungi	Ascomycota		*Ampelomyces* spp.	Many species	leaves	Many species	powdery mildew	(Kiss, 2003)
Fungi	Ascomycota	Hypocreales	*Lecancillium* spp.	monocots and dicots	leaves	-	powdery mildew and various rust fungi	(Ownley et al., 2010)

Kingdom	Division	Order	BCA-species	Host plant	Substrate	Targeted plant pathogens	Common disease name	Reference
Fungi	Ascomycota	Xylariales	*Xylaria* sp *F0010*	*Abies holophylla*	inner bark	*Magnaporthe grisea, Corticium sasaki, Puccinia recondita, Blumeria graminis f.recondita, Blumeria graminis* sp. *hordei*	rice blast, rice sheath blight, wheat leaf rust, barley powdery mildew	(Park et al., 2005)
Fungi	Ascomycota	Hypocreales	*Beauveria bassiana*	monocots and dicots	leaves	Pythium, Rhizictonia, Fusarium	soilborne pathogens	(Ownley et al., 2010)
Fungi	Ascomycota	Capnodiales	*Cladosporium* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Capnodiales	*Clodosporium* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Pezizales	*Geopyxis* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Helotiales	*Helotiaceae* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Helotiales	*Helotiales* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Dothideales	*Hormonema* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Capnodiales	*Mycosphaerella* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Xylariales	*Nemania* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Pezizales	*Pezizales* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Pleosporales	*Rhizosphaera* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Rhytismataceae	*Rhytismataceae* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Pezizales	*Sarcosomateceae* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota		*Xenochalara* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Ascomycota	Lulworthiales	*Zalerion* sp.	*Pinus monticola*	leaves	*Cronartium ribicola*	White pine blister rust	(Ganley et al., 2008)
Fungi	Basidiomycota	Agaricales	*Chondrostereum purpureum*	*Olea europaea*	fruit	*Colletotrichum acutatum*	Anthracnose	(Preto et al., 2017)
Fungi	Basidiomycota	Microstromatales	*Quambalaria cyanescens*	*Olea europaea*	fruit	*Colletotrichum acutatum*	Anthracnose	(Preto et al., 2017)
Fungi	Basidiomycota	Microstromatales	*Quambalaria cyanescens QC 11-3-2*	*Pistacia vera*	fruit/leaves	*Aspergillus flavus, Rhizoctonoa solani, Sclerotina sclerotium*	Aspergillus fruit rot, seedling blight, Sclerotinia shoot blight	(Dolatabad et al., 2017)
Fungi			*Boremia exigua*	*Fraxinus excelsior*	leaves	*Hymenoscyphus fraxineus*	ash dieback	(Kosawang et al., 2018)
Fungi	Ascomycota	Capnodiales	*Cladosporium tenuissimum*	-	leaves	*Puccinia, Cronartium, Uromyces, Hemileia, Melampsora*	rust disease	(Moricca et al., 2005)
Fungi	Basidiomycota	Helicobasidiales	*Tuberculina* spp.	-	-	*Puccinia sylvatica and Tranzschelia prunispinosae*	rust disease	(Bauer et al., 2004)
Fungi	Ascomycota	uncertain	*Verticillium* spp.	-	-	*Hemileia vastatrix, Puccinia recondita, Uromyces dianthi, Verticillum psalliotae, Phakopsora pachyrhizi*	rust disease	(Moricca & Ragazzi, 2008b)
Fungi	Ascomycota	Pleosporales	*Sphaerellopsis filum (Eudarluca caricis*)	-	-	*Puccinia* spp.	rust disease	(Płachecka, 2005)
Fungi	Ascomycota	Hypocreales	*Aphanocladium album*	-	-	*Puccinia graminis* f. sp. *tritici*	wheat stem rust	(Kocl et al., 2008)

Appendix 4. List of known elicitors inducing plant defence response

Elicitor source	Elicitor	Fungal pathogen	Host plant	Reference
abiotic	B*enzothiadiazole (BTH)*	*Puccinia striiformis* f. sp. *tritici*	*Triticum* sp.	(Han et al., 2012)
abiotic	BTH	*Uromyces appendiculatus*	*Phaseolus vulgaris*	(Iriti & Faoro, 2003)
abiotic	BTH	*Uromyces psisi*	*Pisum sativum*	(Barilli et al., 2015)
abiotic	BTH	*Austropuccinia psidii*	Eucalyptus hybrids (*E. grandis* x *E. urophylla*)	(Boava, Laia, et al., 2010)
abiotic	Fungastop	*Sphaerotheca fuliginea*	*Cucumis sativus*	(Alkahtani et al., 2011)
abiotic	Oxalic acid	*Sphaerotheca fuliginea*	*Cucumis sativus*	
abiotic	Photophor	*Sphaerotheca fuliginea*	*Cucumis sativus*	
abiotic	Potassium oxalate	*Sphaerotheca fuliginea*	*Cucumis sativus*	
abiotic	Salicilic acid	*Phytophthora palmivora*	*Hevea brasiliensis*	(Deenamo et al., 2018)
abiotic	Salicilic acid	*Puccinia substrinata*	*Pennisetum glaucum*	(Crampton et al., 2009)
abiotic	Salicilic acid	*Sphaerotheca fuliginea*	*Cucumis sativus*	
abiotic	Salicilic acid + benzothiadiazole (BTH)	*Uromyces viciae-fabae, Ascochyta fabae, Orobranche crenata*	*Vicia faba*	(Sillero, Rojas-Molina, Avila, & Rubiales, 2012)
biotic	λ-carrageenan	*Sclerotinia sclerotorium*	*Arabidopsis thaliana*	
biotic	B2-F	*Fusarium oxysporum* f. sp *lycopersici*	*Solanum lycopersicum*	
biotic	Cerato-populin (Pop1)	*Ceratocystis platani*	*Platanus acerifolia*	
biotic	Chitosan	*several (e.g. Botrytis, Fusarium, Pythium, Colletotrichum, Phytophthora, Alternaria)*	*Several (e.g. Capsicum, Cucumis, Vitis, Solanum, Raphanus* spp.*)*	
biotic	elicitor	*Phytophthora colocasiae*	*Colocasua esculenta*	
biotic	Glucan	*Puccinia arachidis*	*Arachis hypogaeae*	
biotic	Hypersensitive response inducing protein 1 (Hrip1)	*Alternaria tenuissima*	*Nicotiana tabcam* cv. *Xanthi-nc*	
biotic	Laminarin	*Botrytis cinerea* and *Plasmopara viticola*	Vitis vinifera	
biotic	MoHrip1	*Magnaporthe grisea*	*Oriza sativa*	
biotic	MoHrip2	*Magnaporthe grisea*	*Oriza sativa*	(N. U. Khan et al., 2016)
biotic	MoHrip2	*Magnaporthe grisea*	*Oriza sativa*	(N. U. Khan et al., 2016)
biotic	PebC1	*Botrytis cinerea*	*Arabidopsis thaliana*	
biotic	ZemPep1 (elicitor peptide 1)	*Cochliobolis heterostrophus and Colletotrichum graminicola*	*Zea mays*	(Huffaker, Dafoe, & Schmelz, 2011)
biotic	β-1,3 glucan	*Zemoseptoria tritici*	*Triticum* sp.	(Shetty et al., 2009)
biotic	β-1,3 glucan fragments	*Magnaporthe grisea*	*Oriza sativa*	(Yamaguchi et al., 2000)
biotic	β-glucan	*Phytophthora megasperma*	*Glycine max*	(Umemoto et al., 1997)

Appendix 5. List of antifungal peptides

Type of AMP	Antimicrobial Plant Peptide	Plant source	Antifungal effect	Reference
Thionin	Thi2.4	*Arabidopsis thaliana*	*Fusarium graminearum*	
Thionin	α-hordothionin	*Hordeum vulgare*	*Ceratocytis fimbriata*	
Plant defensin	Ah-AMP1	*Aesculus hippocastanum*		
Plant defensin	Ct-AMP1	*Clitoria ternatea*		(K. Thevissen et al., 2003)
Plant defensin	Dm-AMP1	*Dahlia merckii*		
Plant defensin	Dm-AMP2	*Dahlia merckii*		
Plant defensin	Hs-AFP1	*Heuchera sanguinea*		(Terras et al., 1995)
Plant defensin	alfAFP	*Medicago sativa*	*Verticillium dahlia*, *Alternaria solani* and *Fusarium culmorum*	(Gao et al., 2000)
Plant defensin	MsDef1	*Medicago sativa*	*Fusarium graminearum*	(Sagaram et al., 2011)
Plant defensin	MsDef4	*Medicago truncatula*	*Fusarium graminearum*	(Sagaram et al., 2011)
Plant defensin	MtDef5	*Medicago truncatula*	*Fusarium graminearum; Neurospora crassa*	
Plant defensin	PvD1	*Phaseolus vulgaris*	*Fusarium oxysporum, Fusarium solani, Fusarium lateritium, Rizoctonia solani*	
Plant defensin	PgD5	*Picea glauca*	*Verticillium dahlia*, *Botrytis cinerea*, *Rhizoctonia solani*, *Fusarium oxysporum*	
Plant defensin	Drr230a, Drr230c	*Pisum sativum*	*Fusarium solanii*, *F. oxysporum*, *Aschochyta pisi*, *A. pinodes*, *A. lentis*, *Alternaria alternata* and *Leptosphaeria maculans*	
Plant defensin	Rs-AFP1, Rs-AFP2	*Raphanus sativus*	*Alternaria brassicola, Botrytis cinerea*, *Fusarium culmorum*	
Peptaibol	Trichorzianine A1 and B1	*Trichoderma harzianum*	*Botrytis cinerea*	
Lipid transfer protein	LJAMP2	*Leonurus japonicas*	*Alternaria alternate, Colletotrichum gloeosporioides*	
Hevein-like antimicrobial peptides	CaAFP	*Capsicum annuum*	*Fusarium oxysporum, Nectria radicicola*	
Hevein-like antimicrobial peptides	Pn-AMP1, Pn-AMP2	*Pharbitis nil*		
Hevein	Hevein	*Hevea brasiliensis*	*Botrytis cinerea, Fusarium culmorum, Fusarium oxysporum, Phycomyces blakeskeeanus, Pyrenophora tritici-repentis, Pyricularia oryzae, Septoria nodorum, Trochoderma hamatum*	
Fungal defensin	AFP	*Aspergillus giganteus*	*antifungal activity*	
Fungal defensin	Anafp	*Aspergillus niger*	*antifungal activity*	
Fungal defensin	PAF	*Penicillium chrysogenum*	*antifungal activity*	(Oberparleiter et al., 2003)
Cyclopeptides	cyclopeptides	*Phomopsis* sp. K38 ; *Alternaria* sp. E33	*Gaeumannomyces graminis, Rhizoctonia* cerealis, *Helminthosporium sativum, Fusarium graminearum*	*(C. Li et al., 2014)*
Cyclopeptide	tyrocidines	*Bacillus aneurinolyticus*	*Fusarium verticillioides, Fusarium solani, Botrytis cinerea*	(Troskie, de Beer, Vosloo, Jacobs, & Rautenbach, 2014)

Appendix 6. Summary of mycoviruses identified from plant fungal pathogen and their potential to induce hypovirulence

Family	Genus	Virus	Abbreviation	Host	Causing hypovirulence of host	References
Hypoviridae	Hypovirus	*Cryphonectria hypovirus 4*	CHV-4	*Chryphonectria parasitica*	not demonstrated	
Narnaviridae	Mitovirus	*Fusarium circinatum mitovirus 1*	FcMV1	*Fusarium circinatum*	not demonstrated	
Narnaviridae	Mitovirus	*Fusarium circinatum mitovirus 2-1*	FcMV2-1; FcMV2-2	*Fusarium circinatum*	not demonstrated	(Martínez-Álvarez, Vainio, Botella, Hantula, & Diez, 2014)
Narnaviridae	Mitovirus	*Hymenoscyphus fraxineus mitovirus 1*	HfMV1	*Hymenoscyphus fraxineus*	not demonstrated	
Totiviridae	Totivirus	*Puccinia striiformis* virus 1	PsV1	*Puccinia striiformis*	not demonstrated	
Totiviridae	Totivirus	*Puccinia striiformis* virus 2	PsV2	*Puccinia striiformis*	not demonstrated	
Totiviridae	Totivirus	*Puccinia striiformis* virus 3	PsV3	*Puccinia striiformis*	not demonstrated	
Totiviridae	Totivirus	*Puccinia striiformis* virus 4	PsV4	*Puccinia striiformis*	not demonstrated	
Partiviridae	Partivirus	*Verticillium alboatrum* partitivirus 1	VaaPV1	*Verticillium alboatrum*	not demonstrated	
Chrysoviridae	Chrysovirus	*Verticillium dahlia chrysovirus 1*	VdCV1	*Verticillium dahliae*	not demonstrated	
Chrysoviridae	Chrysovirus	*Botryosphaeria dothidea chrysovirus 1*	BdCV1	*Botryosphaeria dothidea*	yes	(L. Wang et al., 2014)
Partiviridae	Partivirus	*Botryosphaeria dothidea partitivirus 1*	BdPV1	*Botryosphaeria dothidea*	yes	(L. Wang et al., 2014)
Narnaviridae	Mitovirus	*Botrytis cinerea mitovirus 1*	BcMV1	*Botytris cinerea*	yes	
Hypoviridae	Hypovirus	*Cryphonectria hypovirus 1*	CHV-1	*Chryphonectria parasitica*	yes	
Hypoviridae	Hypovirus	*Cryphonectria hypovirus 2*	CHV-2	*Chryphonectria parasitica*	yes	
Hypoviridae	Hypovirus	*Cryphonectria hypovirus 3*	CHV-3	*Chryphonectria parasitica*	yes	
Narnaviridae	Mitovirus	*Cryphonectria mitovirus* 1	CpMV1	*Chryphonectria parasitica*	yes	
Reoviridae	Mycoreovirus	*Mycoreovirus 1*	MYRV-1	*Chryphonectria parasitica*	yes	(Suzuki et al., 2004)
Reoviridae	Mycoreovirus	*Mycoreovirus 2*	MYRV-2	*Chryphonectria parasitica*	yes	(Suzuki et al., 2004)
unassigned	New genus of mycoviruses	*Fusarium graminearum* virus 1	FgV1	*Fusarium graminearum*	yes	(Kwon, Lim, Park, Park, & Kim, 2007)
Totiviridae	Victorivirus	*Helicobasidium mompa totivirus*	HmTV1-17	*Helicobasidium mompa*	yes	
Narnaviridae	Mitovirus	*Ophiostoma novo-ulmi mitovirus 3a-Ld*	OMV3a-Ld	*Ophiostoma novo-ulmi*	yes	
Narnaviridae	Mitovirus	*Ophiostoma novo-ulmi mitovirus 4-Ld*	OMV4-Ld	*Ophiostoma novo-ulmi*	yes	
Narnaviridae	Mitovirus	*Ophiostoma novo-ulmi mitovirus 5-Ld*	OMV5-Ld	*Ophiostoma novo-ulmi*	yes	
Narnaviridae	Mitovirus	*Ophiostoma novo-ulmi mitovirus 6-Ld*	OMV6-Ld	*Ophiostoma novo-ulmi*	yes	
Megabirnaviridae	Megabirnavirus	*Rosellinia necatrix megabirnavirus 1*	*RnMBV1*	*Rosellinia necatrix*	yes	
Narnaviridae	Mitovirus	*Sclerotinia sclerotiorum mitovirus 1*	SsMV1	*Sclerotina sclerotiorum*	yes	
unassigned	Botybirnavirus	*Sclerotinia sclerotiorum botybirnavirus* 2	SsBRV2	*Sclerotinia sclerotiorum*	yes	
Reoviridae	unassigned	*Rosellinia anti-rot virus*	RArV	*Rosellinia necatrix*	yes	
Reoviridae	Mycoreovirus	*Rosellinia necatrix Mycoreovirus* 3	MyRV3	*Rosellinia necatrix*	yes	
unassigned	unassigned	*Botryosphaeria dothidea* RNA virus 1	BdRV1	*Botryosphaeria dothidea*	yes	