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BIOLOGY, ECOLOGY AND INTEGRATED MANAGEMENT OF AVOCADO ROOT ROT (*PHYTOPHTHORA CINNAMOMI***) IN ETHIOPIA: A REVIEW**

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A R T I C L E I N F O A B S T R A C T

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Avocado is an economically important crop in Ethiopia, yet its production and productivity are significantly impacted by both biotic and abiotic factors. Among the biotic threats, avocado root rot caused by *Phytophthora cinnamomi* stands out as a particularly destructive pathogen, inflicting considerable damage to avocado plants. This paper reviews integrated pest management strategies for combating avocado root rot in Ethiopia. *P. cinnamomi* thrives in warm, moist conditions, with damage intensifying during the summer when plants are stressed by drought. Locally, the pathogen can spread through soil splash, wind-blown debris, and water runoff. Effective management involves using soil amendments such as organic mulches and gypsum to improve soil structure and drainage, reduce salt levels, and enhance the soil's natural resistance to the pathogen. Comprehensive control measures are essential for managing avocado root rot, including selecting diseasefree sites and nursery plants, applying soil amendments, ensuring proper irrigation, using resistant varieties, and adopting suitable cultural practices. Integrated Pest Management, which incorporates multiple pest control strategies, is critical for minimizing damage and effectively managing avocado root rot. Currently, local landrace avocado varieties in Ethiopia show no resistance to *P. cinnamomi*. Therefore, it is crucial to screen existing local landraces and replace them with resistant varieties to achieve higher yields and better quality.

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INTRODUCTION

The avocado (*Persea americana*) is native to Central America and the West Indies and was introduced to Florida, California, and Hawaii in the early 1800s. It is now cultivated worldwide in regions with suitable growing conditions. Avocados belong to the Lauraceae family, which includes related species such as camphor, sassafras, cinnamon, and laurels. The avocado tree is evergreen, although it may experience significant leaf fall during heavy blossoming or when affected by root rot. Its growth habit ranges from tall and upright to wellshaped and spreading.

Avocado fruit exhibits considerable variation in size, shape, color, texture, and flavor. The edible portion, the flesh between the seed and skin, ranges from cream to yellowish green and should have the consistency of soft butter when ripe. The fruit contains a single seed and is unique in that it does not ripen until harvested, allowing it to remain on the tree for some time after reaching maturity, depending on the variety. Avocados typically

contain between 5% and 40% oil, with the percentage varying by variety, growing area, and seasonal conditions.

In Ethiopia, there is a potential irrigable area of 3.5 million hectares, with a net irrigation area of about 1.61 million hectares, though only 4.6% of this is currently utilized (Haile et al., 2015). Fruits, including bananas, citrus, mangoes, avocados, papayas, and grapefruits, are significant both for domestic consumption and for export. Ethiopia's international involvement in horticultural trade and production is growing at a rate of 7% per year, enhancing its competitive edge in the export market (Berhanu and Dawit Alem, 2013). Since its introduction in 1938 by private orchardists in Hirna and Wondo Genet, avocado production has expanded, and Ethiopia now ranks as the 10th largest producer and 6th largest consumer globally (Faris, 2016). Today, approximately 1,149,074 farmers cultivate over 30,587.70 hectares of avocado land, producing 2,453,356.30 quintals (Jalata, 2021). Despite the favorable agro-ecological conditions for avocado cultivation, production in Ethiopia faces several constraints. Major challenges include root rot disease and the lack of resistant varieties. A study by Garedew and Tsegaye (2011) in the Mana district of the Jimma zone highlighted that avocado production is significantly hindered by these issues and inadequate agronomic practices.

Avocado root rot, caused by the highly destructive pathogen *Phytophthora cinnamomi*, represents a severe threat to global agriculture and ecosystems. This pathogen affects nearly 5,000 plant species (Cahill et al., 2008; Jung et al., 2013) and has caused extensive economic losses across agriculture, forestry, and horticulture, while also harming natural ecosystems and biodiversity. Its impact is evident in chestnut and holm oak forests in Europe (Sghaier-Hammami et al., 2013; Serrazina et al., 2015), avocado and macadamia orchards worldwide (Reeksting et al., 2016; Akinsanmi et al., 2017), and natural vegetation in Australia (Cahill et al., 2008; Jung et al., 2013). In Western Australia, the pathogen threatens about 4,000 native species, nearly half of the local flora (Shearer et al., 2004).

In Ethiopia, the disease has considerable economic consequences. It was first identified in avocado orchards at the Jimma Research Centre (JARC) in the early 1990s. Since then, surveys have confirmed its widespread presence across the Jimma and Iluababor zones in southwestern Ethiopia, resulting in significant crop damage. For example, the coffee diversification initiative at the Limmu Coffee Plantation Enterprise experienced a 74% loss of avocado trees across 44 hectares on three farms due to root rot (Table 1).

Currently, there are no avocado varieties in Ethiopia resistant to *Phytophthora cinnamomi*; only tolerant varieties are available. To mitigate the damage, implementing Integrated Pest Management (IPM) strategies is essential. IPM involves combining various pest control methods to enhance production while ensuring environmental and economic sustainability. This paper reviews IPM strategies for managing avocado root rot in Ethiopia.

Table 1. Incidence of avocado root rot in Jimma and Keffa Zones**.**

Zone	District	Area Planted (ha)	Crop loss (ha)	% loss	Source of plant material
limma	Suntu	∼	ل. 1	75%	JARC
Keffa	Gojeb	30	30	100%	JARC
limma	Cheleleki	1 2Λ	6.08	49%	IARC

Source: JARC crop protection progress report 2010.

PRODUCTION STATUS OF AVOCADO IN ETHIOPIA

Avocado production in Ethiopia primarily caters to the domestic market, which is characterized by low farm gate prices. This situation, along with limited technical expertise in production, has impeded investment in seedling and fruit production. According to the 2021 Meher season data from the Central Statistical Agency (CSA), avocado cultivation has been on the rise over the past five years (Table 2). In the 2016-2017 production

years, Ethiopia produced 649,821 quintals of avocados. By the 2020-2021 production years, production had increased to 2,453,356.30 quintals. The annual production growth rates for avocados were 20%, 25.3%, 4.12%, 23.2%, and 134% for the years 2016-17, 2017- 18, 2018-19, 2019-20, and 2020-21, respectively. The FAO reported in 2022 that Ethiopia produced 245,336 metric tons of avocados from an estimated area of 30,587.70 hectares, with a yield of 80.2 quintals per hectare in 2021. Despite these figures, current acreage, production levels, and productivity remain well below the country's potential. The data reveal a significant yield gap compared to global averages, underscoring the need for enhancements across all production aspects. Ethiopia's current landrace varieties exhibit low yield potential and no resistance to *P. cinnamomi*. To address this gap, there is an urgent need to replace these varieties with ones that are resistant to *P. cinnamomi* and capable of delivering higher yields and improved quality.

Table 2. Avocado production status in Ethiopia.

Year	Area coverage in ha	Production (Qt)			
2016-17	17,834.60	649,821.00			
2017-18	18,021.13	814,318.00			
2018-19	19,758.75	847,936.48			
2019-20	20,875.80	1,044,919.20			
2020-21	30,587.70	2,453,356.30			
Source: (CSA, 2019, Ababa, 2018, Jalata, 2021).					

AVOCADO ROOT AND ITS LOSS HISTORY IN ETHIOPIA

Avocado root rot, caused by *P. cinnamomi*, was first identified in avocado orchards at JARC in the early 1990s. Subsequent surveys have confirmed its widespread distribution across all districts in the Jimma and Iluababor zones in southwestern Ethiopia, leading to significant crop damage. For instance, between 1990 and 2005, the disease resulted in the loss of three to five highly productive avocado orchards at the Jimma Agricultural Research Center, each containing 100-200 trees. Additionally, during a coffee diversification initiative, the Limmu Coffee Plantation Enterprise experienced a 74% loss of avocado trees across 44 hectares on three farms: Suntu, Gojeb, and Cheleleki due to root rot. Survey assessments conducted by the Jimma Agricultural Research Center further underscore the prevalence of the disease in major avocado-producing districts of the Jimma zone (Table 3).

BIOLOGY OF *P. CINNAMOMI*

Life cycle of *P. cinnamomi*

The life cycle of *P. cinnamomi* includes both asexual and sexual stages, depending on environmental conditions. In the asexual phase, the pathogen begins with the sporangium, a vegetative structure that germinates by producing a germ tube. Under optimal conditions; namely, free water and temperatures between 15-38°C,

the sporangium releases mobile, flagellated zoospores. These zoospores, which are short-lived vegetative spores, spread through soil, groundwater, and surface water to infect new hosts. They penetrate the roots of susceptible plants by forming a germ tube that develops into hyphae, which then spread throughout the plant. Zoospores can also move through standing water, where they are attracted to plant roots (Zentmeyer, 1994; Huberli, 2001).

Table 3. Incidence of avocado root rot in different districts of farmers' fields in the Jimma Zone.

District	Kebele (PA)	<u>No. of </u>	Incidence
Seka	Meti	2	20.8
	Atero Gafersa	4	18.2
	Shashamane	2	20.0
	Gibe Bosso	2	6.6
	Buvo kechama	4	9.6
	Kofe	8	18.5
	Sub total	22	15.6
Kersa	Tikur Balto	5	33.3
	Babo Sarte	3	11.6
	Marewa	3	20.0
	Badabuna	3	15.6
	Subtotal	14	20.1
Mana	Dawa	3	20.0
	Haro	2	0.0
	Bilida	4	1.3
	Sombo	7	12.0
	Eladalle	4	17.6
	Dovotoli	5	20.6
	Dovobikila	6	27.4
	Subtotal	31	14.1
	Total	67	

Source: JARC crop protection progress report 2009.

Under warm, moist conditions, the pathogen continues to reproduce asexually, with sporangia producing and releasing more zoospores. In harsh conditions such as hot, dry summers or droughts, the pathogen forms chlamydospores, which are thick-walled resting structures that can survive in the soil for several months. When favorable conditions return (warm and moist), these chlamydospores germinate to produce zoospores, which then spread through moving water to infect plant roots.

In the sexual phase, *P. cinnamomi* produces oospores through the mating of gametes known as oogonia and antheridia. The production of oospores depends on the presence of both mating types at the infection site. Oospores are long-lasting resting structures that can survive in soil for many years. They remain dormant

during unfavorable environmental conditions but germinate when conditions become favorable, producing mycelia. These mycelia then form sporangia and zoospores, continuing the pathogen's life cycle (Zentmeyer, 1994; Teferi and Ayano, 2016).

Figure 1. Life cycle of *P. cinnamomi*.

Symptoms of avocado root rot disease

The first signs of the disease are manifested in the tree canopy. The leaves are small, pale green, often wilted with brown tips, and drop readily. In contrast to *Phytophthora* stem canker, new growth is usually absent. Shoots die back from the tips, and eventually the tree is reduced to a bare framework of dying branches. Tree death may take from a few months to several years, depending on soil characteristics, cultural practices and environmental conditions. When declining trees flower, the trees may defoliate completely and may set a heavy crop of small fruit.

Ecology of the pathogen

P. cinnamomi thrives in moist soil conditions and warm temperatures, but the most severe damage often occurs during summer when plants are stressed by drought. According to Mbaka (2013) soil with poor drainage, high clay content, high water tables, hard pans, clay pans, or areas where water pools after irrigation or rainfall have historically been linked to severe *P. cinnamomi* infection.

Means of movement and dispersal

Locally, *P. cinnamomi* can spread naturally through soil splash, wind-blown soil or debris, and water movement in drainage or irrigation ditches. For more distant dissemination, the pathogen is most likely transported in contaminated soil or plant debris. Propagules can also be

carried on machinery used for cultivation or harvesting, and on seeds. In Australia, movement of contaminated road gravel has been known to initiate new epidemics (Weste, 1975). Additionally, contaminated soil associated with container-grown ornamentals can introduce the pathogen to previously disease-free areas, representing a significant pathway for international spread. Although avocado planting material such as scions and seeds should typically be disease-free, rootstock plants could potentially harbor the pathogen if they are traded in that form.

Figure 2. Avocado root rot disease symptom.

P. cinnamomi **infection strategies Active movement to a potential host**

The spread of *P. cinnamomi* can occur through both hyphal growth and the active movement of biflagellate zoospores. While hyphal growth may facilitate the pathogen's uphill movement (O'Gara et al., 2005); infection is typically initiated by the motile zoospores. The flagella of *Phytophthora* have the characteristic 9+2 microtubular structure found in eukaryotic flagella (Hardham, 1987), and the *P. cinnamomi* genome includes genes encoding eukaryotic flagellar proteins. Notably, genes such as dynein light chain 1 (PcDLC1) and radial spoke protein 6 (PcRSP6) have been identified and cloned (Narayan, 2004; Narayan et al., 2010). Their expression increases shortly after asexual sporulation begins, indicating their role in flagellar assembly during zoosporogenesis (Cope and Hardham, 1994). Silencing of the PcDLC1 homologue in *P. parasitica* (PnDLC1) results in zoospores lacking flagella, demonstrating that disrupting the production of this outer dynein arm component impedes flagellar assembly (Narayan et al., 2010).

Zoospore chemotaxis is crucial for initiating infection, and the *P. cinnamomi* genome contains homologues of three genes involved in this process in *P. infestans* and *P. sojae*: a G-protein α-subunit (GPA1), a GPA1-interacting protein (Hint1), and a G-protein-coupled receptor (GPCR) (GK4). Silencing these genes in *P. infestans* or *P. sojae* reduces zoospore motility duration before encystment and impairs chemotaxis, negative geotaxis, and auto-aggregation (Yang et al., 2013). In contrast, silencing of two other GPCRs, PsGPR11 and PsSAK1, in *P. sojae* does not affect zoospore chemotaxis but does induce encystment (Wang et al., 2010; Yang et al., 2013).

Attachment and protection at the plant surface

P. cinnamomi zoospores are attracted to the elongation zones of plant roots and often preferentially settle in the grooves above epidermal anticlinal walls (Robold and Hardham, 2005). At high densities, these zoospores can exhibit auto-aggregation, clustering at specific sites on the root surface, a process that involves both chemotaxis and bio-convection (Savory et al., 2014). Upon encystment, the zoospores attach to the root surface using a 250-kDa adhesion protein known as PcVsv1, which is stored in small vesicles located ventrally (Hardham and Gubler, 1990; Robold and Hardham, 2005). The expression of the PcVsv1 gene increases during asexual sporulation, coinciding with the appearance of these ventral vesicles. Homologues of the Vsv1 adhesin are present throughout the Oomycetes.

In *P. parasitica*, studies have identified a 12-kDa complement control protein secreted during zoospore encystment (Skalamera and Hardham, 2006). Both *P. parasitica* and *P. cinnamomi* genomes contain single Ccp genes, and the Ccp proteins are housed in an outer shell surrounding an inner core of Lpv glycoproteins within large peripheral vesicles (Gubler and Hardham, 1990; Hardham and Blackman, 2018). During encystment, the smaller Ccp proteins are secreted, while the larger 500- 600 kDa Lpv proteins are retained, illustrating selective protein secretion. Although multiple complement control domains in mammals are involved in cell adhesion, *Phytophthora* Ccp proteins, which have only a single complement control module, are unlikely to have an adhesive role. In *P. cinnamomi*, Lpv proteins seem to function as a protein reserve utilized during germling growth (Gubler and Hardham, 1990). DNA and RNA blots reveal three PcLpv genes that produce transcripts of 11-14 kb in size (Marshall et al., 2001). None of the *Phytophthora* genomes in FungiDB contain Lpv genes that produce transcripts of this length. Among the five predicted *P. cinnamomi* transcripts homologous to cloned partial Lpv genes, two of the largest have long undetermined nucleotide regions. Sequencing of cloned partial PcLpv genes has shown that the C-terminal half of Lpv proteins consists of 12-18 nearly identical 178 amino-acid repeats (Appelgryn, 2014), complicating the complete identification and sequencing of Lpv genes.

Plant penetration and colonization

Cyst germination and chemotropic growth in *P. cinnamomi* occur shortly after zoospore encystment, typically within 20-30 minutes. This process can happen in distilled water, suggesting that cyst germination may be an inherent, programmed response following encystment, even in the absence of external chemical signals. It is anticipated that signaling proteins play a crucial role in regulating gene expression, protein synthesis, and the transition from motility to secretion as the primary cellular activity. Research has shown that silencing GPCRs such as PiGK4 and PsGPR11 not only reduces zoospore motility but also impairs cyst germination, highlighting their involvement in these critical processes (Wang et al., 2010; Yang et al., 2013).

Cell wall-degrading enzymes (CWDEs)

Initial penetration and subsequent colonization of the plant are made possible by the action of a wide range of pathogen degradative enzymes that digest components of the plant cell wall. *Phytophthora* genomes contain large multigene families encoding CWDEs that contain one or more Carbohydrate-Active enzyme (CAZyme) modules (Larroque et al., 2012).

Hyphal growth

After penetrating the plant surface, *P. cinnamomi* hyphae grow both intracellularly and intercellularly through the root cortex and extend into the central vascular bundle. This growth leads to the blockage of the xylem by obstructing hyphae and the deposition of plant materials, which disrupts water transport from the roots to the shoots, resulting in water stress (Ruiz Gomez et al., 2015). The necrosis of infected fine feeder roots further exacerbates the issue, potentially causing rapid plant death (McConnell and Balci, 2015; Oßwald et al., 2014). *P. cinnamomi* hyphae, similar to other tipgrowing cells, extend through the fusion of small transport vesicles at the hyphal apex and the secretion of new membrane and wall material. Unlike many other fungi, *Phytophthora* and other Oomycetes possess cell walls based on a cellulosic framework rather than a chitinous one. Recent studies indicate that *P. cinnamomi* and related species within the *Phytophthora* and

Peronosporales orders have Type I cell walls, which are characterized by their cellulose content and the absence of N-acetylglucosamine (Melida et al., 2013).

FACTORS AFFECTING ROOT ROT

Temperature

The pathogen, *P. cinnamomi* thrives at soil temperatures above 10-12°C and in soil matric potentials greater than -0.9 MPa (Weste and Ruppin, 1977). Consequently, it is less problematic in arid regions or at high elevations where soil temperatures are too low, except in tropical areas. In contrast, higher soil temperatures and adequate moisture conditions favor pathogen activity. Seasonal variations in temperature and soil moisture contribute to increased disease potential during spring and autumn (Shea et al., 1980). Peak pathogen populations around susceptible plant roots are typically associated with summer and winter rainfall in warmer regions (Marks et al., 1975). *In vitro*, *P. cinnamomi* grows between 5°C and 35°C, with optimal growth occurring at temperatures between 25°C and 30°C (Phillips et al., 1985). Temperature also influences *in vivo* growth (Batini and Cameron, 1975). However, resistance in some host species can vary with temperature, meaning that lesion length and temperature may not always align with *in vitro* findings (Shearer et al., 1987).

Moisture

Free water is crucial for the production, dispersal, and germination of *P. cinnamomi* zoospores. While continuous saturation is ideal, periodic showers can provide enough free water in shallow drainage depressions to meet these needs. As soil dries, *P. cinnamomi* forms chlamydospores (Weste and Vithanage, 1978). In water-saturated soils, roots and collars are particularly vulnerable to damage by *P. cinnamomi* (Newhook and Podger, 1972). Epidemics of dieback caused by this pathogen have been linked to years with above-average winter rainfall. Soil dryness tends to inactivate most suppressive microorganisms before affecting *P. cinnamomi*. The lysis of microbial hyphae is most effective at field capacity, while suppression of mycelial growth and chlamydospore production occurs at soil matric potentials of -0.03 MPa and ceases at -0.3 MPa (Malajczuk and Theodorou, 1979; Mackay et al., 1985). Within the host plant, *P. cinnamomi* grows more rapidly in tissues with higher water potential, and lesion expansion is diminished in drought-stressed hosts. However, drought conditions may exacerbate secondary symptoms in the shoots.

Soil characteristics

Soil characteristics significantly influence the growth, reproduction, and inoculum potential of *P. cinnamomi*. Various soil properties can either promote or suppress the pathogen's activity.

Soil characteristics promoting *P. cinnamomi* **Soil texture and composition**

Gravels, sands, and lateritic soils, which are often infertile, low in organic content, and shallow with an impermeable clay pan, provide conditions conducive to disease. These soils often retain moisture, supporting the pathogen's growth.

Topography

Flat terrains or depressions where water accumulates create an ideal environment for *P. cinnamomi* proliferation. In these areas, the pathogen can thrive in water-saturated conditions, especially when the soil contains a dense mass of susceptible roots.

Soil moisture

High soil moisture, especially in shallow soils, can lead to an ideal environment for *P. cinnamomi* if accompanied by warm temperatures. Propagules can survive in soil clumps or root fragments unless the soil dries out completely (Old et al., 1984).

Soil characteristics suppressing *P. cinnamomi* **Soil texture and composition**

Red basaltic soils and red-brown earths, which are deep, well-aerated, and freely draining, are generally suppressive to *P. cinnamomi*. These soils contain high exchangeable cations, high organic components, and support a robust microbial population that may inhibit the pathogen (Broadbent and Baker, 1974; Halsall, 1978).

pH levels

While soil pH has some influence on pathogen activity, it is not a definitive suppressive factor in many cases. Soils with pH ranging from 5.0 to 7.0 are typically within the range where *P. cinnamomi* can thrive. Soils with pH levels outside this range, either more acidic ($pH \leq 4.0$) or more alkaline (pH \geq 8.0), may sometimes show increased suppression, but this correlation is weak (Ko and Shiroma 1989). Specific applications, such as the use of elemental sulfur to lower soil pH to 3.8, have shown effectiveness in controlling *P. cinnamomi* in some crops like pineapples (Pegg, 1977). However, such treatments are not practical for avocados, which have an optimal pH range of 5.0 to 5.5 and are intolerant of conditions below pH 5.0 (Wolstenholme, 2013).

Soil microbiota

Soils with high microbial populations often suppress *P. cinnamomi* through competitive exclusion or antagonistic interactions. Soils rich in beneficial microorganisms can outcompete or inhibit the pathogen's growth (Broadbent and Baker, 1974).

Overall, while soil characteristics like texture, drainage capacity, and microbial populations play significant roles in either supporting or suppressing *P. cinnamomi*, soil pH alone does not act as a primary causal factor in pathogen suppression. The interaction between various soil properties and environmental conditions determines the extent of *P. cinnamomi* activity and the overall disease risk.

Soil organic matter

High soil organic matter is frequently cited as a significant factor in suppressing *P. cinnamomi*, the pathogen responsible for avocado root rot. Several studies have highlighted the relationship between organic matter and disease suppression, suggesting that organic amendments can play a crucial role in managing this pathogen. Given below is the detailed look at how high soil organic matter contributes to the suppression of *P. cinnamomi*.

Key roles of organic matter in suppressing *P. cinnamomi*

Microbial activity

High soil organic matter enhances microbial activity, which can lead to competitive exclusion of *P. cinnamomi* and other pathogens. Organic matter provides a nutrient source for beneficial microbes, which may inhibit the growth of the pathogen either through direct antagonistic interactions or by outcompeting *P. cinnamomi* for resources.

Rhizosphere dynamics

In the rhizosphere (the soil region influenced by plant roots), increased organic matter promotes the proliferation of beneficial microbes that can antagonize *P. cinnamomi*. These beneficial microbes may produce antimicrobial compounds or enzymes that directly target the pathogen.

Types of organic matter

The type and quality of organic amendments used can significantly influence their effectiveness in suppressing *P. cinnamomi*. For instance, humic and fulvic acids, which are products of organic matter decomposition, can affect both soil microbes and plant responses. These substances may enhance plant resistance or directly influence the pathogen (Linderman, 1989; Ribeiro and Linderman, 1991). Various organic materials such as green manures (Baker, 1978), chicken manure (Ajwa and Tabatabai, 1994), sewage sludge (Brendecke et al., 1993), and bioenhanced mulches (Costa et al., 1996) have been shown to reduce disease incidence. The effectiveness of these amendments often depends on their composition and how they interact with soil and plant systems. Studies have demonstrated that adding organic matter to soil can correlate with reduced disease incidence. For example, Costa et al. (1996) found that increasing soil organic matter through mulch application was associated with a decrease in avocado seedling disease incidence. This suggests that organic matter not only improves soil health but also enhances the plant's ability to resist infection.

Soil structure and moisture

Organic matter improves soil structure, leading to better drainage and aeration. This can reduce conditions that are favorable for *P. cinnamomi* growth, such as waterlogged soils. Improved soil structure also enhances root health and reduces stress, making plants less susceptible to infection.

Nutrient dynamics

Organic matter can influence soil nutrient availability, which may affect both the host plant and the pathogen. Healthy, well-nourished plants are generally more resistant to diseases, including those caused by *P. cinnamomi*.

In general, high soil organic matter plays a multifaceted role in suppressing *P. cinnamomi*. It promotes the growth of beneficial microbes that antagonize the pathogen, improves soil structure and nutrient availability, and can directly or indirectly affect the pathogen and host plant interactions. The effectiveness of organic matter in disease suppression depends on its type, quality, and the specific soil and plant conditions. Enhanced microbial activity, improved soil health, and better plant resistance are key mechanisms through which organic amendments contribute to the control of *P. cinnamomi* and the reduction of avocado root rot.

Soil microorganism

Phytophthora species are highly affected by other soil microorganisms, which can be either stimulatory or antagonistic (Malajczuk et al., 1984). Broadbent and Baker (1974) found that the suppressive avocado soils they studied contained higher populations of bacteria, particularly *Bacillus* species, and actinomycetes. In other studies, the lysis of *P. cinnamomi* hyphae in soil has been

positively correlated with increases in microbial populations, including bacteria (Malajczuk et al., 1984). Malajczuk and McComb, (1979) isolated bacteria, actinomycetes, and fungi from both suppressive and conducive soils, as well as rhizosphere samples associated with the susceptible *Eucalyptus marginata* and the less susceptible *E. calophylla*. The highest percentages of antagonistic bacteria and actinomycetes were recorded in non-rhizosphere suppressive loam soil and in rhizosphere soil from *E. marginata* seedlings grown in suppressive loam soil.

Phytophthora spp. is antagonized in several ways by a variety of soil fungi. The most common forms of antagonism involve mycoparasitism and/or production of metabolites that inhibit growth or destroy *P. cinnamomi* propagules (Malajczuk et al., 1984). Ectomycorrhizal fungi may also contribute to the protection of susceptible plant roots from *P. cinnamomi* by: (i) forming a mantle that provides a physical barrier to penetration; (ii) producing antibiotics that inhibit growth and reproduction; (iii) utilizing surplus plant exudates that may act as biochemical signals to *P. cinnamomi* hyphae and zoospores; (iv) providing habitat for other antagonistic rhizosphere microorganisms; (v) improving plant vigor; and (vi) inducing the plant to produce compounds that protect it from infection (Borowicz, 2001). The fungi that form ectomycorrhizal associations with plant roots are usually Basidiomycetes (e.g. genera include: *Amanita*, *Boletus*, *Lactarius*, *Pisolithus*, *Rhizopogon*, *Russula*, *Suillus* and *Thelephora*) and to a lesser extent Ascomycetes, Zygomycetes and anamorphic fungi (Ogle and Brown, 1997). Several antagonistic fungal species are frequently associated with *P. cinnamomi* suppression. These include species in the genera *Penicillium*, *Trichoderma*, *Aspergillus* and, less frequently, *Myrothecium* and *Epicoccum*. Each of these produces metabolites that actively inhibit *P. cinnamomi in vitro* and presumably *in vivo* (Downer et al. 2001).

MANAGEMENT OF AVOCADO ROOT ROT DISEASE Sites selection and soil preparation

Planting an avocado orchard is a long-term investment and requires a high capital outlay in the initial stages. Soil should be prepared well in advance of planting. Severe *P. cinnamomi* is associated with soils that have poor internal drainage, are less than 3 feet deep, have hard pans, clay pans and high clay content. These soils are conducive to inoculum build-up and infection of roots, and should be avoided. Less hazardous soils with a

lay-loam texture and depth of 3-5 feet should be deep ripped and provision made for drainage. Saline soils and soils with high salinity potential should also be avoided since not only does salinity retard growth and reduce yield but it exacerbates avocado root rot (Zentmyer and Ohr, 1978; Menge and Marais, 2000). On sloped land, the construction of interception and diversion drainage ditches, or provision of water tight drainpipes which drain rain water away from the orchard, will help prevent the introduction of *P. cinnamomi* into lower lying orchards. In heavy clay soils, trees can be planted on mounds or ridges.

Soil amendments

Most soils in native habitats of avocados are high in organic matter, and the trees do best in soils with 8% or greater organic matter content. The application of amendments such as organic mulches and gypsum contribute to improving soil structure, thereby improving drainage, helping to remove salts from the soil, and have the added benefit of increasing the soil's suppressiveness to *P. cinnamomi*. The suppressive effect of calcium and organic matter was first discovered in Australia (Broadbent and Baker, 1974). The beneficial effects of organic mulch are thought to be due to the development of high populations of micro-organisms in the soil which are antagonistic to *P. cinnamomi*. Also, avocado roots do best in soils with oxygen content greater than 25% and porous mulches contain high levels of oxygen. Mulches placed in layers 4-6 inches thick under the canopies of the trees has been shown to suppress the pathogen and be beneficial to avocado trees in California (Marais et al, 2002). A study of the effects of calcium on *P. cinnamomi* was conducted in California soils by Messenger et al., (2000) who concluded that calcium primarily acted as a weak fungicide by reducing the size and number of sporangia produced by *P. cinnamomi.*

Disease free nursery trees

Preventing Phytophthora contamination is the basis for producing nursery stock free of Phytophthora and using clean stock eliminates a common pathway through which Phytophthora species are introduced into the field. Prevention is the basis for producing nursery plants that are free of root-infecting Phytophthora species. To manage Phytophthora and other pathogens in nurseries, Swiecki et al., (2018) advised "Don't fight 'em, eliminate 'em" This indicated that, Phytophthora diseases cannot develop if these pathogens are not present.

Irrigation and irrigation water

The avocado tree is extremely sensitive to water-logging due to the high oxygen requirement of its roots. Under such conditions, root growth ceases and the stage is set for largescale destruction of feeder roots. The use of tensiometers or other tools to schedule irrigation is advised. Water from deep wells is unlikely to be contaminated with *P. cinnamomi*, while water from reservoirs and canals can be a source of infection and should be treated with chlorine to eliminate inoculum. When an infection area is identified in an orchard, the diseased trees and the trees at the margins of the diseased area should be irrigated with caution, avoiding over-irrigation. Careful irrigation can retard the spread of the disease and often prolong the life of affected trees (Marais et al., 2002).

Orchard sanitation

Excluding *P. cinnamomi* from a clean avocado orchard is the most economical method of controlling the disease. Movement of soil and water from diseased orchards into healthy ones should be avoided at all costs. The fungus readily moves from orchard to orchard in moist soil on tools, vehicles, bins, ladders, shoes, domestic and wild animals, etc. Barriers in the form of fences and warning signs should be placed between uninfected and infected orchards. Boxes containing copper sulfate should be placed at the property entrance and all foot traffic should dust shoes before entering the grove. Shallow, chlorinated or copper sulfate-treated water baths may also be placed at the entrance to the property for vehicles to drive through when entering the premises. Shovels, soil augers and trowels should be dipped in 70% ethanol or rubbing alcohol before reuse. Always use disinfected equipment in healthy orchards after use in a diseased orchard. Severely affected trees should be removed (Zentmyer and Ohr, 1978; Menge and Marais, 2000).

Resistant rootstocks

A great deal of research has been conducted on detecting and developing resistant rootstocks, particularly in California, South Africa and Israel. Rootstocks such as Duke 7, Thomas, Barr Duke, Toro Canyon, and Merensky 2, exhibit a greater degree of tolerance to *P. cinnamomi* than traditional Topa Topa seedling rootstocks. Not all of these rootstocks yield as well as the traditional sensitive ones in non-infected groves. Trees on resistant rootstocks will survive under disease pressure when used in conjunction with the control measures mentioned above (Menge and Marais 2000; Bijzet and Sippel 2001). While disease-free clonal rootstocks have different levels of tolerance/resistance to PRR and may be

expensive to purchase, they can provide a degree of insurance against devastation by PRR.

Crop replacement

When disease pressure and contributing environmental factors result in economic loss, it may be necessary to remove avocado trees. All varieties of citrus, many deciduous fruit tree crops, macadamia, persimmon, berries, all types of vegetables, and most annual flower crops are not susceptible to PRR and can be planted in old avocado orchard soils (Ohr et al., 1994; Faber and Ohr, 1999).

Biological control

Broadbent and Baker (1974) maintain that high levels of active microorganisms can reduce avocado root rot. Since then many soil-borne microorganisms such as *Myrothecium roridum*, *Trichoderma harzianum*, *Epiccocum purpurascens*, *Catenaria anguillae*, *Humicola fuscoatra*, *Anguillospora pseudolongissma*, *Hypochytrium catenoides*, *Myrothecium verrucaria*, *Streptomyces griseoalbus*, *Micromonospora carbonacea*, *Streptomyces violascens* and *Ceraceomyces tessulatus* have been shown to be inhibitory to *P. cinnamomi* via competition, antibiosis or parasitism (Downer, 1998). Today there are several commercial biocontrol products available with *Trichoderma* or *Gliocladium* as the active biocontrol agent. However, these products are mostly experimental at this time. Evidence indicates these biocontrol microorganisms do not always survive when used in avocado groves. It may be that biocontrol microorganisms, such as these, may add little benefit if mulches with large populations of antagonistic microorganisms are already present. Research is continuing in the search for specific biocontrol microorganisms which target and kill *P. cinnamomi*. Another interesting biocontrol approach is the field production of antagonistic bacteria in field fermentors and their continuous application in irrigation water.

Chemical control

In the 1970s and 1980s, systemic fungicides with specific activity against species of Phytophthora and related fungi revolutionized control of diseases such as PRR. The first of these compounds were metalaxyl (Ridomil ®) and fosetyl Aluminum (Aliette) (Menge and Marais, 2000). The phosphonates, including fosetyl Al and its active breakdown product phosphorous acid and potassium phosphite, have been effective when applied as foliar sprays, trunk paints, trunk injection, or soil application. Trunk injection, first developed in South Africa, has given good results in several avocado producing countries (Wood, et al., 1987).

Table 4. Control of *Phytophthora* root rot by injecting fungicide.

^aAverage rating from 10 trees per treatment. Disease rating on a scale of 0-10, where 0=healthy and 10= dead.

SUMMARY AND CONCLUSION

Avocado root rot, caused by *Phytophthora cinnamomi*, is a highly destructive pathogen with a global presence and a host range of nearly 5,000 species. This pathogen thrives in moist, warm soil conditions, but its impact is most severe during summer when plants are under drought stress. *P. cinnamomi* spreads naturally through soil splash, wind-blown debris, and water runoff in drainage and irrigation systems. Its infection is influenced by temperature, soil moisture, soil characteristics, soil microorganisms, and organic matter. Free water is crucial for the production, dispersal, and germination of zoospores, although periodic rainfall can maintain sufficient moisture in shallow depressions. In dry conditions, the pathogen produces chlamydospores. Soils with high exchangeable cations, high organic content, and robust microbial populations, such as red basaltic soils and red-brown earths, tend to suppress *P. cinnamomi*.

To effectively manage avocado root rot, a comprehensive Integrated Pest Management approach is essential. Key strategies include selecting disease-free sites, managing avocado nurseries, applying appropriate soil amendments, using disease-free planting material, providing optimal irrigation, and adopting phytosanitary practices. Additionally, local landrace avocado varieties currently grown in Ethiopia are not resistant to *P. cinnamomi*. To address this issue, it is necessary to screen the available local landrace varieties and replace them with resistant varieties to achieve higher yields and better quality.

AUTHOR'S CONTRIBUTION

The author collected, sorted out, and arranged the literature into different sections, drew conclusions, made suggestions for future directions, and wrote and proofread the manuscript.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

REFERENCES

- Ababa, A., 2018. Ethiopia fresh fruits market update report. Gain Report Number: ET1827.
- Ajwa, H.A., Tabatabai, M.A., 1994. Decomposition of different organic materials in soils. Biology and Fertility of Soils 18, 175-182.
- Akinsanmi, O.A., Neal, J., Drenth, A., Topp, B., 2017. Characterization of accessions and species of Macadamia to stem infection by *Phytophthora cinnamomi*. Plant Pathology 66(2), 186-193.
- Appelgryn, E., 2014. Characterization of *Phytophthora cinnamomi* from avocado (Master's thesis, University of Pretoria (South Africa)).
- Baker, R.J., 1978. Issues in diallel analysis. Crop Science 18(4), 533-536.
- Batini, F.E., Cameron, J.N., 1975. The effects of temperature on the infection of New Zealand blue lupins by *Phytophthora cinnamomi*. W. Aust. For. Dept. Res. Pap. 25, 6.
- Berhanu, B.B., Dawit Alemu, D.A., 2013. The role of avocado production in coffee based farming systems of South Western Ethiopia: the case of Jimma Zone 86-95.
- Bijzet, Z., Sippel, A.D., 2001. Rootstocks. The cultivation of avocado. Institute for Tropical and Subtropical Crops ARC-LNR. Dynamic Ad, pp. 85-103.
- Borowicz, V.A., 2001. Do arbuscular mycorrhizal fungi alter plant–pathogen relations? Ecology 82(11), 3057-3068.
- Brendecke, J.W., Axelson, R.D., Pepper, I.L., 1993. Soil microbial activity as an indicator of soil fertility: long-term effects of municipal sewage sludge on an arid soil. Soil Biology and Biochemistry 25(6), 751-758.
- Broadbent, P., Baker, K.F., 1974. Behaviour of *Phytophthora cinnamomi* in soils suppressive and conducive to root rot. Australian Journal of Agricultural Research 25(1), 121-137.
- Cahill, D.M., Rookes, J.E., Wilson, B.A., Gibson, L., McDougall, K.L., 2008. *Phytophthora cinnamomi*

and Australia's biodiversity: impacts, predictions and progress towards control. Australian Journal of Botany 56(4), 279-310.

- Cope, M., Hardham, A.R., 1994. Synthesis and assembly of flagellar surface antigens during zoosporogenesis in *Phytophthora cinnamomi*. Protoplasma 180, 158-168.
- Costa, J.D.S., Menge, J.A., Casale, W.L., 1996. Investigations on some of the mechanisms by which bioenhanced mulches can suppress *Phytophthora* root rot of avocado. Microbiological Research 151(2), 183-192.
- CSA., 2019. Central Statistical Agency. Agricultural Sample Survey, 2018-19 Volume I: Report On Area and Production of Major Crops (Private peasant holdings, Meher season), Statistical Bulletin 589, Addis Ababa, pp.54.' http://www. csa.gov.et/survey-report/category/126-eth-agss-2009? Download=349: eth-agss-2009.
- Downer, A.J., 1998. Control of avocado root rot and *Phytophthora cinnamomi* Rands in mulched soils. University of California, Riverside 210.
- Downer, A.J., Menge, J.A., Pond, E., 2001. Association of cellulytic enzyme activities in eucalyptus mulches with biological control of *Phytophthora cinnamomi*. Phytopathology 91(9), 847-855.
- Faris, A., 2016. Review on avocado value chain in Ethiopia. Industrial Engineering Letters 6(3), 33-40.
- Garedew, W., Tsegaye, B., 2011. Trends of avocado (*Persea americana* M) production and its constraints in Mana Woreda, Jimma Zone: a potential crop for coffee diversification.
- Gubler, F., Hardham, A.R., 1990. Protein storage in large peripheral vesicles in *Phytophthora* zoospores and its breakdown after cyst germination. Experimental Mycology 14, 393-404.
- Haile, G.G., Kasa, A.K., 2015. Irrigation in Ethiopia: A review. Academia journal of Agricultural Research 3(10), 264-269.
- Halsall, D.M., 1978. Examination of a forest soil suppressive to *Phytophthora cinnamomi.* Microbial Ecology 360-363.
- Hardham, A., Gubler, F., 1990. Polarity of attachment of zoospores of a root pathogen and pre-alignment of the emerging germ tube*.* Cell Biology International Reports 14(11), 947-956.
- Hardham, A.R., 1987. Microtubules and the flagellar apparatus in zoospores and cysts of the fungus

Phytophthora cinnamomi. Protoplasma 137, 109- 124.

- Hardham, A.R., Blackman, L.M., 2018. *Phytophthora cinnamomi*. Molecular plant Pathology 19(2), 260- 285.
- Huberli, D., 2001. Phenotypic variation of two localized population of *Phytoptora cinnamomi* from Western Australia and how they impact on *Eucalyptus marginata* resistance. PhD. Dissertation, School of Biological Sciences and Biotecnology. Murdoch University, Perth, Western Australia.
- Jalata, Z., 2021. Current status, potentials and opportunities of avocado production as an alternative crop: The case of Ethiopia: A review. Agricultural Reviews 42(3), 336-341.
- Jung, T., Colquhoun, I. and Hardy, G., 2013. New insights into the survival strategy of the invasive soilborne pathogen *Phytophthora cinnamomi* in different natural ecosystems in Western Australia. Forest Pathology 43(4), 266-288.
- Ko, W.H., Shiroma, S.S., 1989. Distribution of *Phytophthora cinnamomi*‐supprcssive soil in nature. Journal of Phytopathology 127(1), 75-80.
- Larroque, M., Barriot, R., Bottin, A., Barre, A., Rougé, P., Dumas, B., Gaulin, E., 2012. The unique architecture and function of cellulose-interacting proteins in oomycetes revealed by genomic and structural analyses. BMC Genomics 13, 1-15.
- Linderman, R.G., 1989. Organic amendments and soilborne diseases. Canadian Journal of Plant Pathology 11(2), 180-183.
- Mackay, A., Weste, G., Sharpe, K., 1985. Survival of *Phytophthora cinnamomi* in buried Eucalyptus roots. Journal of Phytopathology 114(3), 214-223.
- Malajczuk, N., McComb, A.J., 1979. The microflora of unsuberized roots of *Eucalyptus calophylla* R. Br. and *Eucalyptus marginata* Donn ex Sm. seedlings grown in soil suppressive and conducive to *Phytophthora cinnamomi* Rands. I. Rhizosphere bacteria, actinomycetes and fungi. Australian Journal of Botany 27(3), 235-254.
- Malajczuk, N., Pearce, M., Litchfield, R.T., 1984. Interactions between *Phytophthora cinnamomi* and *Rhizobium* isolates. Transactions of the British Mycological Society 82(3), 491-500.
- Malajczuk, N., Theodorou, C., 1979. Influence of water potential on growth and cultural characteristics of *Phytophthora cinnamomi*. Transactions of the

British Mycological Society 72(1), 15-18.

- Marais, L.J., Menge, J.A., Bender, G.S., Faber, B., 2002. *Phytophthora* root rot. Avoresearch a California Avocado Commission Publication 2(1).
- Marks, G.C., Kassaby, F.Y., Fagg, P.C., 1975. Variation in population levels of *Phytophthora cinnamomi* in Eucalyptus forest soils in Eastern Victoria. Australian Journal of Botany 23,435-49.
- Marshall, J.S., Wilkinson, J.M., Moore, T., Hardham, A.R., 2001. Structure and expression of the genes encoding proteins resident in large peripheral vesicles of *Phytophthora cinnamomi* zoospores. Protoplasma 215, 226-239.
- Mbaka, J.N., 2013. The ecology, distribution and population structure of *Phytophthora cinnamomi* associated with root rots and trunk cankers of macadamia in Kenya.
- McConnell, M.E., Balci, Y., 2015. Fine root dynamics of oak saplings in response to *Phytophthora cinnamomi* infection under different temperatures and durations. Forest Pathology 45(2), 155-164.
- Mélida, H., Sandoval-Sierra, J.V., Diéguez-Uribeondo, J., Bulone, V., 2013. Analyses of extracellular carbohydrates in oomycetes unveil the existence of three different cell wall types. Eukaryotic Cell 12(2), 194-203.
- Menge, J.A., Marais, L.J., 2000. Strategies to control *Phytophthora cinnamomi* root rot of avocado. Department of Plant Pathology, University of California.
- Messenger, B.J., Menge, J.A., Pond, E., 2000. Effects of gypsum on zoospores and sporangia of *Phytophthora cinnamomi* in field soil. Plant Disease 84(6), 617-621.
- Narayan, R.D., 2004. Characterization of pre-sporangium stage sporulation genes in the oomycete plant pathogen: *Phytophthora cinnamomi*.
- Narayan, R.D., Blackman, L.M., Shan, W., Hardham, A.R., 2010. *Phytophthora nicotianae* transformants lacking dynein light chain 1 produce non-flagellate zoospores. Fungal Genetics and Biology 47(8), 663-671.
- Newhook, F.J., Podger, F.D., 1972. The role of *Phytophthora cinnamomi* in Australian and New Zealand forests. Annual Review of Phytopathology 10(1), 299-326.
- O'Gara, E., Howard, K., Wilson, B., Hardy, G.S.J., 2006. Management of *Phytophthora cinnamomi* for

biodiversity conservation in Australia: Part 1. A Review of Current Management.

- Ogle, H., Brown, J., 1997. Plant-microbe symbioses. Plant pathogens and plant diseases. pp. 21-37.
- Old, K.M., Oros, J.M., Malafant, K.W., 1984. Survival of *Phytophthora cinnamomi* in root fragments in Australian forest soils. Transactions of the British Mycological Society 82(4), 605-613.
- Oßwald, W., Fleischmann, F., Rigling, D., Coelho, A.C., Cravador, A., Diez, J., Dalio, R.J., Horta Jung, M., Pfanz, H., Robin, C., Sipos, G., 2014. Strategies of attack and defence in woody plant *Phytophthora* interactions. Forest Pathology 44(3), 169-190.
- Pegg, K.G., 1977. Soil application of elemental sulphur as a control of *Phytophthora cinnamomi* root and heart rot of pineapple. Australian Journal of Experimental Agriculture 17(88), 859-865.
- Phillips, D., Weste, G., 1985. Growth rates of four Australian isolates of *Phytophthora cinnamomi* in relation to temperature. Transactions of the British Mycological Society 84, 183-85.
- Reeksting, B.J., Olivier, N.A., Van den Berg, N., 2016. Transcriptome responses of an ungrafted *Phytophthora* root rot tolerant avocado (*Persea americana*) rootstock to flooding and *Phytophthora cinnamomi*. BMC Plant Biology 16, 1-19.
- Ribeiro, O.K., Linderman, R.G., Shattock, R.C., Shaw, D.S., Cooke, L.R., 1991. Chemical and biological control of *Phytophthora* species in woody plants. Phytophthora, 399-410.
- Robold, A.V., Hardham, A.R., 2005. During attachment P*hytophthora* spores secrete proteins containing thrombospondin type 1 repeats. Current Genetics 47, 307-315.
- Ruiz Gómez, F.J., Navarro‐Cerrillo, R.M., Sánchez‐Cuesta, R., Pérez‐de‐Luque, A., 2015. Histopathology of infection and colonization of *Quercus ilex* fine roots by *Phytophthora cinnamomi*. Plant Pathology 64(3), 605-616.
- Savory, A.I., Grenville-Briggs, L.J., Wawra, S., Van West, P., Davidson, F.A., 2014. Auto-aggregation in zoospores of *Phytophthora infestans*: the cooperative roles of bioconvection and chemotaxis. Journal of the Royal Society Interface 11(94), 20140017.
- Serrazina, S., Santos, C., Machado, H., Pesquita, C., Vicentini, R., Pais, M.S., Sebastiana, M., Costa, R., 2015. Castanea root transcriptome in response to

Phytophthora cinnamomi challenge. Tree Genetics and Genomes 11, 1-19.

- Sghaier-Hammami, B., Valero-Galvàn, J., Romero-Rodríguez, M.C., Navarro-Cerrillo, R.M., Abdelly, C., Jorrín-Novo, J., 2013. Physiological and proteomics analyses of Holm oak (*Quercus ilex* subsp. ballota [Desf.] Samp.) responses to *Phytophthora cinnamomi*. Plant Physiology and Biochemistry 71, 191-202.
- Shea, S.R., Gillen, K.J., Leppard, W.I., 1980. Seasonal variation in population levels of *Phytophthora cinnamomi* Rands in soil in diseased, freely-drained *Eucalyptus marginata* Sm sites in the northem jarrah forest of south-westem Australia. Journal of Environmental Protection and Ecology 2, 135-56.
- Shearer, B.L., Crane, C.E., Cochrane, A., 2004. Quantification of the susceptibility of the native flora of the South-West Botanical Province, Western Australia, to *Phytophthora cinnamomi*. Australian Journal of Botany 52(4), 435-443.
- Shearer, B.L., Shea, S.R., Deegan, P.M., 1987. Temperaturegrowth relationships of *Phytophthora cinnamomi* in the secondary phloem of roots of Banksia grandis and Eucalyptus marginata. Phytopathology 77(5), 661-665.
- Škalamera, D., Hardham, A.R., 2006. PnCcp, a *Phytophthora nicotianae* protein containing a single complement control protein module, is sorted into large peripheral vesicles in zoospores. Australasian Plant Pathology 35, 593-603.
- Swiecki, T.J., Bernhardt, E.A., Frankel, S.J., 2019. Phytophthora root disease and the need for clean nursery stock in urban forests: Part 3. Prevention and management. Western Arborist 45(1), 40-50.
- Teferi, D., Ayano, A., 2016. Significance of *Phytoptora*

disease with special emphasis to avocado and pine apple in South Western Ethiopia: A Review. Significance 6(7).

- Wang, Y., Li, A., Wang, X., Zhang, X., Zhao, W., Dou, D., Zheng, X., Wang, Y., 2010. GPR11, a putative seventransmembrane G protein-coupled receptor, controls zoospore development and virulence of *Phytophthora sojae*. Eukaryotic Cell 9(2), 242-250.
- Weste, G., 1975. Pathogenicity of *Phytophthora cinnamomi* towards *Nothofagus cunninghamii*. Australian Journal of Botany 23(2), 277-283.
- Weste, G., Ruppin, P., 1977. *Phytophthora cinnamomi*: population densities in forest soils. Australian Journal of Botany 25(5), 461-475.
- Weste, G., Vithanage, K., 1978. Seasonal variation in numbers of chlamydospores in Victorian forest soils infected with *Phytophthora cinnamomi*. Australian Journal of Botany 26(5), 657-662.
- Wolstenholme, B.N., 2013. Ecology: climate and soils. In The avocado: botany, production and uses. Wallingford UK: CABI. pp. 86-117.
- Wood, R., Bennett, I.C., Blanken, P.A., 1987. Injectable formulations of phosetyl-Al developed for root rot control in avocado trees in South Africa. South African Avocado Growers' Association Yrb 10, 97-99.
- Yang, X., Zhao, W., Hua, C., Zheng, X., Jing, M., Li, D., Govers, F., Meijer, H.J.G., Wang, Y., 2013. Chemotaxis and oospore formation in *Phytophthora sojae* are controlled by G‐protein‐coupled receptors with a phosphatidylinositol phosphate kinase domain. Molecular Microbiology 88(2), 382-394.
- Zentmyer, G.A., Ohr, H.D., 1978. Avocado root rot. Leaflet 2440. Division of Agricultural Sciences. University of California, Berkeley.