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REVIEW

Soil amendments for management of Phytophthora root rot in avocado and their impact on the soil microbiome

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Abstract
Phytophthora root rot is a major problem for avocado growers around the world. This review summarises the current control measures and their impact on the soil microbiome. The fungicide phosphite is widely used in the avocado industry, and reports from several countries indicate that *Phytophthora cinnamomi* is developing resistance. For this reason, alternative control measures have been investigated. Applying organic mulches and soil dressings of calcium or silicon provides a level of control. Biological control through the application of suppressive microbes has been actively investigated over many years, but reports of successful field deployment are rare. This review examines the effects on the soil microbiome of these control measures and assesses the future directions for research.

Keywords Soil additives · *Phytophthora cinnamomi* · Biocontrol · Silicon mulch · Suppressive soils

Introduction

Avocado (*Persea americana*) is a warm climate tree, and its fruits are utilised worldwide for direct consumption, edible oil and the preparation of beauty products (Schaffer et al. 2013). Annual production in 2018 was 5.7 million tonnes (Sommaruga and Eldridge 2021). Soil-borne diseases that impact avocado production include white root, Verticillium wilt and Rhizoctonia root rot (Zentmyer 1984; Perez-Jimenez 2008; Dann et al. 2013), but the one of most concern is Phytophthora root rot caused by the oomycete *Phytophthora cinnamomi* and other *Phytophthora* species. This disease occurs in all the major avocado-growing regions of the world (Dann et al. 2013) and if not controlled, may kill all trees in an orchard (Zentmyer 1980).

Phosphite (also known as phosphonate) is the primary chemical used to control Phytophthora root rot in avocados (Pegg et al. 1987; Ramirez-Gil et al. 2017, 2018). Orchards are frequently sprayed with phosphite several times a year, leading to the emergence of resistant *P. cinnamomi* strains (Dobrowolski et al. 2008; Hunter et al. 2022). *Phytophthora cinnamomi* strains resistant to other fungicides, metalaxyl, mefenoxam, dimethomorph, and cymoxanil have also emerged (Parra and Ristaino 2001; Thomidis and Elena 2001). Although some new fungicides are becoming available (Belisle et al. 2019), an integrated approach for managing *P. cinnamomi* in avocado orchards (Pegg and Whiley 1987) is the best option and has been widely adopted. It promotes root health by planting *P. cinnamomi*-resistant rootstocks, careful soil selection and site preparation, organic and inorganic amendments, irrigation management, and chemical control (Wolstenholme 1979; Wolstenholme and Sheard 2010). However, even with integrated management, the control of *P. cinnamomi* in avocado orchards still relies heavily on applying phosphite.

Increasing awareness of the value of sustainable agriculture has stimulated research into ways of reducing the applications of chemical pesticides. Identifying and harnessing the disease suppression abilities of soil microbes is an attractive alternative for disease control. Many studies have identified microbes from the rhizosphere or root endosphere that can inhibit *P. cinnamomi in vitro*. Fewer have shown these organisms to be effective in glasshouse trials, and even fewer have demonstrated effectiveness in the field (Table 1).

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Attempts to use single organisms for biocontrol for other woody species have also frequently failed when applied in the field, and as a result, the thrust of the research effort is now to assemble cohorts of suppressive organisms which have different, complementary modes of action and which can co-exist in the soil (Raaijmakers and Mazzola 2016). An alternative approach is manipulating the soil environment so introduced organisms can multiply and express their disease suppression traits. These two approaches could be complementary and soil health could be improved using both methods. This review will focus on the effects on the soil microbiome of various control measures used for *P. cinnamomi* in avocados: applications of organic and inorganic soil amendments or suppressive microbes and spraying with pesticides. Prospects for using soil microbes for biological control of Phytophthora root rot in avocados will be discussed.

Soils suppressive or conducive to soil-borne pathogens

Some soils are naturally suppressive to disease due to their microbial populations, which inspired research into using soil microbes for disease control (Mazzola 2002; Cook 2014). These soils may have either general or specific suppression ability. Weller et al. (2002) explained the difference: “General suppression owes its activity to the total microbial biomass in soil and is not transferable between soils. Specific suppression owes its activity to the effects of individual or select groups of microorganisms and is transferable”. Soil microflora can contribute significantly to the suppression of pathogens directly by hyperparasitism (Davies et al. 2008), microbiostasis (Jambhulkar et al. 2015), production of antibiotics, metabolites, toxins (Garbeva et al. 2006, 2011; Adesina et al. 2007), competition for substrates (Cook and Baker 1983), or direct destruction of pathogen propagules (Jambhulkar et al. 2015). Indirect protection against diseases can result from the induction of systemic host resistance (Jambhulkar et al. 2015), the release of volatile compounds as signalling molecules in intraspecific interactions (Schmidt et al. 2015), or improved growth of plants through microbial production of growth hormones and siderophores (Bhattacharjee and Dey 2014). Gomez Exposito et al. (2017) provide an extensive list of organisms shown to provide specific suppression of a pathogen in vitro or under glasshouse conditions. In disease-suppressive soils, species of Proteobacteria and Actinobacteria are amongst the most abundant (Mendes et al. 2011; Liu et al. 2016). However, the theoretically possible transfer of specific suppression to conducive soils by soil transplantation or inoculation with microbial cultures has proved difficult for annual crop species and even more so for tree species (Cazorla and Mercado-Blanco 2016). As the use of one or two organisms to induce specific suppression has been largely unsuccessful, the research focus is changing to manipulation of the whole microbiome and utilising consortia of suppressive organisms to engineer the soil to function in a manner closer to one with general suppressive ability (Whipps 2001).

Microbes that suppress *Phytophthora*

Fungi, bacteria and oomycetes that inhibit the growth or reproduction of *P. cinnamomi* have been found in soils, rhizosphere soils or root endospheres (Table 1). The organisms shown to be effective both in vitro and in pot trials with avocado are *Bacillus cereus, Paenibacillus polymyxa Trichoderma harzianum, T. hamatum, T. kongingiopsis* and *T. asperellum* (Hakizimana et al. 2011; Andrade-Hoyos et al. 2020). There are few reports of field studies. One short study in Mexico showed that four soil treatments with suppressive *Trichoderma* species, six months apart, reduced damage observed on infected trees to a greater extent than Ridomil (Lara-Chavez et al. 2012). An extensive study in South Africa showed that *in vitro Aspergillus candidus, T. hamatum, Paecilomyces lilacinus, Bacillus azotoformans* and *B. megatenum* reduced *P. cinnamomi* damage. However, the fungal species were more effective for avocado seedlings in the glasshouse than the bacteria. Subsequent field tests over seven years demonstrated that A*spergillus candidus* and *T. hamatum* established and survived best (Duvenhage 1999) and either separately or together with *Paecilomyces lilacinus* improved root health and plant condition, depending on the avocado variety. Unfortunately, in this trial, untreated control trees had a low level of diseased roots. Yang et al. (2001) studied the effect of treating 30-year-old avocado trees with *Pseudomonas fluorescens* through irrigation water once a week for four months. After this treatment, the rhizosphere and endosphere of roots had no *Phytophthora* and a population of *Pseudomonas, Polangium* and *Cytophaga* similar to healthy untreated roots, but the long-term health of the trees was not reported. The association of particular microbial groups on healthy roots does not necessarily mean they suppress *Phytophthora*, as the differences may reflect differences in root exudates due to infection/tree health (Yang et al. 2001).

Various culture-independent DNA-based analyses are now available that provide information on how the microbial community composition and metabolic activity changes in avocado soil in response to soil additives (e.g.Yang et al. 2001). Another population study reported that infection causes a shift toward a higher proportion of bacteria than fungi in the top ten taxa, and changes the relative abundance

Table 1 Microbial suppression of *Phytophthora cinnamomi* by microbial species or their culture filtrates in vitro, and disease suppression in glasshouse or field trials for avocado or other plant species

Suppressive microbe (source)	In vitro	In planta	Notes	References
Trichoderma hamatum *T. pseudokoningii, T. virens*[a] (soil)	Filtrate from *T. hamatum* and *T. virens* inhibited mycelial growth	Filtrate suppressive when applied to chestnut shoots in an excised shoot bioassay	*T. hamatum* and *T. pseudokoningii* are mycoparasites. Filtrate from *T. hamatum and T. virens* also inhibited mycelial growth of *P. citricola*	Chambers and Scott (1995)
Streptomyces violascens *Micromonospora* spp. (soil)	Inhibited mycelial growth. *Micromonospora* culture filtrate also inhibitory	Reduced damage to *Banksia grandis* seedlings in pots of inoculated soil	*S. violaceae* produced an antibiotic and the Micromonospora species, cellulases. The effect was synergistic.	El-Tarabily et al. (1996)
Aspergillus candidus, Trichoderma hamatum, Paecilomyces lilacinus, Bacillus azotoformans, B. megatenum (soil from healthy trees in diseased area)	Isolates had been selected on the basis of mycelial inhibition but data not shown.	In glasshouse all suppressed infection of lupin, but on avocado seedlings bacteria were less effective than the fungi. In a 7 year field trial of avocado *A. candidus* and *T. hamatum* either separately or together with *P. lilacinus*, improved root health and plant condition	Suppression in the field varied with avocado cultivar and year.	Duvenhage et al. (1991); Duvenhage and Kotzé (1993); Duvenhage and Kohne (1997); Duvenhage (1999)
Penicillium funiculosum (soil)	Hyphal lysis	Soil inoculation of azalea rooted cuttings gave weak-moderate control of disease	*P. funiculosum* is a microparasite and produced diffusible antibiotics and promoted plant growth. In the glasshouse, two applications over 12 weeks were needed as inoculum density declined after 4 weeks.	Fang and Tsao (1995a)
Pythium nunn (soil)	Inhibition of mycelial growth, lysis	Not effective in azalea rooted cuttings	In vitro mycoparasitism of hyphae, sporangia chlamydospores and sex organs. *Pythium nunn* was effective for *P. parasitica* on azalea when using a high innoculum concentrations and providing a food source in the potting mix.	Fang and Tsao (1995b)
Trichoderma virens (avocado orchard soil)	n/a	Avocado seedlings in inoculated soil had 33% healthy roots, infested controls 0%.		Costa et al. (2000)
Pseudomonas fluorescens	n/a	Bacterial flora of root tips of 30-year-old treated trees lacked *P. cinnamomi* and was similar to that of healthy trees and different from diseased trees	Supplied in irrigation water once a week for 4 weeks	Yang et al. (2001)
Bacillus cereus (*Arbutus unedo* endosphere)	Suppression of mycelial growth	n/a		Martins et al. (2021)
Bacillus subtilis (avocado rhizoplane)	Some strains showed moderate inhibition of mycelial growth	n/a		Cazorla et al. (2007)
Muscodor crispens (*Ananas anassoides* endophyte)	Stopped mycelial growth	n/a	Also inhibited *P. palmivora* in vitro produced volatiles that suppress *Pythium ultimum, Sclerotinia sclerotiorum Mycosphaerella fijiensis Xanthomonas axonopodis* in vitro	Mitchell et al. (2009)
Bacillus cereus, Paenibacillus polymyxa, Trichoderna harzianum, Trichoderma hamarum (avocado endophytes)	Inhibited mycelial growth	Suppressive in glasshouse when 9-month-old avocado rootstocks or tissue cultured plants were inoculated	Inoculation with both a bacterium and a fungus gave better results than either separately. Decreased disease incidence to 2–40% cf. 94–100% for positive controls. Particularly effective in tissue cultured plants that are endophyte free before inoculation	Hakizimana et al. (2011)

Table 1 (continued)

Suppressive microbe (source)	In vitro	In planta	Notes	References
Trichoderma erinaceum, T. agressivum, T. arundinaceum	n/a	Reduced damage to infected avocado trees in orchard to a greater extent than Ridomil	Four soil treatments 6 months apart	Lara-Chavez et al. (2012)
Bacillus aff. acidifera *B. dentensis* (soil from infected and healthy avocado trees)	Inhibited mycelial growth *B. acidifera* more effective than *B. dentensis*	n/a	*B. acidifera* produced volatile pyrazine in vitro, also plant growth promotors	Mendez-Bravo et al. (2018)
Bacillus subtilis/Bacillus amyloliquefaciens, Bacillus mycoides, (rhizosphere soil of avocado)	Inhibited mycelial growth	n/a		Guevara-Avendano et al. (2018)
Trichoderma asperellum, *T. harzianum, T. koningiosis,* *T. hamatum* (endophytes from avocado)	All reduced mycelial growth	When applied to soil in glasshouse all reduced avocado seedling deaths	Mycoparasitism and abiosis	Andrade-Hoyos et al. (2020)
Trichoderma hamatum (endophyte from *Cinammon vernum*)	Reduced mycelium growth	When applied to soil in glasshouse significantly reduced avocado seedling deaths		Andrade-Hoyos et al. (2020)
Drechslera biseptata, Epicoccum nigrum and Fusarium avenaceum (soil)	Fungus or culture filtrate stopped mycelial growth	Filtrate used on seeds or seedlings of *Lupinus luteus* reduced disease impact	*E. nigrum and F. avenaceum* promoted plant growth	Garcia-Latorre et al. (2022)

[a] *Trichoderma virens* (syn. *Gliocladium virens*)

of the top ten taxa of both bacteria and fungi (Shu et al. 2019). Solis-Garcia et al. (2021) found that *P. cinnamomi* infection did not affect species richness, diversity or community structure in the rhizosphere but did change relative abundance, increasing the abundance of Burkhoderiales and decreasing Actinobacteria, *Bacillus* species and Rhizobiales. They also found an increase in opportunistic fungi. In contrast, Farooq et al. (2022b) reported that infection decreased bacterial abundance and diversity and that Actinobacteria and Proteobacteria were higher in relative abundance after infection. They also found that soil treatments of mineral mulch or spraying plants with phosphite suppressed Phytophthora root rot similarly and had different impacts on the bacterial microbiome.

Thus far, suppressive organisms have been sought mainly from soils and roots in agricultural environments. However, some organisms that suppress disease also confer resistance to abiotic stress (Timmusk and Wagner 1999), so bioprospecting in extreme environments might discover organisms that suppress pathogens. The halophytes *Halomonas elongata* and *Bacillus pumilis* inhibited the growth of *P. citrophthora* in *Citrus x clementina* (Zouaoui et al. 2019) and dark septate endophytes tolerant of trace element contamination of soils reduced the in vitro growth of *P. citricola* (Berthelot et al. 2019). Thus exploration of extreme habitats may reveal microbes capable of suppressing *P. cinnamomi.*

Mechanisms of action of microbes associated with disease-suppressive soils

Chemical antibiosis

Metabolites from many soil bacteria and fungi have antibiotic properties (Gomez Exposito et al. 2017; Raaijmakers et al. 2002; Whipps and Lumsden 2001). Although the production and action of these antibiotics have been intensively studied in vitro, their production in the soil environment has not been conclusively demonstrated, let alone shown to occur at inhibitory levels (Gomez Exposito et al. 2017). Their function at subinhibitory concentrations in soil may lie in cell-to-cell communication (Davies 2006). A notable aspect of chemical inhibitors is the wide range of chemicals produced (Whipps and Lumsden 2001). Some of these compounds can suppress diseases caused by entirely different pathogens, even across different phyla. For example, species of *Trichoderma* and *Muscador* can suppress *Phytophthora, Pythium, Sclerotinia, Mycosphaerella, and Xanthomonas* (Mitchell et al. 2009; Andrade-Hoyos et al. 2020). This illustrates the possibility that a suppressive soil microbe may positively or negatively impact many soil organisms, whether beneficial or pathogenic. However, some metabolites are particularly potent against zoosporic pathogens such as *Phytophthora*. Species of *Pseudomonas* produce biosurfactants that lyse naked cells, such as zoospores (Stanghellini and Miller 1997). Strains of the same suppressive species may vary widely in the ability to produce an antibiotic, and closely related species may inhibit a pathogen through different mechanisms; of five species of *Paraburkholdaria* equally effective against *Rhizoctonia* in soil, only one did so through the production of inhibitory volatiles (Carrion et al. 2018). The flexibility of microbial metabolism is notable too, and makes experimentation and application of results difficult. Production of suppressive metabolites can depend on the plant to which the microbe is applied and the pathogen present (Woo and Lorito 2007).

Many active compounds from *Pseudomonas* and *Bacillus* species are also notable, but other taxa may be equally as versatile, and the current data may, in part, reflect the extensive research involving *Pseudomonas* and *Bacillus* (Whipps and Lumsden 2001; Cawoy et al. 2011). Interestingly, many suppressive species (or their close relatives) are also endophytes (Table 1), and it is difficult to disentangle the contribution to disease suppression from microbes in the rhizosphere or the endosphere of a plant. As discussed below, using biological control organisms as endophytes is attracting increasing attention as it may provide better disease control than soil bacteria.

New metatranscriptomic techniques provide information on microbial metabolism in the soil rather than under the artificial conditions of in vitro culture. Metatranscriptomics analysis has not yet been applied to the avocado/*P. cinnamomi* pathosystem, but has provided information on microbial metabolism in soils that suppress *Rhizoctonia solani* (Raaijmakers and Mazzola 2016; Carrion et al. 2018; Hayden et al. 2018). These studies have illustrated the power of the technique to pinpoint the soil organisms important for producing key metabolites responsible for reducing disease expression.

Competition for nutrients

Non-pathogenic soil organisms may suppress pathogenic organisms through competition by obtaining soil nutrients more effectively (Heydari and Pessarakli 2010). The competition may be for macro- and micro-nutrients in the soil matrix and those secreted by the plant. For example, some non-pathogenic strains of *F. oxysporum* can out-compete the pathogenic strain for carbon and iron and reduce the pathogen's impact. Their suppressive ability correlates with their siderophore production level (Loper and Buyer 1991). Organisms that owe their suppressive ability to the speedy utilisation of secreted nutrients include *Enterobacter cloacae* which rapidly colonises the surface of germinating seeds of several horticultural species preventing *Pythium ultimum* damage (Kageyama and Nelson 2003), and *Pseudomonas putida* which suppresses *F. oxysporum* wilt in cucumber through its ability to colonise root surfaces rapidly (Anderson et al. 1988).

P. cinnamomi is a weak saprophyte, and increasing the abundance of competitive saprophytes may be an effective management strategy. In addition, root damage may be reduced by introducing non-pathogenic organisms that rapidly colonise the root surface. There are no examples of applying these strategies to *P. cinnamomi*, and there are no studies of interspecies competition in *Phytophthora.* Investigating the potential of non-pathogenic *Phytophthora* to suppress *P. cinnamomi* through competition for nutrients may be rewarding.

Parasitism and lysis

Although in vitro studies have shown that many organisms, especially fungi, can be parasitic on soil pathogens by releasing enzymes that destroy the host cell wall (Adams 1990), the effectiveness of this mechanism in soil has been questioned. No conclusive studies demonstrate the role of parasitism in specific disease suppression in soil (Gomez Exposito et al. 2017). Many suppressive organisms are capable of lysis, antibiosis, and parasitism. The widely used in vitro screening methods usually detect an inhibition zone rather than the direct interaction between a pathogen and a mycoparasite. Necrotrophic parasitic fungi with a broad range of nutritional strategies are more often successful biocontrol agents and more competitive in the soil environment than parasites that require a living host (Karlsson et al. 2017).

Early research on *P. sojae* and *P. cactorum* oospores showed a great diversity of microbes that parasitize them; amoebae, other oomycetes, Actinomycetes and Chytridiomycetes (Waterhouse 1940; Sneh et al. 1977; Chakraborty et al. 1983). Most information is available on the effect of *Trichoderma* species. *In vitro, Trichoderma* species parasitize *Phytophthora;* the intertwining of hyphae is followed by the degradation of walls and cytoplasm of *Phytophthora* hyphae, oospores, and chlamydospores by lytic enzymes and antibiotic substances released from the *Trichoderma* (Andrade-Hoyos et al. 2020). Mycoparasites must be used cautiously as biocontrol agents as they may also parasitise beneficial soil fungi such as mycorrhizae.

Surprisingly, amongst the oomycetes, some species of *Pythium* are parasitic and suppressive of some pathogens. *Pythium nunn* can protect orange trees from *P. parasitica*, and *Pythium oligandrum* inhibits *P. megasperma* and *P. parasitica. Pythium oligandrum* was highly effective against *P.cinnamomi in vitro* but not for infested potted azalea plants (Fang and Tsao 1995b). *Pythium oligandrum* is the biological component of the commercial product Polyversum^{R}. Its mode of action is most unusual. It behaves like an oomycete pathogen, quickly colonising root tissue and producing oligandrin, an elicitor of plant defence (Mohamed et al. 2007).

The *Pythium* then rapidly degenerates without harming the plant. Further, it is a virulent mycoparasite and produces cellulases that destroy the walls of *P. parasitica* and lytic substances that degrade cellular structure of *P. megasperma* without hyphal contact or wall destruction. In addition, it promotes plant growth through auxin production (Benhamou et al. 2012). The selective advantage of this unusual *modus operandi* is not clear. The biology of non-pathogenic oomycetes is rarely studied, and it is not known how many other species of soil oomycetes share these valuable attributes, particularly stimulation of host defence.

Induction of systemic resistance in the host plant

Some non-pathogenic bacteria and fungi (free-living or mycorrhizal) can induce systemic resistance in a host plant. In some cases, resistance is long-lasting and gives a high level of disease control, but more often, it is inconsistent and provides a low level of control (Walters et al. 2013; Pieterse et al. 2014). Organisms known for this trait include species of *Pseudomonas, Bacillus* and *Trichoderma* (Da Rocha and Hammerschmidt 2005; Alabouvette et al. 2009; Bakker et al. 2013). *Fusarium oxysporum* induced resistance to *P. capsici* in peppers (Silvar et al. 2009). Using a model system of tomato, *Trichoderma* and *Phytophthora*, La Spada et al. (2020) demonstrated that *Trichoderma asperellum* and *T. atroviride* induced plant defence genes effective against *P. nicotianae* and were also mycoparasites. Also of interest is that a zoospore suspension of *P. cryptogea* applied to leaves of tomato induced systemic resistance against *F. oxysporum* (Attitalla et al. 2001). Microbially induced resistance in avocados against *P. cinnamomi* is unknown, but research to identify such soil microbes appears attractive. In order to be practical, induced defence throughout the root system would need to occur in response to an application of an organism to the foliage. This simplified delivery system could result in better contact between the organism and the host tissue than in soil applications, as the biocontrol agent would face less competition on the foliage than in the soil. It would also be interesting to test whether a killed suspension of *P. cinnamomi* mycelium and zoospores would induce systemic resistance if applied to the leaves of avocado. However, several aspects concerning this strategy must be resolved before its real value can be determined. Resident microbes may result in plants in the field already having a level of resistance to some pathogens, and applying additional microbial treatments may make little difference. Moreover, the cost to plant metabolism of maintaining a high induction level without a pathogen may reduce productivity (Walters et al. 2013).

Agricultural practices affecting disease suppression and beneficial soil microbes

Any amendment to soil, including organic substrates, fertilizers and pesticides, will affect its chemical and physical properties and thus directly or indirectly, affect the microbial communities composition and activity.

Organic soil additives

Suppressive soils from natural environments are generally high in organic matter, and raising the organic content in agricultural soils is one way of improving their general disease suppressiveness (Vida et al. 2020). The commonly used organic inputs in avocado orchards are composted animal manures (sheep, cow, chicken) (Ramírez-Gil and Morales-Osorio 2020; Carreon-Abud et al. 2015), almond shell mulch, vegetable compost, blood meal (Bonilla et al. 2012), wood mulch (Mohale et al. 2022) and biochar (Zwart and Kim 2012). The 'Ashburner System' of *Phytophthora* control involves several cycles of incorporation of green manure crops and application of chicken manure and NPK fertilizer to the soil before planting avocado, and after planting, maintaining the high soil organic matter by retention of litter and further application of composts (Pegg 1977). The degree of disease suppression achieved using an organic amendment is a combination of the physical and chemical properties of the compost and the soil and changes in the abundance, composition and metabolism of the soil microbes. A three-way interaction between compost microbiota (composition, diversity and functionality), pathogens and plants lead to a new equilibrium (Hardy and Sivasithamparam 1995; Aviles et al. 2011; Bonanomi et al. 2010).

Disease suppression resulting from adding organic materials may result from a combination of increased plant vigour and suppression of pathogens. Plant growth may be improved by the organic material buffering changes in moisture content, the increased microbial activity resulting in greater availability of nutrients, higher levels of nitrogen fixation, and microbial production of plant growth hormones and siderophores (Zhang et al. 1998; Hoitink and Boehm 1999; Van Wees et al. 2008).

The complexity of the possible impacts of an organic amendment is illustrated by the results of the addition of biochar (Lehmann et al. 2011), the application of which decreases root damage in oak and maple (Zwart and Kim 2012). Biochar has been shown to enhance plant growth-promoting microorganisms (Graber et al. 2010; Kolton et al. 2011) and arbuscular mycorrhizal fungi (Warnock et al. 2007) and improve the growth and yield of avocado (Crowley 2012; Jones et al. 2012). Biochar makes waterlogged soils less conducive for *Phytophthora* by increasing water infiltration and improving aeration, increasing the microbial biomass and changing the balance to one dominated by bacteria (Jones et al. 2012), alters the functions of microbial communities (Bonanomi et al. 2015) and results in disease suppression (Lehmann et al. 2011; Thies et al. 2015).

Volatile organic compounds originating from metabolism of soil microbes or compost can beneficially alter the soil microbial population (Kasuya et al. 2006; Klein et al. 2007). The degradation of crop residues or seed meal from some *Brassica* species releases volatile toxic chemicals, mainly glucosinolates and isothiocyanates (Neubauer et al. 2014; Fourie et al. 2016), capable of inhibiting mycelial growth, decreasing sporangial production and chlamydospore viability. *Brassica* residues reduced hyphal growth of *P. cinnamomi* in vitro and inoculum levels in pot soils for up to 9 days. When *Brassica* was applied as a pre-planting soil fumigation technique in the field, *P. cinnamomi* infection of *Leucadendron* was reduced, but chemical fumigation was more effective (Dunne et al. 2003a, b). The effect of *Brassica* residues has also been observed for *P. cinnamomi* on lupin and oak (Rios et al. 2017), P. *nicotianae* on tobacco, and *P. capsici* on squash (Ji et al. 2012; Morales-Rodriguez et al. 2014) The possibility of using *Brassica* residue for controlling *P. cinnamomi* in avocados is being investigated (Avocados Australia 2021), and it is also being considered as a means of reducing the population of resident soil microbes before the introduction of suppressive organisms such as *Trichoderma* (*Trichoderma* is resistant to the volatiles) (Mazzola and Freilich 2017).

Beneficial organisms may be introduced to the soil in the compost itself, or the changed physical conditions induced by the organic additive may enhance the relative abundance of beneficial species already present in the soil. Composted eucalyptus bark and organic mulch used in avocado orchards contain many actinomycetes antagonistic to *P. cinnamomi* (Hardy and Sivasithamparam 1995; You et al. 1996). Although composts may increase microbial abundance and activity overall and result in increased general suppressiveness, there is also frequently an increase in microbes known to be suppressive of a specific pathogen such as *Phytophthora*, i.e. the bacteria *Pseudomonas, Streptomyces Bacillus, Paenibacillus* and *Enterobacter*, and the fungi *Trichoderma* and *Penicillium* (Gomez Exposito et al. 2017).

Soils naturally suppressive to *Phytophthora* are high in calcium (Broadbent and Baker 1974) and soil dressings of calcium, gypsum, or limestone are known to suppress *Phytophthora* in woody tree species. Calcium application has proven effective for avocado (Messenger et al. 1997; Silva et al. 2016) as well as for jarrah (Khdiar et al. 2022), citrus (Campanella et al. 2002), oak (Serrano et al. 2012), pistachio (Mostowfizadeh-Ghalamfarsa et al. 2018), *Banksia* (Stasikowski et al. 2014; Khdiar et al. 2022) and blueberries (Yeo 2014). Most of these studies were glasshouse trials, but the work on blueberry and avocado includes field observations. A calcium chelate was as effective as phosphite in controlling *P. cinnamomi* (Khdiar et al. 2022). Calcium reduces sporangial production and zoospore motility, induces premature encystment in the pathogen, and reduces plant root exudates that attract the zoospores (Messenger et al. 2000a, b). Stasikowski et al. (2014) showed that externally supplied calcium disrupts calcium signalling pathways in *Phytophthora*, reducing its pathogenicity and that when calcium was applied to soil, it enhanced the protective effect of spraying with phosphite. There is no information on the effect of calcium on beneficial microbes in avocado orchard soils, but it has been shown to increase populations of suppressive organisms in other crops (e.g. peanut) (Zhang et al. 2021).

Application of silicon to the soil reduces the severity of a number of diseases in several species, including *P. cinnamomi* root rot of avocado, ink disease of chestnut seedlings (Pozza et al. 2015; Carneiro-Carvalho et al. 2017; Dann and Le 2017; Farooq et al. 2022a; Bekker et al. 2006, 2007) and *P. sojae* root rot of soybean (Rasoolizadeh et al. 2018, 2020). Silicon also controls several rice leaf pathogens as effectively as fungicides (Tubana et al. 2016). Silicon inhibits *Phytophthora* mycelial growth in vitro, although the high concentration required would be unrealistic for field applications (Carneiro-Carvalho et al. 2017; Bekker et al. 2006). Silicon increases root growth and production of phenolics in avocados (Anderson et al. 2004; Bekker et al. 2007, 2014) and in other species, it stimulates several plant metabolic processes related to disease suppression. These include the host defence response (Liang et al. 2007), enzymatic activity, hormone release and synthesis of antimicrobial compounds (Fauteux et al. 2005; Ahammed and Yang 2021), accumulation of flavonoids, phenols and lignin in root tissues (Fortunato et al. 2015), antioxidant enzyme activity (Carneiro-Carvalho et al. 2020) and the formation of physical barriers in plant cell walls (Fawe et al. 2001). Finally, it has an impact through changes in the soil microbiome. In the rhizosphere of *P. cinnamomi* infested avocado plants treated with a silica-based mulch, there was an increase in the proportion of Actinobacteria and Chloroflexi, phyla known to include many species that suppress *Phytophthora* (Farooq et al. 2022b). Application of a silica-based mulch may be cheaper than multiple sprays of phosphite each year. For avocados growing in Queensland, the application of 2 tonnes per hectare of silicate-based mulch effectively controlled Phytophthora root rot for at least ten months, but the total longevity of the effect was not reported (Dann and Le 2017). Bekker et al. (2014) also found that soil drenches of potassium silicate significantly improved the health of infected avocado trees, but three drenches in each growing season were required. The application of silicon-based nanoparticles also appears to be a promising line of research (Rajput et al. 2021).

Herbicides and pesticides

Many agricultural chemicals used for pest and disease control eventually end up in the soil, where they affect the composition and metabolic activity of the microbiome, usually detrimentally (Hussain et al. 2009; Lo 2010; Floch et al. 2011; Munoz-Leoz et al. 2011; Kaur and Garg 2014). The main chemicals commonly used in avocado orchards are glyphosate for weed control, phosphite, and metalaxyl to suppress Phytophthora root rot. Although not soil amendments, it is appropriate to consider these treatments here as they may cause changes to the soil microbiome.

The effect of phosphite on soil organisms is multi-pronged. A direct impact on *P. cinnamomi* and non-target organisms is possible as the chemical inhibits several *Phytophthora* species and other oomycetes (*Peronospora, Plasmospora* and *Pythium*), some fungal species (e.g. *Fusarium, Armillaria, Puccinia, Ralstonia*and *Phakospora*) and some bacteria (Thao and Yamakawa 2009; Gill et al. 2018). Phosphite can be metabolised as a source of phosphorous by some bacteria and fungi, which may enhance their growth. Knowledge of which soil organisms have this capability is sparse and not well substantiated, but they include *Pseudomonas* and *Rhizobium*, which are known to be suppressive to *Phytophthora* (McDonald et al. 2001; Achary et al. 2017). Phosphite mainly reduces *Phytophthora* infection by stimulating the host plant's defence system, but concentrations in root tips may be sufficiently high to directly affect the pathogen (Guest and Grant 1991; Van den Berg et al. 2021). Changes in plant metabolism cause changes in root exudates (e.g. Kremer et al. 2005). Phosphite treatment likely changes root exudates, affecting the soil microbiome. In tomatoes, root exudates are altered by *Trichoderma atroviride*, stimulating this fungus's growth and inhibiting *P. cinnamomi* (Macías-Rodríguez et al. 2018). It would be interesting to know if avocado root exudates change following the application of phosphite and, if so, the impact on the soil microbiome. Farooq et al. (2022b) found that applying phosphite spray to avocado leaves increased the overall abundance of soil bacteria in the rhizosphere but did not change their diversity or the relative abundance of the different phyla. In contrast, metalaxyl and related products and their residues are generally deleterious to microbial communities as they reduce microbial numbers and enzymatic activity and suppress groups, including beneficial organisms such as the Actinomycetes well as the target pathogen (Demanou et al. 2004; Sukul 2006).

The herbicide glyphosate may have positive or negative effects on the soil microbe mass and respiration depending on the rate of application and soil conditions (Haney et al. 2000). Soil fungi metabolise it (Lane et al. 2012) and this may increase the abundance of saprophytic fungi,*Fusarium* and *Pythium* (Meriles et al. 2006; Schlatter et al. 2017), but it has not been reported to affect *Phytophthora* directly. Like phosphite, it, too, may indirectly affect the soil microbiome by changing root exudates and increasing the mass of necrotic root material in the soil (Kremer et al. 2005). Farooq et al. (2022a) noted that glyphosate applied to weeds in potted avocados reduced avocado shoot and root dry weights and suggested that repetitive spraying of glyphosate in the field may exacerbate the effect of the *P. cinnamomi*.

Extension of results from in vitro to the glasshouse and from the glasshouse to the field

Treating soil with organic mulches or calcium has successfully reduced the Phytophthora root rot of avocados in the field, and there is one field study of the successful use of a silicon-based mineral mulch. However, despite the wide range of potential biocontrol species for avocados (Table 1), there are few examples in the scientific literature of successful biocontrol in the field. Initial evaluation of potential suppressive microbes is usually done in vitro as this is a quick, economical way of screening many microbes before selecting a few for testing in pot trials. Such studies are valuable to identify antagonists that owe their suppressive abilities to antibiosis resulting from soluble or volatile chemicals, and microscopic observations may also detect mycoparasitism. However, in vitro results may not reflect the full range of interactions that will occur in pot trials or in the field where the conditions of temperature, nutrient availability and population density are very different, and interactions with competing organisms may affect metabolism. Also, when assessing oomycetes in pot trials, it is usual to include a period of flooding to stimulate zoospore production and movement, but if not carefully controlled, flooded soil can become anoxic and affect the health of host roots (Davison and Hardy 2022). Additionally, an organism may lose the ability to suppress *Phytophthora* during the repetitive subcultures required to obtain the quantity of inoculum necessary for large-scale trials. This happened in the case of the suppressive ability of *Burkholderia gladioli* against *Pythium ultimum* (Bae et al. 2007). Depending on in vitro screening also means that species that have a mechanism of action effective in the field but not in vitro will be missed (Carrion et al. 2018). Testing control of the pathogen using culture filtrates in pot trials is common but gives little more information than in vitro trials and provides no insight into whether the microbe can compete in soil and produce sufficient levels of suppressive chemicals to inhibit *P. cinnamomi* in the field. It may lead to identifying compounds that might be formulated as fungicides.

Establishing trials in the field exposes the control organisms to different conditions than those experienced in a glasshouse pot trial (Forero et al. 2019; Johnson et al. 2003; Heinze et al. 2016; Howard et al. 2017). In the glasshouse, controlled temperatures, fertilisation and watering provide different (usually less stressful) conditions for the plant and the soil microbes compared to the field. This may result in differences in plant morphology and physiology in the glasshouse and the field (Poorter et al. 2016) and impact the metabolism of the microbes. For example, increased fertilization and water availability can cause some arbuscular fungi to become parasitic (Johnson et al. 2003; Schmidt et al. 2011). The restricted growing space and the time a tree species can be realistically grown under glasshouse conditions also affect the results. Under glasshouse conditions, infected plants are often harvested two weeks or so after infection to assess the extent of root damage before the roots disintegrate (Davison and Hardy 2022) and such trials do not measure the organism(s) ability to survive in the field in the longer term. Experiments may use field soil in pots to simulate field conditions as closely as possible, but plant growth in unaltered field soil in pots is not usually possible. The disturbance during collection destroys soil structure and results in a poorly draining medium, and it is usually necessary for field soil to be mixed with another medium such as sand, perlite or potting mix to increase porosity and provide a substrate suitable for plant growth in pots. In an orchard, the volume of soil that a biocontrol organism must reach vastly differs from that in a pot. Avocado has a shallow root system, with 60% of the roots in the top 60 cm of soil (Salazar-Garcia and Cortés-Flores 1986), and should thus be more suitable for biological control of root disease than many other tree crops. However, there are few papers on avocado (or any tree crop) in which reports of a high level of success in the field have followed up promising results from soil additives in glasshouse trials.

Most publications on microbial suppression of *P. cinnamomi* (Table 1) give only data on in vitro studies. Fang and Tsao (1995b) reported a poor correlation between results from in vitro and pot trials. A good correlation between in vitro suppression and control of *P. cinnamomi* in pot trials was reported in four cases (Fang and Tsao 1995a; El-Tarabily et al. 1996; Hakizimana et al. 2011; Andrade-Hoyos et al. 2020). There are three studies involving field trials (Table 1). Of these, only the South African work included comparisons of effects in vitro, pot trials and the field, but the data provided do not allow comparison of the same suppressive species in all three environments. Pot trials showed that the selected bacterial species for avocado were not as effective as the fungi for suppressing *Phytophthora*. *Aspergillus candidus* and *Trichoderma* were more advantageous in the field than *Paecilomyces lilacinus* (Duvenhage 1999). The question arises as to why so many in vitro results have not been tested further in the glasshouse and why there is so little information on field trials using experimental microbes or commercial products. Is this because of the cost, difficulty and time required to conduct these experiments or because negative results, for some reason, have not reached the scientific literature? This is an area where the publication of negative or positive results is badly needed to guide further research.

Collinge et al. (2022) and Whipps and Lumsden (2001) review the development and success of commercial microbial products for plant disease control in general and list several products that have enjoyed commercial success. Whipps and Lumsden (2001) suggest that the legislative requirements for registration of a new pesticide are so onerous that some products containing disease-suppressive microbes are marketed as growth promotors or fertilizers rather than fungicides. The few products listed against *Phytophthora* species have been applied in annual crops, and none are available for Phytophthora root rot in avocados. The high cost of developing commercial products and delivery systems and the limited target may result in potentially effective microbes not being tested further for commercial use. This will not change until the market drivers change; climate change might result in the disease becoming more severe and widespread, demand for organic produce may increase, government legislation may demand less use of chemical pesticides, or legislation concerning the release of a biopesticide simplified.

Future directions and research gaps

The complexity of the interactions resulting from using soil additives to control Phytophthora root rot in avocados is illustrated in Fig. 1. Many impacts or mechanisms require confirmation as they have only been shown in vitro, in other host species, or other pathogens (Fig. 1). A fuller understanding of the effects of perturbations in soil ecology following the addition of soil additives will enable better design of beneficial communities of microbes. Some research gaps are outlined below:

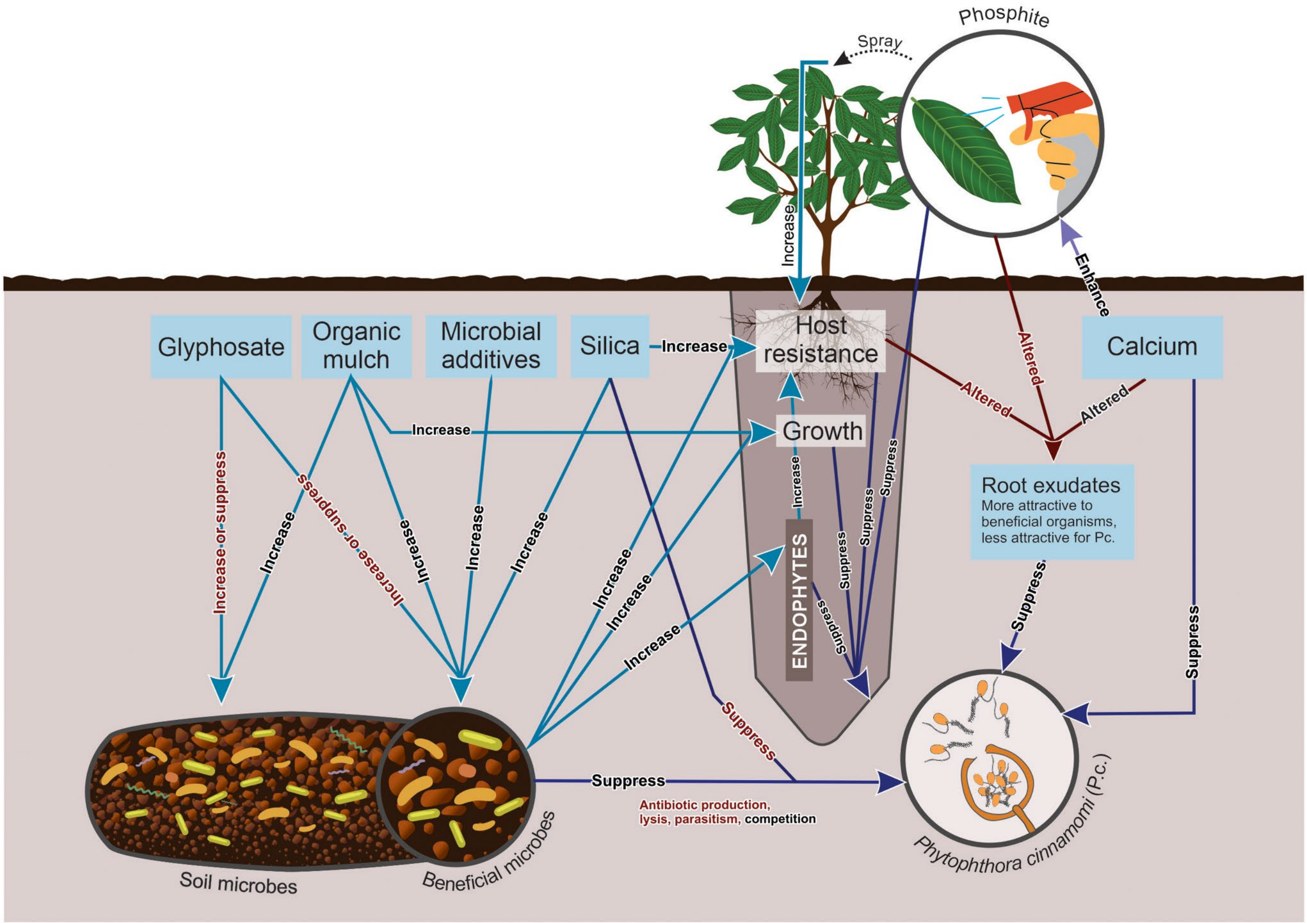

Fig. 1 Interaction between soil additives, soil microbes, *Phytophthora cinnamomi* and the avocado root (in grey). Proven effects or mechanisms are indicated by black labels and those assumed as they are known only from in vitro studies or work on other species by red labels

1. The most promising additive, and one that may complement current disease control measures, is silicon. More information is needed regarding the rate and timing of silica applications and tests in different soil types and climatic conditions.
2. It has become apparent that for tree crops, applying a single microbial species, no matter how effective in vitro, is rarely effective in the field (Cazorla and Mercado-Blanco 2016). However, past research has identified several species that might be used effectively in combinations. The use of both a bacterium and a fungus gave more suppression of *P. cinnamomi* in avocado and *Banksia grandis* than either of the organisms used separately (El-Tarabily et al. 1996; Hakizimana et al. 2011), while two strains of *Bacillus amyloliquefaciens* gave better control of *P. capsici* in *Capsicum annuum* than either strain separately (Yang et al. 2015). The use of species consortia with several different modes of action is being investigated to establish synthetic communities of suppressive organisms for various diseases (Mazzola and Freilich 2017; Gomez Exposito et al. 2017). Members of these consortia also need to be compatible and able to thrive in the ecological parameters of the orchard soil. This is a complex task, but it will provide the best chance of biocontrol of *P. cinnamomi* in avocados.
3. Further investigation is needed into whether biocontrol microbes lose their suppressive traits when repeatedly sub-cultured and, if so, how culture methods can be modified to reduce or eliminate this problem. Regardless of whether a single organism or a group is being utilized, it is essential to know that the suppressive capabilities are expressed at the time of application to the soil. Confirmation of suppressive compounds being produced at inhibitory levels in soil, as distinct from in vitro, is also needed.
4. When the new ground is being prepared, or an infected site is cleared for replanting, *Phytophthora* in the soil can be reduced or eliminated by solarization (Lopez-Herrera et al. 1997), treatment with brassica residues (Fourie et al. 2016) or by removing large woody residue and all living plant roots (including annual weeds)

for 2–3 years (Dunstan et al. 2020),. These treatments may reduce the abundance in the entire microbiome and thus facilitate the establishment of populations of the desired suppressive organisms. However, as Mazzola and Freilich (2017) point out, solarization and brassica treatments may also suppress resident beneficial microbes or increase the abundance of a pathogen other than *Phytophthora*. A study of the changes in the total microbiome due to these elimination/suppression methods would be valuable, as well as information on the population changes following the addition of suppressive microbes.

5. While applying beneficial organisms to nursery stock is relatively straightforward, methods to ensure the persistence of these organisms once plants are transferred to the field may require some manipulation of the established resident microbes using the above techniques. The best methods of application of suppressive microbes to established trees need to be developed. Thus far, irrigation with a microbial solution has been widely used (e.g., (Yang et al. 2001) but some type of soil injection may also be appropriate, and provision of a food source (as used by Fang and Tsao 1995a in the glasshouse) may also increase survival in the field.
6. Further attention should be given to the best way to introduce endophytes, as many suppressive organisms are endophytes (Table 1). The endophytic environment in an avocado root should be more similar between plants growing in different soils and climatic conditions than in the surrounding rhizosphere or soil environments. Also, the diversity and abundance of microbes in the avocado endosphere are much lower than in the rhizosphere (Farooq et al. 2022b). Endophytes may be effective over a broader range of growing regions than free-living microbes. It may be easier for a suppressive microbe to establish an effective population in the endosphere than in the rhizosphere, where there is more competition for nutrients and ecological niches. Inoculating endophyte-free tissue cultured plantlets of avocado rootstock would be ideal for establishing a community of the desired organisms (Hakizimana et al. 2011). However, experiments are needed to determine compatible mixes of endophytes that would confer disease suppression and whether they survive the competition from organisms introduced by grafting and planting to the field. Their distribution in the root system as the plant matures and their persistence over time must also be investigated. Molecular techniques are available to study fluctuations of bacterial density populations and the relative abundance of the component taxa under different conditions. Endophytes can be introduced into seedlings through spraying leaves, but it is unknown whether spraying endophytes onto the foliage of mature trees results in the successful colonization of root endospheres.
7. As many biocontrol agents are effective against more than one pathogen species, tests should be conducted to determine whether the organisms suppressing *P. cinnamomi* also suppress other avocado diseases such as white rot, Verticillium wilt or Rhizoctonia root rot. Conversely, the microorganisms that suppress other *Phytophthora* species are frequently in the same genera as those that suppress *P. cinnamomi*, so they may also provide another source of potential suppressors.

Conclusions

Current practices by avocado orchardists to suppress Phytophthora root rot through manipulating the soil's physical and biological properties have been partially successful, but orchardists still rely on heavily frequent applications of phosphite, a compound to which the pathogen is gradually developing resistance. The application of silicon may replace the necessity for some or all phosphite sprays during a year, thus delaying the development of pathogen resistance. It has rarely been possible to induce a specific suppressive soil by applying one or a few suppressive microbes, but this research has provided knowledge of many suppressive organisms. These known and yet-to-be-discovered organisms hold the potential to establish artificial microbial ecosystems that can naturally control the disease. Additionally, exploring the manipulation of the endophytic microbiome as a means to suppress *P. cinnamomi* should be pursued. While promising results may arise from laboratory and greenhouse experiments, it is crucial to conduct field trials and publish the outcomes, regardless of whether they are positive or negative. Although effectively utilizing microbes to suppress Phytophthora root rot in avocados still requires further development, the potential benefits are substantial. The availability of advanced tools to assess changes in the entire soil microbiome will facilitate progress in this area.

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Data availability The data are available if required from the corresponding author.

Code availability R statistical software was used for data analysis, and code is available if required.

Declarations

Ethical Statement This manuscript did not involve any work/study with human participants/animals performed by any of the authors.

Consent to participate All Authors agreed to the submission of this manuscript.

Conflict of interest The authors declare that they have no conflicts of interest in the submitted paper.

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