Fine root characteristics in kauri-dominated forests affected by *Phytophthora agathidicida*

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Abstract

Fine roots (≤ 2 mm diameter) are a small but functionally important portion of belowground biomass in forest ecosystems, contributing to net primary productivity, carbon transfer, and nutrient cycling. Yet, fine roots are poorly quantified in Southern Hemisphere forests. Kauri (*Agathis australis*), an ecologically and culturally significant species, is threatened by the pathogen *Phytophthora agathidicida* (PA) which causes kauri dieback. Considering infection begins within living tissue of the fine roots, knowledge on fine roots is crucial to understanding tree responses to PA. Soil core samples were used to assess standing fine root density (mg cm^{-3}) at 22 trees across six plots in the Waitākere Ranges Regional Park. Ingrowth cores (N = 12) were used to estimate fine root production (mg cm^{-3} $year^{-0.5}$) and turnover ($year^{-0.5}$). Tree and soil properties were assessed at each tree. Soil cores and ingrowth cores were processed by extracting fine roots and sorting them into four root groups: kauri, non-kauri, unidentified, and leftovers. Root chemical analyses (kauri roots only) included total C, total N, C/N ratio, and micronutrients.

Mean total standing fine root density (16.94 mg cm^{-3} ± 3.59 mg cm^{-3}) was greater than global estimates. Fine root production (7.41 mg cm^{-3} $year^{-1}$ ± 1.48 mg cm^{-3} $year^{-1}$) and turnover (3.45 $year^{-1}$ ± 1.79 $year^{-1}$) were within the range of global data. A positive correlation was found between standing fine root density and organic humic layer (Oh) temperature, and between fine root production and kauri fine root C/N. Standing fine root density was significantly greater in trees where PA had not been detected (P = 0.01). Fine root production and turnover was significantly greater (P = 0.03) in non-kauri fine roots than in kauri fine roots. The findings suggest that PA results in a reduction of kauri fine roots while non-kauri fine roots are not affected by the pathogen. This may have considerable effects on the functioning of kauri-dominated forest ecosystems.

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Chapter 1. Introduction

1.1. Kauri-dominated forest ecosystems and *Phytophthora agathidicida*

Kauri (*Agathis australis* (D.Don) Lindl.) is an ancient conifer endemic to the North Island of Aotearoa – New Zealand. Kauri-dominated forests are one of the most diverse forest types in Aotearoa – New Zealand (Ogden, 1995; Wyse, 2012), often distinct species assemblages are observed in kauri stands or within the dripline of individuals (Wyse, 2012; Wyse *et al*., 2014).

As a foundational species, kauri have an immense influence on soil processes, modifying environmental conditions due to tannin-rich, acidic litter with relatively low litter decomposition rates (Wyse *et al*., 2014). In undisturbed kauri forests, deep, acidic (pH value ca. 4) organic layers form from kauri litter build-up. With maturity, the soil organic layer accumulates high levels of carbon and nitrogen (Blakemore *et al*., 1987; Silvester & Orchard, 1999; Padamsee *et al*., 2016). However, tree growth is often nitrogen-limited in kauri-dominated ecosystems due to the immobilization of N (Silvester, 2000). This occurs through rainfall washing acidic leachates from the litter and organic layer into the underlying soil which inhibits nitrification, resulting in low levels of biologically available nitrogen (Silvester, 2000; Wyse, 2012; Wyse & Burns, 2014). Under podsolising conditions, the mineral soil layer becomes increasingly depleted of nutrients and biomass which accumulate in the litter and organic humic layer. The organic and mineral soil layers of kauri are acidic relative to both New Zealand soils (Wyse, 2012) and other coniferous species (Vanguelova *et al*., 2004; Helmisaari *et al*., 2009). Nutrient intake is aided by mycorrhizal fungi associations on fine roots (Padamsee *et al*., 2016).

The soil conditions formed by kauri trees often results in distinctive species assemblages in the vicinity of kauri. According to Wyse *et al*. (2014), non-kauri species can be divided into three groupings depending on their stress tolerance to low nitrogen and other conditions (e.g. low pH) associated with kauri: stress-tolerant species dependent on kauri presence; species dependent on areas with kauri absent; and those with distributions unaffected by kauri. The assemblage of species near kauri may vary with kauri tree maturity and degree of influence on the surrounding soil conditions. Thus, the response of fine roots to nitrogen availability may be species dependent.

Previous studies regarding kauri soils have mainly focused on litter (Silvester & Orchard, 1999; Wyse & Burns, 2013) and soil chemistry (Silvester, 2000; Jongkind *et al*., 2007; Verkaik & Braakhekke, 2007) but little is known about root characteristics besides their role in influencing soil CO_2 efflux in kauri-dominated forests (Schwendenmann & Macinnis-Ng, 2016), and the arbuscular mycorrhizal fungi associated with fine roots (Padamsee *et al*., 2016). The kauri fine root system is widespread throughout the litter and organic layers of the forest (Steward & Beveridge, 2010; Jia *et al*., 2021). With maturity, the root system of kauri shifts from a well-developed tap root to widely branching lateral roots and deep peg roots (Steward & Beveridge, 2010). The influence of individual kauri extends to the dripline, limiting the ability of many species to become established beneath the tree canopy (Wyse *et al*., 2014).

Generally, a sizable portion of fine root biomass occurs in the organic (O) soil horizon; however, the proportion of root biomass in the O horizon relative to the other soil horizons, varies widely across different ecosystems (Fujimaki *et al*., 2005; Zang *et al*., 2011; Gao *et al*., 2021). This has been observed in kauri-dominated forests by Silvester & Orchard (1999) who found that the majority of fine root mass in kauri forests occurs in the soil organic humic layer, and that often a dense mat of fine roots occurred between the soil organic fermented and soil organic humic layer, contributing to forest floor depth and volume (Figure 1). Past studies suggest that the variation in fine root biomass in the O horizon is linked to the tree species community composition, climatic and edaphic conditions (Leuschner & Hertel, 2003; Finér *et al*., 2011; Gao *et al*., 2021).

The litter and soil layers in this study follow the layers operationally defined by Silvester & Orchard (1999). The forest floor is defined as a combination of the litter layer, the organic fermented (Of) layer, and the organic humic (Oh) layer (Figure 1). The mineral layer is the soil layer beneath the forest floor. The litter layer is composed of largely intact organic material. The Of layer is composed of partially decomposed organic material and the Oh layer is composed of largely black friable organic particles that are small and can be moulded.

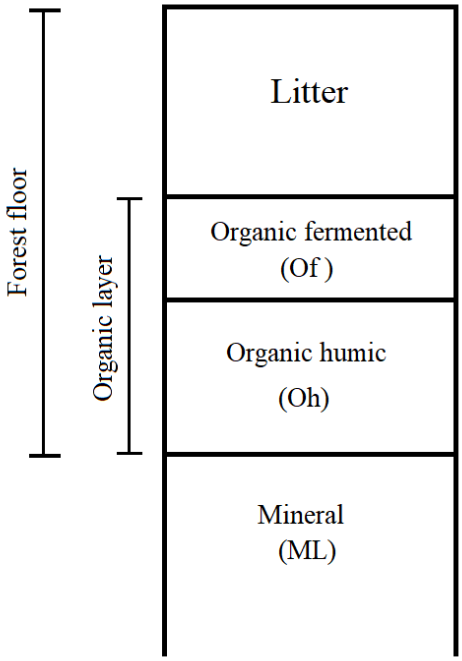

Figure 1. Diagram of the litter and soil layers beneath a kauri tree. The relative heights of the layers are for illustrative purposes only and do not correspond to actual depths.

Kauri dieback is a lethal root and collar dieback disease caused by the oomycete pathogen *Phytophthora agathidicida* (PA) (Bradshaw *et al*., 2020) that threatens kauri and consequently, given the role of kauri as foundational species, kauri-dominated forests (Wyse *et al*., 2014; Weir *et al*., 2015; Hood, 2021). The disease is a key concern in New Zealand due to its impact on forest ecosystems and on the culturally significant taonga species kauri (Black *et al*., 2018; Bradshaw *et al*., 2020).

Phytophthora agathidicida infection begins within living tissue of the fine roots and progresses further through the root system to eventually form a canker at the root collar, inhibiting vascular function, and causing mortality (D'Souza *et al*., 2021). Bradshaw *et al* (2020) suggest that PA is attracted to kauri root exudates released from the fine roots. The stages of the disease occur over a considerable period of time as kauri offer some physiological resilience through their large size, long lifespan, and ability to form root anastomoses with neighbouring trees (Bauder & Leuzinger, 2019) for the exchange of water and nutrients (D'Souza *et al*., 2021). Visual symptoms, therefore, signify the late, chronic stage of infection as PA likely infects the fine roots for a lengthy period before impacts on the aboveground components become visible (Bradshaw *et al*., 2020; D'Souza *et al*., 2021). Surveillance methods to determine kauri tree health largely rely on aboveground visual symptoms such as defoliation and presence of

bleeding lesions in the trunk (Waipara *et al*., 2013). If fine roots are one of the first sites infected, fine root biomass and productivity may be important indicators to determine how PA has affected the functioning of individual trees in the earlier stages of infection, and what feedbacks may result from a change in kauri tree influence on their surrounding environment and consequently the wider forest ecosystem.

1.2. The role of fine roots in forest ecosystems

The term 'fine roots' generally refers to roots that are non-woody and thinner than 2 mm in diameter, although other diameter thresholds may also be used (Finér *et al*., 2011; Zang *et al*., 2011; Olesinski *et al*., 2012; Shively *et al*., 2022). Fine roots are regions of high metabolic activity and more active sites of resource uptake than coarse roots (Emmet *et al*., 2014; Freschet *et al*., 2021). They are the main facilitators responsible for the uptake of water, nutrients, and water from the soil and are therefore significant in influencing terrestrial productivity (Jackson & Schulze, 1997; McCormack *et al*., 2015; Li *et al*., 2021a).

Belowground root systems are major contributors to total gross primary productivity and carbon storage in forest ecosystems (Bardgett, 2011; Addo-Danso *et al*., 2016). The critical role of fine roots in tree growth, nutrient cycling, C transfer, and the development of soil as a substrate is well known (Ehrenfeld *et al*., 1997; Vanninen & Mäkelä, 1999; Zang *et al*., 2011). For example, fine roots have been found to explain the majority of spatial variation in soil CO_2 efflux in a kauri-dominated forest (Schwendennmann & Macinnis-Ng, 2016). Thus, small changes in fine root growth can affect C cycling in forests and cause feedbacks that affect terrestrial productivity on much larger scales (Cairns *et al*., 1997; Li *et al*., 2021a). Despite the relatively large influence of the root system on carbon fluxes and forest productivity, root components are understudied in forest ecosystem research, and fine roots have been particularly poorly quantified (Nadelhoffer & Raich, 1992; Phillips *et al*., 2008). Fine roots constitute a small (2%–5%) but functionally important portion of total biomass (DeAngelis *et al*., 1981; Vogt *et al*., 1995; Helmisaari *et al*., 2002) accounting for approximately 33%–60% of annual net primary production in forest ecosystems (Brunner & Godbold, 2007; Xiao *et al*., 2008; Meng *et al*., 2018).

Root systems and fine roots, in particular, have a degree of plasticity in morphology and resource allocation in response to environmental stressors, such as the presence of neighbouring species and environmental fluctuations (Holdaway *et al*., 2011; Valverde-Barrantes *et al*., 2013; Jia *et al*., 2021). Adaptations vary by species (Valverde-Barrantes *et al*., 2013) and the ability to modify allocation and morphology can reduce trait overlap and maximise species coexistence (Jia *et al*., 2021).

1.3. Standing fine root biomass and density

Root biomass refers to the standing belowground root mass of a plant per unit *area* whereas fine root density is the root mass per unit *volume*; the latter was used for the purpose of this study. Quantification of fine root biomass and density are important in understanding the role of fine roots in contributing to primary productivity and C cycling, and is essential for unravelling the interactions between the aboveground and belowground systems in terrestrial ecosystems (Cairns *et al*., 1997; Helmisaari *et al*., 2007; Lwila *et al*., 2021). Fine root biomass plays a large role in plant species performance due to their role in soil resource uptake and can be good indicators of changing environmental conditions (Valverde-Barrantes *et al*., 2017; Weemstra *et al*., 2020). For example, Bowen (1985) and Finér *et al*. (2007) observed a strong relationship between fine root biomass and aboveground biomass and Weemstra et al. (2020) found that fine root mass and longevity were important factors in explaining interspecific differences in tree growth.

The main environmental factors that tend to influence fine root biomass are air temperature, precipitation, geographical location, stand age and elevation (Leuschner & Hertel, 2003; Yuan & Chen, 2010; Finér *et al*., 2011; Jagodziński *et al*., 2016; Fortier *et al*., 2019; Gao *et al*., 2021). Fine root biomass tends to differ by biome and forest type (Lei *et al*., 2012); generally fine root biomass is greatest in tropical forests followed by temperate forests, and lowest in boreal forests (Finer *et al*, 2011; 2007; Gao *et al*., 2021). Furthermore, deciduous trees tend to produce more fine root biomass than conifers (Leuschner & Hertel, 2003; Finer *et al*., 2007).

Measuring fine root biomass and density comes with a number of challenges, including the difficulty of distinguishing between roots of different species, between living and dead roots (Helmisaari *et al*., 2007), and varying estimates depending on the sampling methods used

(Makkonen & Helmisaari, 1999; Addo-Danso *et al*., 2016). Large temporal and spatial variability in root longevity add complexity to the quantification of fine root density and biomass (Helmisaari *et al*., 2007).

1.4. Fine root production and turnover

Fine root production refers to the mass of fine roots per unit area per unit time, i.e. how fast fine roots grow, and fine root turnover is the rate at which fine root biomass is replaced per unit time. Fine roots contribute up to 40% of total ecosystem productivity (Vogt *et al*., 1993; Vogt *et al*., 1995) and up to 75% of annual net primary production (Gill & Jackson, 2000; Finér *et al*., 2011). The measurement of root production and turnover is important for understanding the role of fine roots in C and nutrient cycling and accumulation, as well as the relationships between above- and belowground production (Nadelhoffer & Raich, 1992; Burke & Raynal, 1994; Meng *et al*., 2018).

The main factors affecting fine root growth are nitrogen (N) and water availability which are crucial for plant growth and development, and species diversity (Bardgett & De Vries, 2014; Li *et al*., 2021a). Nadelhoffer (2000) and Yuan & Chen (2012) suggest an increase in soil nitrogen could stimulate fine root production and turnover, however, other studies found that production and turnover did not vary or decreased with greater nitrogen availability as nitrogen-rich environments where roots had high metabolic activity lead to greater carbon allocation for the roots, resulting in the prolonged lifespan of fine roots (Gower *et al*., 1992; Burton *et al*., 2000).

While fine root production and turnover may increase in more nutrient-rich (fertile) sites, fine root biomass has been observed to decrease with site fertility (Danjon *et al*., 2013; Shively *et al*., 2022). An increase in carbon and nitrogen allocation for fine root growth, resulting in greater production and turnover, reduces fine root longevity and consequently lowered measures of fine root biomass (Li *et al*., 2021b). Shively *et al*. (2022) suggests lower root biomass is a result of the reduced resource allocation to the structure and protection of fine roots, leading to more rapid root mortality. As young fine roots are more metabolically active than older fine roots hence more efficient in nutrient uptake, it may not be the most

energetically cost-effective strategy to maintain older, less efficient roots (Blair & Perfecto, 2001).

The influence of species diversity on fine root production and turnover is inconsistent (Lei *et al*., 2012). Fine root production increased with greater species richness in some forest stands (Brassard *et al*., 2011; Brassard *et al*., 2013; Ma & Chen, 2017) but not in others (Domisch *et al*., 2015). This may be the effect of species-specific variations in morphology and physiology of fine roots, allowing adaptations to different environmental niches (Bakker *et al*., 2009). Root systems and fine roots, in particular, have a degree of plasticity in morphology and resource allocation in response to environmental stressors, such as the presence of neighbouring species and environmental fluctuations (Holdaway *et al*., 2011; Valverde-Barrantes *et al*., 2013; Jia *et al*., 2021). Adaptations vary by species (Valverde-Barrantes *et al*., 2013) and the ability to modify resource allocation and morphology can reduce trait overlap and maximise species coexistence, resulting in a stabilization or increase fine root production (Rewald *et al*., 2018; Jia *et al*., 2021).

Water availability is a fundamental factor in plant growth in plants (McCormack & Guo, 2014). The response of fine roots to an increase in water availability varies depending on the how strongly water is a limiting factor in a given system. In drought-prone forests, an increase in water availability prolongs root lifespan and increases productivity (Meier & Leuschner, 2008). In comparison, the addition of water to an environment of low water stress may see no change in fine root characteristics or reduce fine root turnover given oversaturation (Leppälammi-Kujansuu *et al*., 2014).

Fine root production and turnover are difficult to measure due to requiring long-term labour-intensive methods of measurement (Burke & Raynal, 1994), often differ significantly in magnitude between methods (Hendricks *et al*., 2006), and are subject to high variability (Lei *et al*., 2012; Lukac, 2012). For example, the seasonality in fine root production and fine root turnover complicates how estimates of production and turnover can fully capture the continuous growth and mortality of fine roots (Konôpka *et al*., 2005).

1.5. Root system response to soil-borne pathogens

The impact of soil-borne pathogens varies by species (both host and pathogen) and can range from predominantly fine root damage (Scott *et al*., 2019) to tree dieback and mortality (Brasier, 1996; Shafizadeh & Kavanagh, 2005). Soil-borne pathogens generally constrain growth and longevity of host trees and consequently forest ecosystems (Chavarriaga *et al*., 2007; Emmet *et al*., 2014).

The *Phytophthora* genus comprises over sixty species of plant pathogens that cause root and collar rot diseases in a broad range of host plants and trees (Erwin & Ribeiro, 1996; Fleischmann *et al*., 2004). Pathogens in the *Phytophthora* genus share similar infection cycles and most *Phytophthora* species infect the host from the fine roots (Fleischmann *et al*., 2004). Studies in central Europe reported that *Phytophthora quercina* in combination with other *Phytophthora* species such as *Phytophthora cambivora* and *Phytophthora citricola*, cause a severe loss in feeder roots in the deciduous oak species *Quercus robur* and *Quercus petraea,* demonstrating that this pathway of infection can cause severe root loss in the form of fine root decay (Jung & Blaschke, 1996; Jung *et al*., 2013). *Phytophthora cinnamomi* was associated with fine root loss in *Quercus ilex* trees in western Spain (Corcobado *et al*., 2013) and an average 15% loss of fine root biomass in *Castanea dentata* (Marsh.) Borkh., seedlings in North American forests (Rhoades *et al*., 2003). In New Zealand, *Phytophthora pluvialis* and *Phytophthora cinnamomi* cause a reduction in fine root growth and production of fine root tips in *Pinus radiata* roots (Scott *et al*., 2019). The majority of forest trees infected by soil-borne pathogens lack easily detectable visual symptoms until the chronic stage of infection (Allikäme *et al*., 2017). *Inonotus tomentosus* and *Armillaria mellea* soil-borne forest pathogens can develop for 20–40 years, and *Heterobasidion annosum* for 7–8 years, before showing easily detectable symptoms (Davison, 2011).

There is a knowledge gap in our current understanding of kauri dieback concerning research into changes in fine roots with PA presence. Changes in standing fine root density, fine root production, and fine root turnover may be useful in increasing understanding on how PA interacts and affects kauri trees' belowground functioning (Bradshaw *et al*., 2020).

1.6. Aims and hypotheses

Phytophthora agathidicida infection eventually leads to mortality and there is currently no known cure (D'Souza *et al*., 2021; Froud *et al*., 2022). Therefore, there is a need for greater understanding of the impacts of the pathogen to inform management of kauri dieback. A key challenge in the research on kauri dieback is determining the larger-scale and longer-term ecosystem impacts of PA. This study aimed to determine whether the pathogen impacts fine root characteristics, and what flow-on effects this may have for kauri-dominated forest functioning.

The objectives of this study are to:

i) quantify the standing fine root density, fine root production and fine root turnover (fine root characteristics) of kauri trees affected by PA in three sites in the Waitākere Ranges Regional Park;

ii) determine what environmental variables are influencing differences in these fine root characteristics;

iii) evaluate the impacts of *Phytophthora agathidicida* on fine roots and apply this knowledge to predict long-term impacts on kauri-dominated forests in response pathogen pressure.

As aforementioned, fine roots are one of the first sites infected by *P. agathidicida* (Bradshaw *et al*., 2020) and infection generally causes tree mortality (D'Souza *et al*., 2021). Therefore, it is hypothesized that there will be a reduction in fine root biomass, production, and turnover of kauri fine roots at symptomatic trees and/or where PA has been detected compared to control trees (hypothesis 1). Given a reduction in kauri fine roots, a reduction in the competitive advantage and suppressive effects of kauri trees on species in their surrounding environment is expected. Therefore, it is further hypothesised that there will be more non-kauri fine roots (higher standing fine root density and production) and that they will have greater longevity (lower fine root turnover) at symptomatic trees and/or where PA has been detected compared to control trees (hypothesis 2).

Chapter 2. Methods

2.1. Study area

This study was conducted in three sites in the Waitākere Ranges Regional Park: Cascades Kauri Area (hereafter Cascades), Huia, and Piha (Figure 2). The sites were established in 2011–2015 by Bruce Burns and George Perry (University of Auckland) for long-term monitoring of plant species composition and kauri demography. Each site comprised two plots, one of which was symptomatic and one of which was non-symptomatic (control) at the time of establishment, based on tree health assessments (canopy health score) (Table A1). All study sites have been closed to the public since 2 December 2017, following the placement of a rāhui over the wider Waitākere Ranges Heritage Area by mana whenua Te Kawerau ā Maki (Tiakina Kauri, 2017).

Figure 2. Map of the locations of the three field sites in the Waitākere Ranges Regional Park, situated to the west of the city of Auckland: Cascades, Piha and Huia. (Adapted from a map made in ArcGIS by Marijke Struijk, CC BY 4.0).

The Waitākere Ranges Regional Park is a regenerating forest area in the Auckland region, encompassing approximately 21,000 ha of continuous vegetation (Bishop *et al*., 2013). The area lies on a dissected plateau with an average elevation of 240 m (Searle, 1948; Diamond, 1955) and a maximum elevation of 460 m (Esler & Astridge, 1974). The geological history of the area can be traced back to the formation of the Waitākere Volcano in the early Miocene period between 22 and 15 million years ago and its eruption ca. 16 million years ago (Bishop *et al*., 2013). The Waitākere Ranges Regional Park sits on the now heavily eroded eastern side of the Waitākere volcano; consequently, the dominant soil type of the Waitākere Ranges is Waitākere volcanic soil (Bishop *et al*., 2013).

The Waitākere Ranges has a warm and temperate climate with an average daily maximum temperature of 23 °C in the warmer months (December-February) and an average daily minimum of 9 °C in the colder months (June-September). The region experiences mild summers, cold and wet winters, tends to be partly cloudy year-round, and receives an average annual rainfall of 1500 mm to 2300 mm (Chappell, 2014).

Prior to human settlement, forest vegetation in the region likely lacked distinctive vegetation patterns due to the absence of significant geological discontinuities and major altitudinal differences (Esler, 1983). Large quantities of kauri were present throughout the region (Beever, 1981), but disturbances in the form of extensive logging and post-European settlement, Māori activities and land clearance have influenced the vegetation composition (Esler, 1983). The Waitākere Ranges Regional Park is now largely composed of secondary forest with a few tall individual emergent kauri trees and small fragments of unharvested or lightly harvested kauri stands (Esler, 1983).

Besides kauri, common plant species in the Waitākere Ranges include: *Alsophila dealbata* synonym *Cyathea dealbata* (ponga/silver tree fern), *Coprosma arborea* (māmangi), *Cyathea medullaris* (mamakū), *Dacrydium cupressinum* (rimu), *Geniostoma ligustrifolium* (hangehange), *Myrsine australis* (māpou), *Phyllocladus trichomanoides* (tānekaha), *Rhopalostylis sapida* (nīkau) and *Vitex lucens* (pūriri) (McKelvey& Nicholls, 1959; Esler, 1983; Wyse & Burns, 2014).

2.1.1. Cascades

The Cascades plots are located in the northern section of the Waitākere Ranges Regional Park within the Cascades Kauri Area. Both the symptomatic and control plots were adjacent to the Upper Kauri track. The Cascades site represents the most mature forest of all three sites, with larger kauri trees (Figure 3), and a deeper forest floor and soil organic humic layer than Huia and Piha (Table 1). The more abundant non-kauri species at each plot were *Rhopalostylis sapida* (nīkau), *Coprosma repens* (māmāngi), *Hedycarya arborea* (pigeonwood) and *Syzygium maire* (maire).

Figure 3. A kauri tree from the Cascades control site in the Waitākere Ranges Regional Park. Image by Jaynie Yang (CC BY 4.0).

2.1.2. Huia

The Huia plots are located on the southern end of Waitākere Ranges Regional Park. The Huia sites represent an intermediate size class (Figure 4). The tree size, forest floor depth and soil organic humic layer depth (see Section 2.3.) (Figure 1) were in between those at Cascades and Piha edge of the Waitākere Ranges Regional Park, adjacent to the Puriri Ridge (Table 1). The more abundant non-kauri species at each plot were *Rhopalostylis sapida* (nīkau), *Phyllocladus trichomanoides* (tānekaha), *Kunzea ericoides* (kānuka) and *Leptospermum scoparium var. scoparium* (mānuka).

Figure 4. A view of the kauri-dominated forest at the Huia symptomatic site in the Waitākere Ranges Regional Park. The kauri tree marked with red tape is one of the target trees used in this study. Image by Jaynie Yang (CC BY 4.0).

2.1.3. Piha

The Piha sites are located on the west coast of the Waitākere Ranges Regional Park and are approximately 1.5 km from New Zealand's southern coastline. The symptomatic plot is adjacent to the Maungaroa Ridge track and the control plot is adjacent to the McKenzie track. This site represents the least mature stand in this study. The forest at this site tends to be densely packed with smaller kauri trees, lacks a dense understorey (Figure 5), and has the shallowest forest floor and soil organic humic layer (Table 1). The more abundant non-kauri species at each plot were *Coprosma arborea* (māmāngi), *Veronica* species (koromiko), *Phyllocladus trichomanoides* (tanekaha) and *Carex zotovii* (hook sedge).

Figure 5. Sparse understory of the kauri forest stand at the Piha control site. Image by Jaynie Yang (CC BY 4.0).

Table 1. Tree- and environmental variables at the six plots included in this study. All values are the median of the four trees at each plot.

Location	**Plot type**	**Health score**	**DBH** (cm)	**Soil moisture** (%)	**Organic layer depth** (cm)	**Litter depth** (cm)
Cascades	Symptomatic	2.6	81.0	23.7	10.6	5.6
	Control	2.5	120.0	21.2	8.9	4.1
Huia	Symptomatic	2.8	35.4	45.8	2.8	3.5
	Control	1.9	30.6	38.2	3.3	3.1
Piha	Symptomatic	2.9	24.2	31.8	1.9	3.1
	Control	2.3	26.1	22.1	2.5	2.4

2.2. Plot and tree selection

At each of the three study sites, two 40 m × 50 m plots, representing a symptomatic and non-symptomatic (control) plot, were established (2011–2015). These six plots were used for the field experiments presented in this thesis. Symptomatic plots were sites where PA was deemed to be present at the time of plot establishment, as determined by the canopy health assessment of the kauri trees, other visible symptoms of kauri dieback (e.g. base bleeds) and soil samples (B. Burns 2022, pers. comm., 8 September). The control plots were sites where visual symptoms of the pathogen were absent at the time of establishment. For the purpose of this thesis, the word 'plot' will refer to the control and symptomatic plots, and 'site' will refer to field sites (Cascades, Huia, Piha) used in this study.

At each plot, four kauri were selected as target trees to be used in this study. The selection criterion was based on achieving maximum distance from one target tree to another to minimise overlap of any potential confounding factors between trees such as resource sharing (Klein *et al*., 2016). The selected kauri trees were those located closest to one of each of the four corners of the plot. There was a total of 24 kauri trees at all the plots combined. Soil samples were taken from each tree and tested for PA presence in 2022. Samples were tested for detection using the loop-mediated isothermal amplification (LAMP) assay which targets the detection of a portion of the mitochondrial apocytochrome b coding sequence in PA DNA (Winkworth *et al.*, 2020).

2.3. Tree and environmental characteristics

The height and diameter at breast height (DBH) of each tree were measured and recorded. Tree height was measured using a clinometer and 50 m tape, and DBH was measured at 1.35 m above the root collar. The slope was measured using a clinometer. Canopy health scores were attributed by experienced surveyors following Dick & Bellgard's (2012) canopy health assessment, modified to include half points (Froud *et al*., 2022) (Table A1). The canopy health score is based on using visible symptoms of kauri dieback in the canopy to estimate if, and how badly, a kauri tree has been infected. The scale ranges from 1, representing a healthy kauri tree with no visible signs of kauri dieback, to 5, representing a kauri tree that is dead.

A series of environmental characteristics was measured and sampled at or close to the sampling point of each tree. This included canopy cover, soil volumetric water content, and air and soil temperature.

Canopy cover was estimated using the 'CanopyApp' app on a mobile phone (University of New Hampshire, 2014). A picture of the canopy was taken in the app from approximately a metre off the ground at the sampling point, canopy cover was estimated following the instructions in the app, which involved the selection of leaf colours to identify the canopy in any given photo, allowing an estimation of the percentage of canopy cover in an image. The soil volumetric water content was measured once during the sampling of soil cores and again during the retrieval of the fine root ingrowth cores (HydroSense II, Campbell Scientific Inc., Logan, Utah, United States). Temperature readings of the air, the soil organic layer horizon and the soil mineral layer horizon (Figure 6) were taken alongside soil moisture measurements (Soil Temperature Probe, Novel Ways Ltd., Taupō, New Zealand).

Forest floor depth was measured using a thin metal rod. The rod was pressed straight down into an area of undisturbed forest floor until resistance was felt, signalling the boundary to the mineral soil layer. The rod was then marked at the top of the litter layers, and the inserted length measured using a measuring tape to determine the forest floor depth. A small area of the litter layer and organic fermented layer was then wiped away, and the same method was used to determine the organic humus layer depth. The Oh depth was then calculated as the forest floor depth minus the depth of litter and fermented litter. A separate measure of the Oh layer was taken using a soil ring; this value corresponded to the specific depth of the Oh soil used to estimate standing fine root density. This ring measurement was taken twice and will be henceforth referred to as the core depth.

Figure 6. Soil auger sample showing the boundary (dashed red line) and difference in colour between the mineral layer on the left and organic humic layer on the right of the boundary. The organic humic layer can be differentiated using colour and compaction of the soil. As the mineral layer is composed of more mineral components, such as a clay-like substrate, it is denser than the organic humic soil. See also the absence of intact litter and organic material in the organic humic layer. Image by Jaynie Yang (CC BY 4.0).

2.4. Standing fine root density

2.4.1. Sampling

Sampling and measurements were conducted in the Oh layer at the 24 target kauri trees. For consistency, all samples were collected at a predetermined sampling point for each tree, which was at a distance of half the length of the canopy size of each tree in the north-facing compass direction. Samples were not taken closer to the trunk to minimise damage to the main body of the tree while remaining within the root zone. Fine root density was obtained for all target kauri trees ($N = 24$) across the three sites in spring-summer from early November to late December 2021. Two trees were omitted from the dataset due to insufficient fine root material in the samples. Soil samples were obtained using a metal soil ring corer (10 cm diameter) placed on undisturbed soil near the sampling point for each tree; this was repeated for a total of two samples spaced approximately 15 cm apart. All material that was part of the litter layer and Of layer (Figure 1) was removed from the core interior then the Oh layer was extracted by hand and brought back to the lab in paper bags. Samples were stored in the freezer until processing.

2.4.2. Fine root separation

Fine roots were separated from soil samples, primarily following the root processing steps detailed in Freschet *et al*. (2021). Roots were sorted into four groups: kauri, non-kauri, unidentified, and leftovers. This was based on morphological characteristics outlined in Table 2. Both live and dead roots were included due to the difficulty of differentiating the roots after freezing.

Frozen soil samples were soaked for a minimum of 2 hours and gently stirred throughout the soaking period to detach soil and organic matter. After soaking, large roots (> 2 mm) and identifiable organic matter (e.g. leaves, bark, seed pods) were discarded. Long fine roots and floating roots were picked out using tweezers and transferred to paper towels to dry. Next, the water mixture was poured over a set of three sieves of decreasing size (2 mm, 1 mm and 250 µm), and a gentle flow of water was used to clear roots of soil and debris. Fine roots were individually extracted from each sieve and placed on paper towels to dry in groups corresponding to the root groups in Table 2 and Figure 7. Roots were then stored in paper bags and oven-dried to constant mass at 60 °C for a minimum of 72 hours. After drying, roots were weighed (Adventurer™ Precision AX4202, OHAUS Corporation, New Jersey, United States) to obtain the dry fine root mass to 3 decimal places.

The standing fine root density was calculated as dry fine root mass (mg) divided by the total volume of the Oh layer (cm^{-3}) in the two soil cores. Fine root density is referred to as 'standing fine root density' to avoid confusion with values from ingrowth cores (see Section 2.5.).

$$standing\ fine\ root\ density\ = \frac{dry\ fine\ root\ mass\ (mg)}{2\pi\ \times\ 5^{2}\ (cm) \times\ median\ core\ depth\ (cm)}$$

Total standing fine root density was then determined as the sum of kauri, non-kauri and unidentified fine roots. Although the root group 'leftovers' was a significant component of total fine root density, this group has been excluded from further data analyses due to the highly variable composition of material in the group, from laboratory observations. This group may contain some very small fine root material but lacks discernible roots and is composed of a significant portion of small soil particles, organic matter, kauri root nodules and other material indiscernible to the naked eye. In the data analysis, kauri standing fine root density represents the standing fine root density for roots in the kauri group (Table 2), while non-kauri standing fine root density represents roots in the non-kauri and unidentified root groups. This decision was made to ensure the maximum of all fine roots sorted from soil cores were accounted for in this study.

Table 2. Criteria used to distinguish between the four fine root groups. Also see Figure 7.

Group	Morphological criteria
Kauri	Roots that vary from orange to dark red-black when wet and are typically covered in uniformly sized and evenly distributed root nodules. Nodules are similar in colour to the root epidermis. Side branches gradually decrease in size with root order. Removal of the darker root epidermis will reveal a white inner layer.
Non-kauri	Roots that are distinctly different from the characteristics described for kauri roots, including pinnately branched roots, roots which fall outside the orange to red-black colour spectrum, absence of root nodules, uniformly sized roots, clustered branching of side branches, etc.
Unidentified	Any roots that share some but not all characteristics of kauri roots.
Leftovers	Small debris caught in the smallest sieve (250 μm) that could not be distinguished into other groups, composed mostly of organic matter, small soil particles, and separated kauri root nodules in the soil core samples, and fine peat material in the ingrowth core samples.

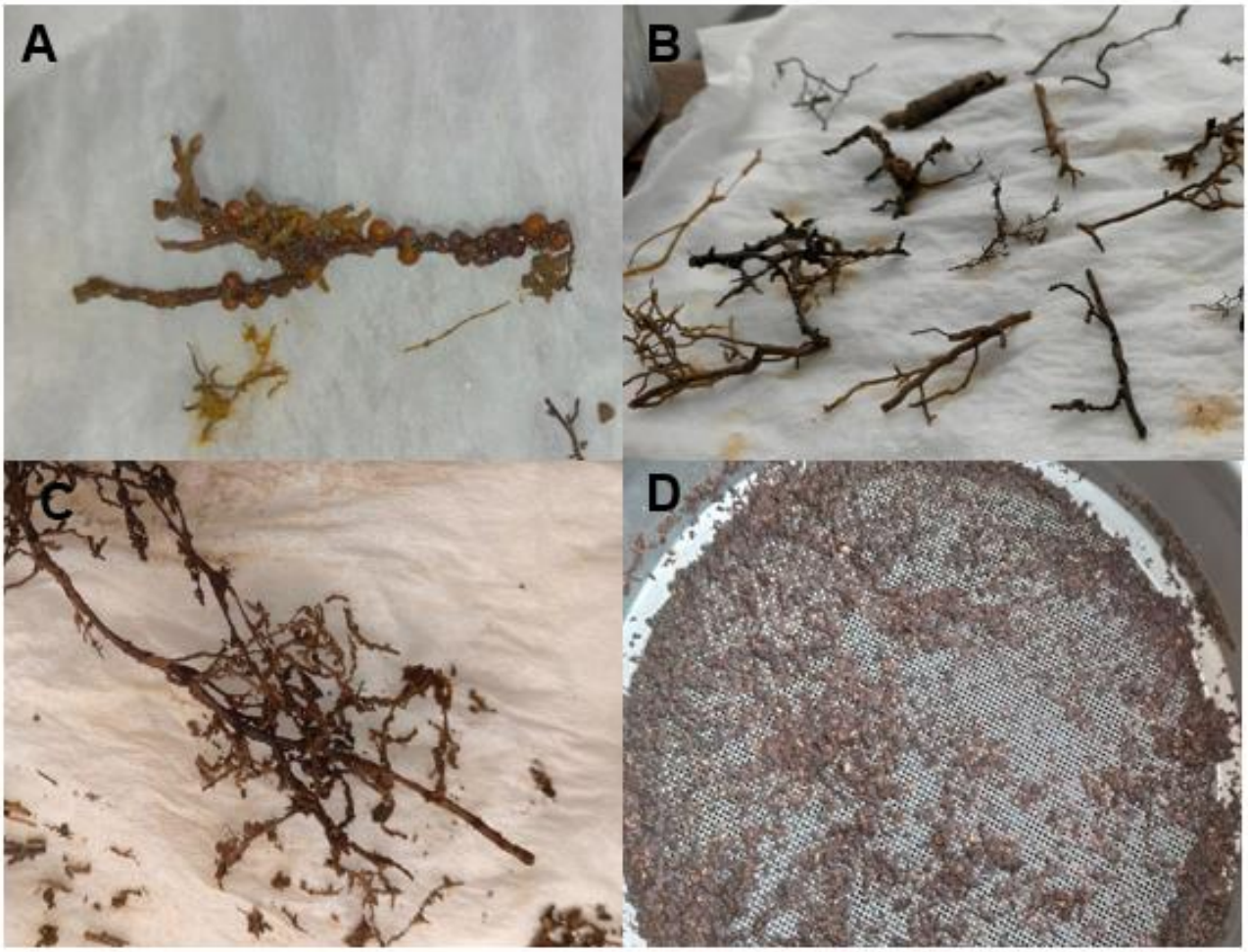

Figure 7. A) A kauri fine root, note the numerous root nodules and orange-red colouring. B) An assortment of non-kauri fine roots. C) An unidentified root which shares the orange-red colouring of kauri roots but lacks other characteristics. D) A root sample in the 1 mm sieve after visible roots have been removed this will be washed into the 250 μm sieve and be classified as leftovers. Images by Jaynie Yang (CC BY 4.0).

2.4.3. Carbon, nitrogen and nutrient analyses

Kauri and non-kauri fine root samples were ground into a fine powder for total C, total N and nutrient analyses using a mill (Foss Tecator Cyclotec 1093, Foss™, Hillerød, Denmark). Analysis of fine root C and N concentration was performed using an elemental analyser (Vario EL III, Elementar, Langenselbold, Germany), calibrated using acetanilide calibration standard and tomato leaves standard.

Kauri and non-kauri fine root samples with more than 2.0 g of material left after C and N analysis ($N = 7$) were further analysed for the following nutrients: phosphorus (P), potassium (K), sulphur (S), calcium (Ca), magnesium (Mg), sodium (Na), iron (Fe), manganese (Mn), zinc (Zn), copper (Cu), boron (B), and molybdenum (Mo). Aliquots of 2.0 g were weighed out for each powdered sample (Adventurer™ Analytical AX224, OHAUS Corporation, New Jersey, United States), which were digested in a 2:1 mixture of Hydrogen Peroxide and Nitric Acid (v:v) by closed-vessel microwave-assisted digestion. The digests were then diluted with deionised water and analysed by inductively-coupled plasma optical emission spectrometry (ICP-OES) (iCAP 6000, ThermoFisher Scientific Inc, Massachusetts, United States). Mo was analysed by ICP mass spectrometry (ICP-MS) (iCAP 6000, ThermoFisher Scientific Inc, Massachusetts, United States).

2.5. Fine root production and turnover

Fine root productivity is commonly estimated from fine root ingrowth cores (Hendricks, *et al*., 2006; Brassard *et al*., 2011). Fine root ingrowth cores were installed beneath each of the kauri trees at each of the plots, at half-canopy distance from the trunk.

2.5.1. Fine root ingrowth core construction and installation

The majority of the fine root ingrowth cores used in this study (10 of 12) were constructed with plastic mesh based on the methodology outlined by the Kellogg Biological Station (n.d.), and Chen *et al* (2018). Metal cores were used for two trees and were produced using a laser cutter by the University of Auckland's Technical Services Workshop. Metal cores are composed of stainless steel, each core was 20 cm in length, 1.5 cm thick, 4 cm in diameter, and had 0.5 cm hole spacing resulting in over

1300 holes. Holes in the metal cores had a 3 mm diameter. Plastic cores were made from 20 cm × 30 cm plastic mesh, holes were 4 mm× 4 mm in size. Mesh was rolled up to produce a cylinder, which was then zip-tied in place using cable ties. The resulting plastic cylinders were 20 cm high and had an average diameter of 4.5 cm (Figure 8). Two squares of mesh cut from Netlon bags were attached to the base of each cylinder using a cable tie. All cores were then given a numbered metal tag attached to the top of the core using polypropylyne garden string.

Cores were filled up to 10 cm with a 2:1 ratio of sandy substrate (Dalton's 15 L propagation sand) to commercially harvested peat (Yates Hauraki Gold Peat 50 L Bale) to mimic the bulk density of the mineral layer. The rest of the core was filled with locally commercially harvested peat (Yates Hauraki Gold Peat 50L Bale) to represent a similar substrate to the organic layer, as recommended by Freschet *et al*. (2021). All sand and peat materials were oven-dried (60 °C) for a minimum of 24 hours.

Fine root ingrowth cores were buried at the sampling point of each kauri trees at each plot. A hole was created using a metal soil auger (4.5 cm diameter) until a depth of 10 cm in the mineral layer. The hole was slightly widened to fit a core using a long flat head screwdriver and the core was inserted into the hole and any gaps backfilled with the excavated soil until a snug fit was achieved. Care was taken to ensure the backfill soil corresponded to the soil layer. Cores were then tied to plastic stakes for ease of location come retrieval. Fine root ingrowth cores were buried in November and December 2021. The cores were buried for 6 months during the New Zealand spring-summer period to capture the maximum root growth potential. Installation of the cores was delayed by a month due to New Zealand's shifts in alert level in response to the COVID-19 pandemic halting fieldwork activities.

2.5.2. Fine root ingrowth core retrieval and processing

Fine root ingrowth cores were retrieved May–June 2022. The cores (Figure 8) were retrieved by creating incisions around the perimeter of the core using a thin, sharp 20 cm long knife. The core was pulled out by hand and stored in plastic zip lock bags and frozen until processing. Ingrowth cores from two non-adjacent trees were processed for each plot, two of the four trees from each plot were omitted from the productivity and turnover dataset due to time constraints.

Plastic ingrowth cores were removed from the outer plastic mesh while frozen. All zip ties were cut using a combination of scissors and a sharp craft knife, and the bottom Netlon mesh removed allowing the ingrowth core to remain intact as a long cylinder. The core was separated into two sections: the mineral layer which was typically 10 cm in length from the bottom of the core, and the Oh layer. The layers could be distinguished by colour, as the Oh layer was typically a darker brown, and by abundance of small sand and stone particles in the mineral layer. The layers were separated using a craft knife to first score the boundary between the layers, then cut using a sharp knife. The metal cores could not be taken apart, thus the cores were thawed and the Oh layer scooped out using a spoon, assuming a mineral layer of 10 cm. Only the Oh layer was used in this study. Once freed from the plastic and metal ingrowth core structures, the loose core material was soaked in warm water until no longer frozen and processed following the same methodology in section 2.4.2. into the root groups described in Table 2. In addition to the buried cores, an unused plastic core was frozen and processed following the same method to capture any material that could be identified as root in the peat substrate used to fill the cores ("blank" measurement).

Figure 8. A plastic fine root ingrowth core freshly retrieved after 6 months of burial showing root growth into the core. Roots on the outside of the core, such as in the image, were carefully cut off and not included in this study. Image by Jaynie Yang (CC BY 4.0).

Fine root production was calculated as dry fine root mass (mg) sorted from the fine root ingrowth cores, divided by the total volume of the ingrowth core Oh layer (cm^{-3}) multiplied by incubation time ($year^{-0.5}$).

$$fine\ root\ production\ =\ \frac{dry\ fine\ root\ mass\ (mg)}{\pi\ \times\ 4.5^{\,2}\ (cm)\times ingrowth\ core\ Oh\ layer\ depth\ (cm)\ \times incubation\ time\ (year^{-0.5}\ )}$$

The fine root production values calculated for the unused plastic core were subtracted from all the corresponding total, non-kauri, unidentified, and leftovers fine root production values for the ingrowth cores that were buried in the ground, to ensure production estimates were not inflated by roots in the peat substrate material.

Fine root turnover was calculated as fine root production (mg cm^{-3} $year^{-0.5}$) divided by the standing fine root density (mg cm^{-3}).

$$fine\ root\ turnover\ =\ \frac{fine\ root\ production\ (mg\ cm^{-3}\ year^{-0.5}\ )}{standing\ fine\ root\ density (mg\ cm^{-3}\ )}$$

Total fine root production and turnover will be the sum of kauri and non-kauri fine root production and turnover values and will exclude unidentified and leftovers root group (Table 2). The unidentified root group comprised a small proportion (2%) of the total dry weight of fine roots in the ingrowth cores thus will be excluded. The leftovers root group will be excluded for the same reasons described for standing fine root density (see Section 2.4.2.).

2.5.3. Soil properties

Soil samples from the Cascades and Piha sites (collected in 2021), and Huia soil samples (collected in 2022) were dried in the oven at 40 °C for several days. Sample preparation for bulk density and pH measurements involved the weighing of 3 g of soil from each soil sample (and 2 g from one smaller sample), these were then placed into a centrifuge tube. Bulk density was calculated as the dry soil

weight (g) divided by the volume of the soil (cm^3) in the centrifuge tube (Al-Shammary *et al*., 2018). To measure pH, all tubes were filled with distilled water following a 1:10 soil:distilled water ratio, mixed vigorously using a vortex mixer and left to settle overnight. pH was measured using the Sension+ PH3 Basic laboratory pH & ORP Meter (Hach Co., Colorado, United States). The pH meter was calibrated before use using calibration standards, and pH measurements were replicated three times to ensure accuracy of results.

2.6. Data analysis

Due to the low number of samples for each site when classified into control and symptomatic plot types (N = 2) or PA presence (Table 3), fine root production and turnover was analysed using the pathogen detection status rather than being grouped by site, allowing for more robust statistical analyses with a larger sample size.

Tests for the normality of the data were carried out using the Shapiro-Wilk normality test and Q–Q plots for visual assessment of the data distributions. The P-value of the Shapiro-Wilk normality tests was less than 0.05 therefore the data were not normally distributed. To analyse the difference in fine root density, fine root production and fine root turnover between groups (site, plot type, PA detection status), the Kruskal–Wallis test (dplyr v. 1.0.5. in R; Wickham *et al*., 2021) was used to test whether there was a significant difference and Pairwise Wilcoxon Rank Sum Tests (stats v. 3.6.2 in R) were used to test where the significant was, between sites. A correlation matrix (corrplot v. 0.92 in R; Wei & Simko, 2021) was used to examine relationships between variables (Table A2) and standing fine root density, production and turnover for the kauri, non-kauri and total fine root groupings. A significance level of $P < 0.05$ was used for all analyses. All analyses were performed in R (v. 4.04) (R Core Team, 2021).

Chapter 3. Results

3.1. Total standing fine root density

There was a significant difference between sites, with standing fine root density (excluding the leftovers group) being greater at Piha than at Cascades ($H(2) = 7.51$, $P < 0.01$) and greater at Huia than at Cascades ($H(2) = 10.38$, $P = 0.03$) (Figure 9). No significant differences were found in total standing fine root density between pathogen detection statuses and plot type ($P > 0.05$) (Table A3).

The mean standing fine root density, excluding the leftover debris root group, at Piha was 17.41 mg cm^{-3} ± 8.02 mg cm^{-3}, which is more than five times greater than that at Cascades, where it was 5.74 mg cm^{-3} ± 1.47 mg cm^{-3} (Figure 9). There was greater variance of standing fine root density in Piha (7.52 mg cm^{-3} to 66.52 mg cm^{-3}) compared to the Cascades (1.87 mg cm^{-3}–11. 34 mg cm^{-3}) and Huia (2.14 mg cm^{-3}–28.69 mg cm^{-3}) sites.

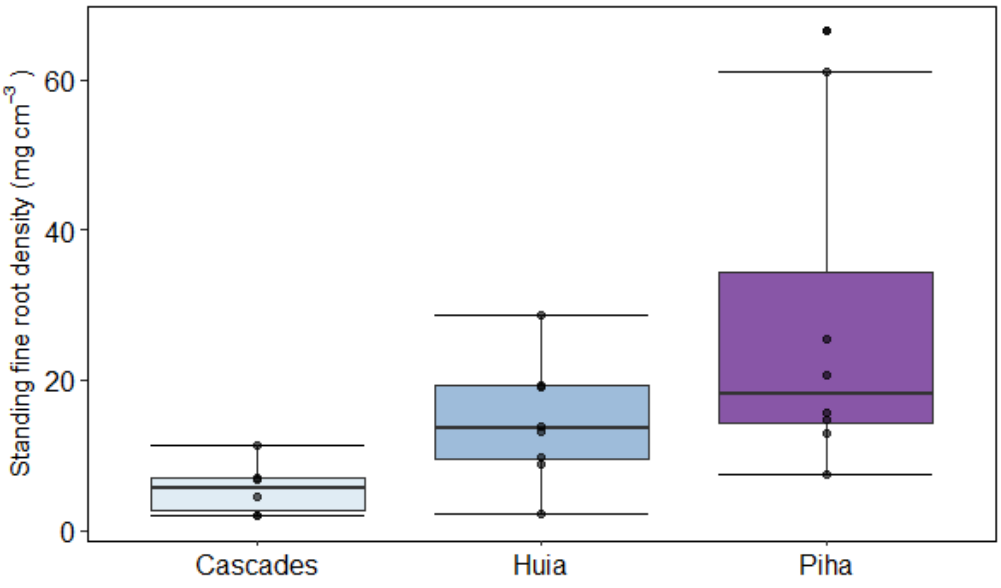

Figure 9. Standing fine root density (mg cm^{-3}) of kauri trees from the Cascades, Huia and Piha field sites, including the fine root groups of kauri, non-kauri, and unidentified. Lower and upper hinges correspond to the 25th and 75th percentiles

3.1.1. Kauri and non-kauri standing fine root density

Kauri and non-kauri standing fine root density did not differ significantly in the Cascades, Huia or Piha sites ($P > 0.05$) (Table A3). There was a significant difference in kauri standing fine root density between pathogen detection statuses where standing fine root density was greater in trees not detected with PA (mean ± SE = 15.22 mg cm^{-3} ± 4.95 mg cm^{-3}) than in detected trees (mean ± SE = 4.79 mg cm^{-3} ± 1.55 mg cm^{-3}) ($H(1) = 6.04$, $P < 0.01$) (Figure 10A). Kauri standing fine root density was also significantly greater in control plots (mean ± SE = 12.94 mg cm^{-3} ± 3.66 mg cm^{-3}) than in symptomatic plots (mean ± SE = 3.33 mg cm^{-3} ± 1.04 mg cm^{-3}) ($H(1) = 8.80$, $P = 0.01$). Non-kauri standing fine root biomass at trees where PA was detected did not differ significantly from non-kauri standing fine root biomass at trees where PA was not detected (Figure 10B).

Across all root groups and pathogen detection statuses, standing fine root density values from the Piha site showed greater variability compared to Cascades and Huia (Table 3). Kauri standing fine root density had greater variability than non-kauri standing fine root density ranging from 0.00 mg cm^{-3} to 21.98 mg cm^{-3} in PA-detected sites and from 4.03 mg cm^{-3} to 48.54 mg cm^{-3} at sites where PA has not been detected. In comparison, non-kauri standing fine root density ranged from 0.39 mg cm^{-3} to 18.19 mg cm^{-3} in PA-detected sites and from 0.21 mg cm^{-3} to 9.79 mg cm^{-3} in non-detected sites.

The ‘unidentified’ fine root group contributed the smallest proportion to overall root density composition (Table 3) except for one tree at Piha. The kauri and leftovers root groups were the largest contributions to overall fine root composition.

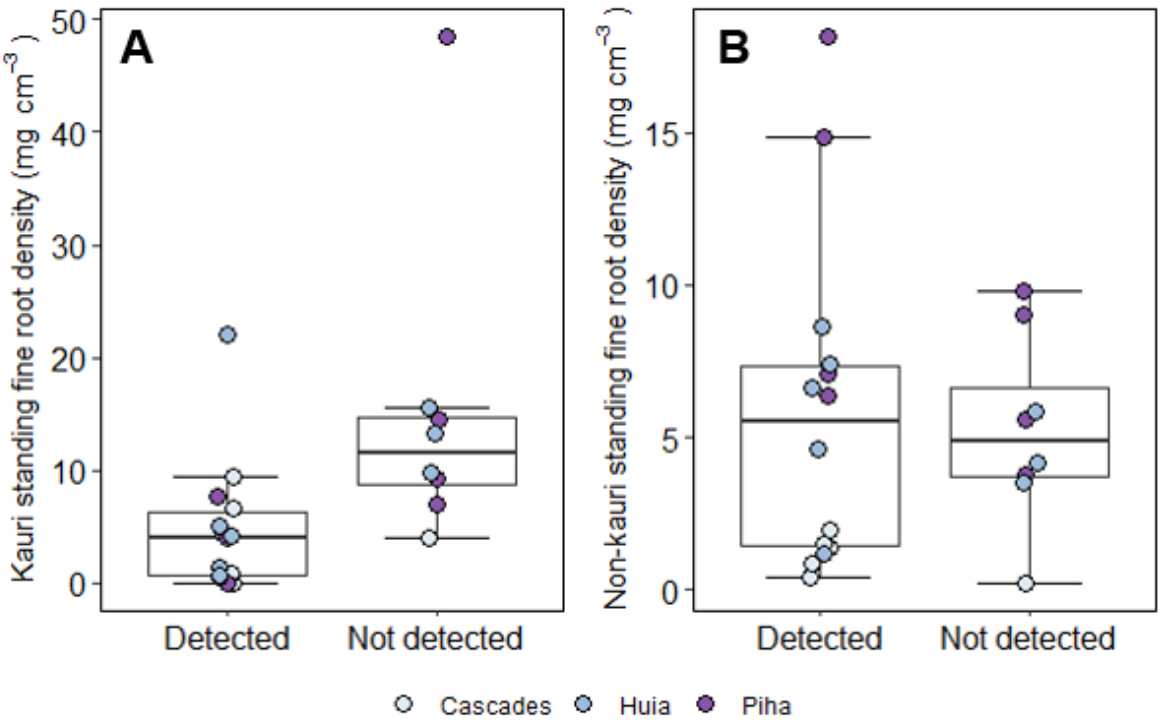

Figure 10. Standing fine root density (mg cm^{-3}) of A) kauri and B) non-kauri fine roots grouped by pathogen (PA) detection status. Sites are differentiated by the colour of the point, light blue represents Cascades, darker blue represents Huia and purple represents Piha. Lower and upper hinges correspond to the 25th and 75th percentiles. All corresponding figures will be colour-coded by site following the same colours.

Table 3. Mean and total standing fine root density grouped by site and PA detection status. Values are the mean ± SE, except when *N* = 1. SE is standard error of the mean.

Site	**Plot type**	***N***	**Standing fine root density** (mg cm^{-3})				**Total fine root density** (excluding leftover debris) (mg cm^{-3})
			Kauri	**Non-kauri**	**Unidentified**	**Leftover**	
Cascades	Detected	5	4.29 ± 1.77	1.22 ± 0.27	0.29 ± 0.17	6.31 ± 2.64	5.80 ± 1.78
Cascades	Not Detected	1	4.03	0.21	0.18	2.91	4.42
Huia	Detected	5	6.64 ± 3.92	5.70 ± 1.30	0.17 ± 0.07	13.48 ± 3.65	12.52 ± 4.42
Huia	Not Detected	3	12.82 ± 1.68	4.49 ± 0.69	0.13 ± 0.07	12.01 ± 1.67	17.45 ± 1.79
Piha	Detected	4	3.03 ± 1.78	11.61 ± 2.91	10.09 ± 9.56	23.17 ± 5.62	24.73 ± 12.20
Piha	Not Detected	4	19.82 ± 9.70	7.04 ± 1.42	4.49 ± 3.26	11.68 ± 2.98	31.35 ± 12.01

3.1.2. Total carbon, nitrogen, and micronutrients

Total C concentration in kauri fine roots ranged from 40.73 % ± 0.02 % to 49.30 % ± 1.53 %, and between 39.40 % ± 0.92 % and 47.70 % ± 1.86 % in non-kauri fine roots. Non-kauri roots had significantly greater C concentration than kauri roots across sites, PA detection status and plot type ($H(1) = 4.9$, $P = 0.02$). In contrast, there was little variation in kauri fine root C concentrations between sites and between PA detection status (Table 4).

No significant differences were found in N concentrations in kauri and non-kauri fine roots across sites, PA detection status, or plot types. Kauri fine root N concentrations ranged from 0.94 % (Huia, Detected) to 1.31% (Huia, Not detected), and non-kauri fine root N concentrations ranged from 0.94 % (Piha, Not detected) to 1.19 % (Cascades, Detected). The variance in N concentrations in kauri and in non-kauri roots was similar (Table 4). The C/N ratio was greater, although not significant, in sites where PA had been detected (Table 4) and did not differ significantly across sites, plot type, and root type.

There was little variation in the P, K, S, Na, Zn, B and Mo concentrations in fine roots across sites and PA detection status (Table 5). No significant differences were found in any micronutrients across sites, PA detection status and plot type. The greatest variation of fine root micronutrients was in the Fe and Mn concentrations. Fe ranged from 1907.50 mg kg^{-1} (Cascades, Detected) to 18696.33 mg kg^{-1} (Huia, Not detected) and Mn ranged from 71.08 mg kg^{-1} (Cascades, Detected) to 539.14 mg kg^{-1} (Huia, Not detected).

Fine roots at Huia had greater Ca and Mg concentrations than the Cascades, and Fe, Mn, Zn and Cu content were lower at sites where the pathogen had been detected (Table 5) but were not significantly different.

Table 4. Total carbon (C) and nitrogen (N) concentrations (%) of kauri and non-kauri fine roots from the Cascades, Huia, and Piha sites. Values are the mean ± standard error with the exception of sites where $N = 1$.

		Kauri				Non-kauri			
Site	**PA detection status**	***N***	**Total C** (%)	**Total N** (%)	**C/N ratio**	***N***	**Total C** (%)	**Total N** (%)	**C/N ratio**
Cascades	Detected	4	49.1 ± 0.9	1.1 ± 0.0	44.8 ± 1.1	4	45.1 ± 1.6	1.1 ± 0.0	39.6 ± 1.0
Cascades	Not detected	1	47.3	1.2	38.6	1	49.4	1.1	46.7
Huia	Detected	5	43.6 ± 0.9	1.0 ± 0.1	41.9 ± 2.1	5	40.7 ± 1.8	1.1 ± 0.0	38.3 ± 2.3
Huia	Not detected	2	41.8 ± 0.4	1.2 ± 0.1	34.3 ± 2.1	2	40.4 ± 0.9	1.1 ± 0.0	34.6 ± 0.8
Piha	Detected	1	44.7	1.1	40.7	2	39.6 ± 1.3	0.9 ± 0.0	35.1 ± 0.2
Piha	Not detected	2	40.7 ± 0.0	1.0 ± 0.0	39.3 ± 1.2	2	39.6 ± 0.9	0.9 ± 0.9	35.1 ± 2.7

Table 5. Micronutrient content of kauri fine roots for the Cascades and Huia sites. Samples from Piha could not be analysed because there was insufficient root material in the samples. Values are the mean of *N*.

Site	**PA status**	***N***	**P** (%)	**K** (%)	**S** (%)	**Ca** (%)	**Mg** (%)	**Na** (%)	**Fe** (mg kg^{-1})	**Mn** (mg kg^{-1})	**Zn** (mg kg^{-1})	**Cu** (mg kg^{-1})	**B** (mg kg^{-1})	**Mo** (mg kg^{-1})
Cascades	Detected	3	0.03	0.05	0.14	0.31	0.11	0.06	2435.39	178.97	24.92	10.61	7.37	0.09
	Not detected	1	0.04	0.10	0.13	0.32	0.21	0.07	18696.33	426.52	33.48	20.94	8.44	0.06
Huia	Detected	1	0.04	0.10	0.12	0.41	0.28	0.05	12669.37	286.06	34.10	14.76	7.52	0.11
	Not detected	2	0.04	0.07	0.13	0.59	0.24	0.07	16418.91	482.83	35.77	18.22	9.52	0.09

3.2. Fine root production and turnover

3.2.1 Fine root production

Fine root production (kauri plus non-kauri roots) at trees where the pathogen had been detected was significantly greater compared to non-detected trees ($H(1) = 4.81$, $P = 0.03$) (Figure A1A) The mean fine root production (excluding unidentified and leftover debris root groups) of trees where PA had not been detected was 4.41 mg cm^{-3} $year^{-0.5}$ ± 1.10 mg cm^{-3} $year^{-0.5}$ and detected trees ($N = 5$) was 2.93 mg cm^{-3} $year^{-0.5}$ ± 0.98 mg cm^{-3} $year^{-0.5}$. There were no significant differences in fine root production between sites nor between control and symptomatic plot types ($P > 0.05$). Trees where PA had been detected had greater variation in fine root production than non-detected trees ranging from 0.09 mg cm^{-3} $year^{-0.5}$ to 7.98 mg cm^{-3} $year^{-0.5}$, in comparison to non-detected which ranged from 0.1 mg cm^{-3} $year^{-0.5}$ to 9.67 mg cm^{-3} $year^{-0.5}$).

Non-kauri fine root production (mean ± SE = 2.15 mg cm^{-3} $year^{-0.5}$ ± 0.62 mg cm^{-3} $year^{-0.5}$) was significantly greater than kauri fine root production (mean ± SE = 0.38 mg cm^{-3} $year^{-0.5}$ ± 0.12 mg cm^{-3} $year^{-0.5}$) ($H(1) = 4.82$, $P = 0.03$) (Figure 11A; Figure 11B). Kauri (Figure 11A) and non-kauri fine root production (Figure 11B) showed no significant differences between sites, PA detection status, or plot type (Table A3). The mean kauri fine root production at trees where PA has been detected ($N = 5$) was 0.46 mg cm^{-3} $year^{-0.5}$ ± 0.21 mg cm^{-3} $year^{-0.5}$ and at trees where PA has not been detected ($N = 4$) it was 0.24 mg cm^{-3} $year^{-0.5}$ ± 0.15 mg cm^{-3} $year^{-0.5}$. The mean non-kauri fine root production at PA-detected trees ($N = 7$) was 6.66 mg cm^{-3} $year^{-0.5}$ ± 0.92 mg cm^{-3} $year^{-0.5}$ and at PA-not-detected trees ($N = 5$) it was 5.63 ± 1.78 mg cm^{-3} $year^{-0.5}$. Both kauri and non-kauri fine root production share a similar variance between trees at which PA was and was not detected, but this variation was greater in non-kauri (Figure 11A) than in kauri fine root production (Figure 11B).

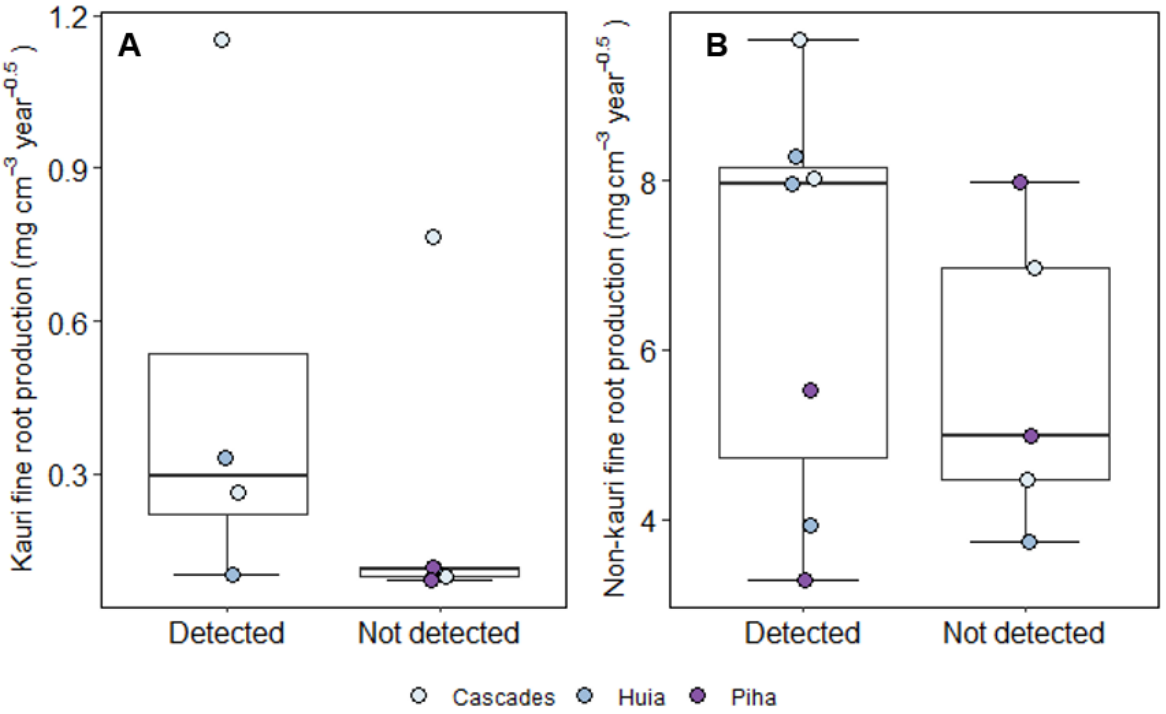

Figure 11. Fine root production (mg cm^{-3} $year^{-0.5}$) for A) kauri and B) non-kauri fine root groups, grouped by pathogen (PA) detection status and colour-coded by site. Lower and upper hinges correspond to the 25th and 75th percentiles.

3.2.2. Fine root turnover

There were no significant differences in fine root turnover rates, of both kauri and non-kauri fine roots, between site and plot type (Table A3). Furthermore, no significant difference was found between fine root turnover rates of trees at which PA has been detected (N = 7, mean ± SE = 3.76 $year^{-0.5}$ ± 1.13 $year^{-0.5}$) and trees at which PA has not been detected (N = 5, mean ± SE = 4.79 $year^{-0.5}$ ± 3.61 $year^{-0.5}$). Variation in fine root turnover of trees at which PA has not been detected (33.17 $year^{-0.5}$) was more than double that of the turnover of trees at which PA has been detected (12.69 $year^{-0.5}$) (Figure A1B).

Non-kauri fine root turnover was significantly greater than kauri fine root turnover ($H(1)$ = 13.2, P < 0.01) (Table A3). The mean kauri fine root turnover in trees where PA has been detected (N = 4) was 0.27 $year^{-0.5}$ ± 0.12 $year^{-0.5}$ and the mean at trees where PA has not been detected (N = 4) was 0.06 $year^{-0.5}$ ± 0.04 $year^{-0.5}$ (Figure 12A). In comparison, the mean non-kauri fine root turnover for PA-detected trees (N = 7) was 3.74 $year^{-0.5}$ ± 1.62 $year^{-0.5}$ and for

non-detected trees (N = 4) it was 9.52 year$^{-0.5}$ ± 7.06 year$^{-0.5}$ (Figure 12B). There were no significant differences in kauri and non-kauri fine root turnover between PA detection status, site, and control and symptomatic plot type. Although there were no significant differences between sites, the higher turnover rates in non-kauri fine roots tended to occur at Cascades and the lower turnover rates at the Huia and Piha sites (Figure 12B). This is not reflected in kauri fine root turnover (Figure 12A).

Similar to what was observed in fine root production, the variance in turnover rates was greater in non-kauri fine roots than in kauri roots. Non-kauri fine root turnover ranged from 0.74 year$^{-0.5}$ to 33.19 year$^{-0.5}$ at PA-detected trees and from 1.10 year$^{-0.5}$ to 12.72 year$^{-0.5}$ at trees where PA has not been detected, whereas kauri fine root turnover rates ranged from 0.02 year$^{-0.5}$ to 0.53 year$^{-0.5}$ at PA-detected trees and from 0.02 year$^{-0.5}$ to 0.19 year$^{-0.5}$ at trees where PA has not been detected.

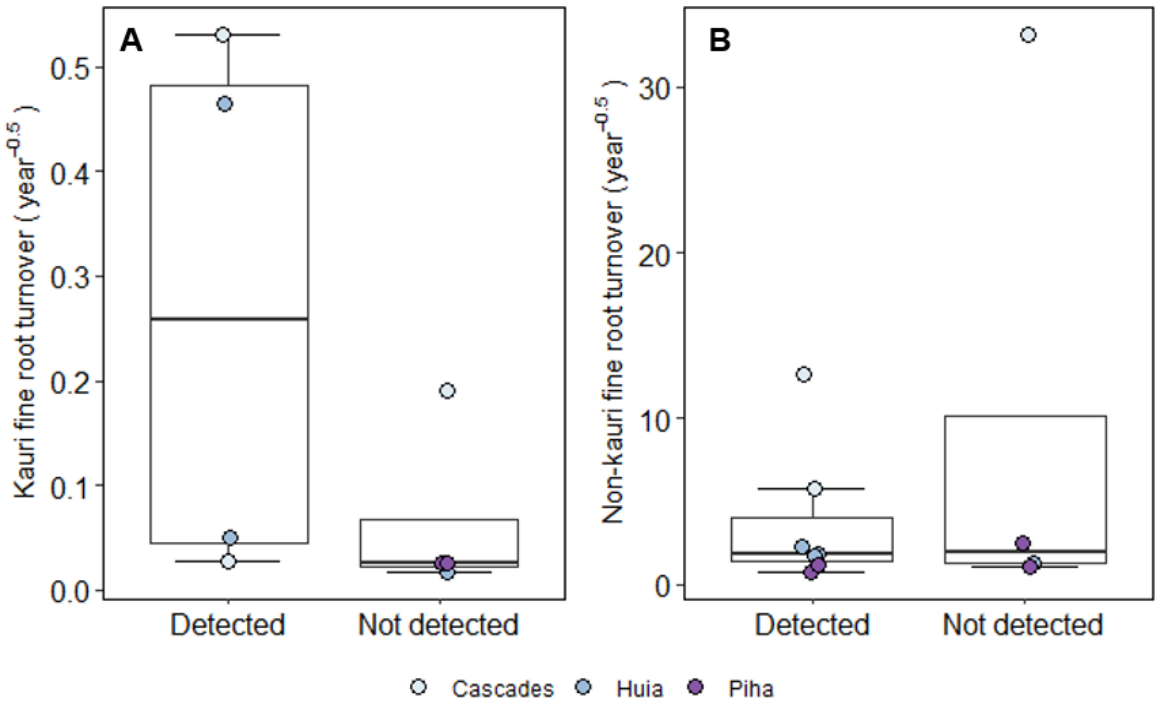

Figure 12. Fine root turnover (year$^{-0.5}$) for A) kauri and B) non-kauri fine root groups, grouped by pathogen (PA) detection status and colour-coded by site. Lower and upper hinges correspond to the 25th and 75th percentiles.

3.3. Correlations

Total standing fine root density and kauri standing fine root density were positively correlated with Oh temperature ($P < 0.05$). Kauri standing fine root density was negatively correlated with kauri C/N ratio ($P < 0.05$). Non-kauri standing fine root density was correlated with Oh depth ($P < 0.05$) (Figure 13A), forest floor depth, soil N, kauri C, tree height and DBH ($P < 0.01$) (Table 6).

Total fine root production and non-kauri fine root production were positively correlated with kauri fine root C concentration and C/N ratio (Table 7; Figure 13B). Kauri fine root production was positively correlated with Oh depth and forest floor depth ($P < 0.02$). Total fine root turnover and non-kauri fine root turnover were positively correlated with Oh depth, tree height and DBH, but not forest floor depth (Table 7).

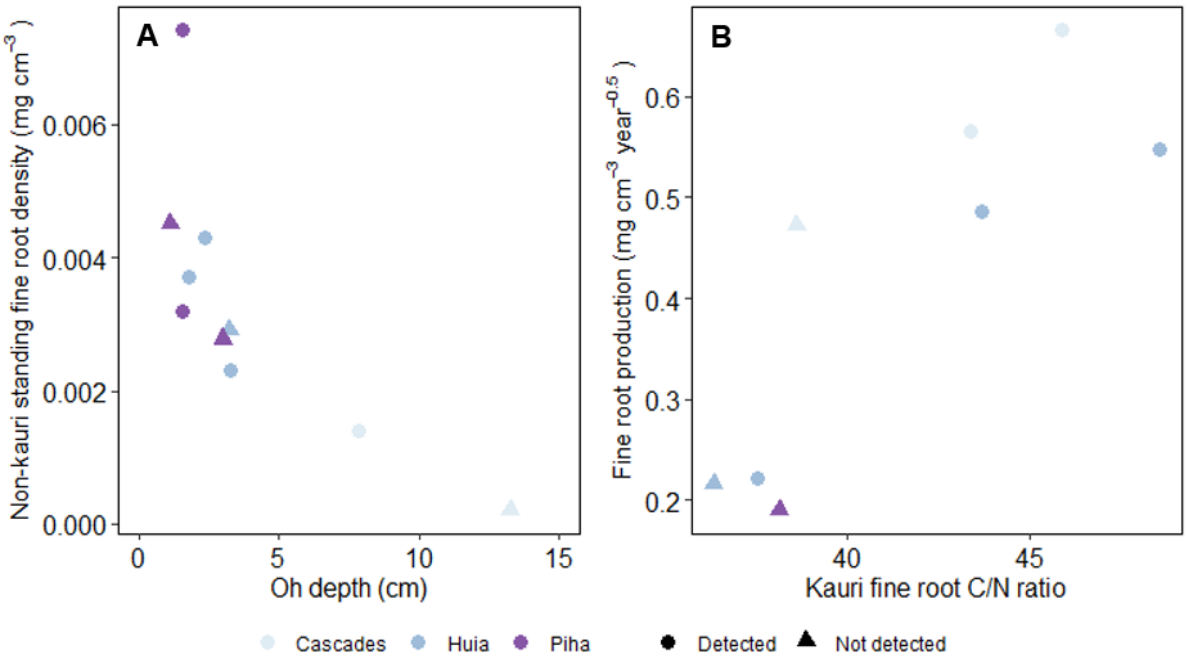

Figure 13. Scatterplots of A) Non-kauri standing fine root density (mg cm^{-3}) and Oh depth (cm) and B) fine root production (mg cm^{-3} year$^{-0.5}$) and kauri fine root C/N. Points are colour-coded by site: light blue representing the Cascades, the dark blue representing Huia and purple representing Piha; and shape: circle for PA detected and triangle for sites where PA had not been detected. Lower and upper hinges correspond to the 25th and 75th percentiles.

Table 6. Correlation analysis between standing fine root density (frd) and biophysical characteristics. Statistically significant values are shaded with dark orange ($P \leq 0.01$) to pale orange ($P \leq 0.05$). See Table A2 for more details.

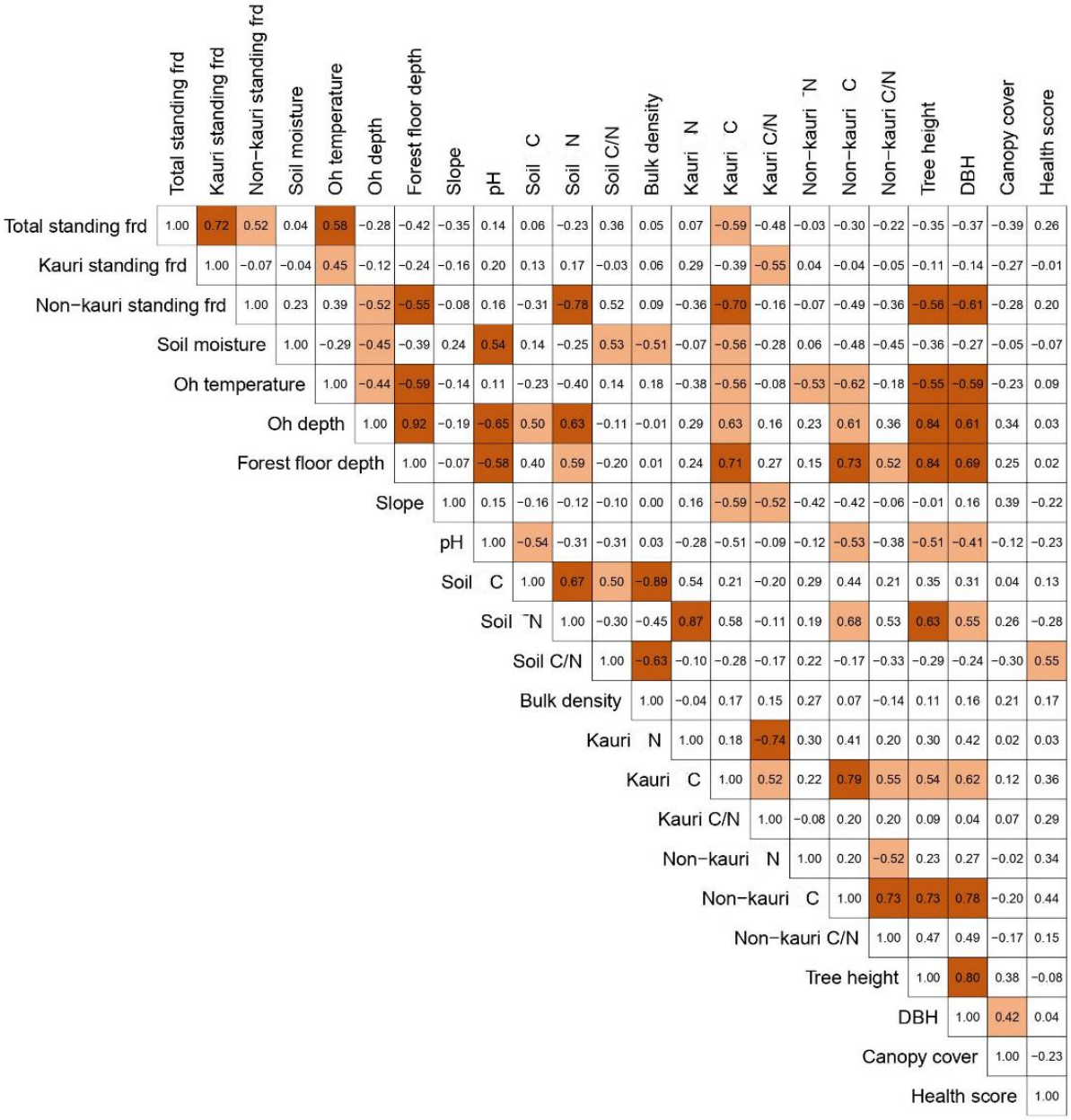

Table 7. Correlation analysis of fine root production and turnover against soil characteristics, and biophysical characteristics. Statistically significant values are shaded with dark orange ($P \leq 0.01$) to pale orange ($P \leq 0.05$). See Table A2 for more details.

	Soil moisture	Oh layer temp.	Oh depth	Forest floor depth	Slope	Soil pH	Soil C	Soil N	Soil C/N	Bulk density	Kauri N	Kauri C	Kauri C/N	Non-kauri N	Non-kauri C	Non-kauri C/N	Tree height	DBH	Canopy cover	Canopy health score
Total fine root production	-0.18	-0.05	0.50	0.41	-0.43	-0.07	0.24	0.70	-0.66	0.12	-0.26	0.72	0.84	0.48	0.41	0.09	0.38	0.23	0.28	0.51
Kauri fine root production	-0.56	0.09	0.88	0.73	-0.15	-0.48	0.57	0.72	-0.45	-0.23	0.38	0.74	0.30	-0.33	0.54	0.70	0.62	0.23	0.38	0.23
Non-kauri fine root production	-0.03	-0.14	0.47	0.36	-0.24	0.16	-0.05	0.25	-0.38	0.19	-0.48	0.38	0.76	0.17	0.14	-0.01	0.17	0.15	0.29	0.34
Total fine root turnover	-0.51	0.26	0.73	0.63	0.24	-0.57	0.80	0.76	-0.04	-0.20	0.47	0.46	-0.06	-0.11	0.63	0.61	0.93	0.73	0.55	0.06
Kauri fine root turnover	-0.10	-0.16	0.57	0.64	-0.04	-0.09	0.34	0.49	-0.41	-0.22	-0.22	0.53	0.72	-0.25	0.34	0.46	0.25	-0.07	0.14	0.55
Non-kauri fine root turnover	-0.52	0.26	0.72	0.63	0.26	-0.57	0.81	0.75	0.00	-0.22	0.49	0.44	-0.10	-0.15	0.63	0.62	0.92	0.73	0.54	0.04

Chapter 4. Discussion

4.1. Standing fine root density

The mean total standing fine root density (excluding leftovers) across all kauri trees in this study was 16.94 mg cm^{-3} ± 3.59 mg cm^{-3} (N = 22), which is greater than what has been observed in other conifer-dominated forests (12.2 mg cm^{-3}) (Bauhus & Messier, 1999) (Table A4) and greater than the mean fine root density of temperate forests in the northern hemisphere (10.68 mg cm^{-3} ± 0.36 mg cm^{-3}) (Wang *et al*., 2019). However, the results are within the range of root density estimates (5.36 mg cm^{-3} to 29.25 mg cm^{-3}) reported for a kauri-dominated forest in the Huia area, Waitākere Ranges Regional Park (van der Westhuizen, 2014). The mean total fine root density was greater than the values reported in the soil organic layer (Finér *et al*., 2017) and lower than the values reported for standing fine root density in the soil mineral layer in temperate mixed forests (Bauhus & Messier, 1999; Finér *et al*., 2017). Fine roots in the soil organic layer are typically more exposed to environmental fluctuations and stressors than deeper roots which results in greater root mortality, particularly in the upper soil organic layer (Braddeley & Watson, 2005). The deep litter and soil organic layers typically produced by kauri may provide greater protection for fine roots to environmental stressors, thereby supporting greater standing fine root density in the Oh layer.

The were significant differences in total standing fine root density between Cascades and the other sites, and there was a general increase in mean fine root density from Cascades to Piha, which represent the most and least mature stand in this study respectively (Table 3, Figure 9). These results suggest that stand maturity may be a factor influencing fine root density. This differs from previous studies reporting that fine root biomass increases with stand maturity (Vanninen and Mäkelä 1999; Helmisaari *et al*., 2002; Claus & George, 2005; Fujimaki *et al*. 2007; Hu *et al*., 2021). Fine roots reach peak biomass at the point of canopy closure and then generally continue to decline at a slow rate to eventually reach a stable biomass (Yuan & Chen, 2010; Jagodzinski & Kalucka, 2011). The higher fine root density at Piha could be due to the Cascades forest stand being closer to the stage of stable biomass. Further research into the relationship between standing fine root density and stand maturity is needed as these observations were generally made in studies using fine root biomass values (i.e. g m^{-2}) (Yuan & Chen, 2010; Jagodzinski & Kalucka, 2011).

Fine root density varies considerably across different forest ecosystems, between species, and within the same species (Vogt *et al*., 1983; Bauhus & Messier, 1999; Noguchi *et al*., 2007; Jagodzinski *et al*., 2016; Finér *et al*., 2017). The results of this study found similar findings, demonstrated by the high variability in standing fine root density between sites; Piha exhibited significantly greater standing fine root density than the Cascades site ($P < 0.01$).

4.2. Fine root production and turnover

The annual mean total fine root production across all kauri trees was 7.41 mg cm^{-3} $year^{-1}$ ± 1.48 mg cm^{-3} $year^{-1}$. Non-kauri fine root production (12.46 mg cm^{-3} $year^{-1}$ ± 1.24 mg cm^{-3} $year^{-1}$) was significantly greater than kauri fine root production (0.67 mg cm^{-3} $year^{-1}$ ± 0.25 mg cm^{-3} $year^{-1}$) (Figure 11). Annual fine root turnover values were extrapolated from the half year results found in this study to allow comparison with literature. The annual mean fine root production of kauri fine roots lies within the range reported for fine root production of Scots pine forests (0.0 mg cm^{-3} $year^{-1}$ to 3.56 mg cm^{-3} $year^{-1}$) (Konôpka *et al*., 2005).

Fine root production was reported as density in this study due to the difference in Oh layer depth between sites limiting the use of a standard Oh depth for ingrowth core burial. Values have been converted into *area* estimates (see Appendix) to allow comparison with other studies on fine root production; estimates are likely to differ from actual biomass values as a result of the inconsistency of Oh depth. Total annual fine root production of kauri stands in this study (543 g m^{-2} $year^{-1}$ ± 113.5 g m^{-2} $year^{-1}$) was highly variable ranging from 13.83 g m^{-2} $year^{-1}$ to 1527.13 g m^{-2} $year^{-1}$. Production was within the range of estimates reported for mixed coniferous forest stands (45 g m^{-2} $year^{-1}$ to 482 g m^{-2} $year^{-1}$) (McKay & Malcolm, 1988; Burke & Raynal, 1994; Jackson *et al*., 1997; Hertel *et al*., 2013) and temperate European forests (250 g m^{-2} $year^{-1}$ to 428 g m^{-2} $year^{-1}$) (Finér *et al*., 2011; Neumann *et al*., 2020). Mean annual kauri fine root production was 56.84 g m^{-2} $year^{-1}$ ± 20.75 g m^{-2} $year^{-1}$ and lies within the range reported for Norway Spruce (19 g m^{-2} $year^{-1}$ to 715 g m^{-2} $year^{-1}$) (McKay & Malcolm, 1988; Majdi & Andersson, 2005).

The high variability in fine root production in different kauri stands (sites) supports findings in past fine root studies which show high variability between and within tree species and forest types (Noguchi *et al*., 2007; Lei & Bauhus, 2012; Wang *et al*., 2018). This suggests stand-

related factors such as stand age, management history and microclimate, may be substantial influences on fine root production. Some of the variation in fine root production between studies is likely a result of differences in methodology for sampling and calculation of estimates (Vogt *et al*., 1998; Hendricks *et al*., 2006). The review by Hendricks *et al*. (2006) on methods for estimating fine root production concluded that ingrowth cores generally underestimate values and that the minirhizotron technique is a more reliable method. However, it is not possible to obtain information on fine root chemistry as the minirhizotron technique is a non-destructive fine root sampling method (Majdi, 1996). Rates of fine root production in past studies may be lower due to the use of a different definition of fine roots, for example, Majdi & Andersson (2005) classified fine roots as those ≤ 1 mm in diameter. Fine root production values are thus missing the contributions of fine roots in the 1 mm–2 mm size class. The inconsistency in defining 'fine roots' in forest literature makes comparisons between studies difficult.

The mean annual fine root turnover was 3.45 year^{-1} ± 1.79 year^{-1} and ranged from 0.02 year^{-1} to 33.19 year^{-1}. A global analysis of fine root turnover for terrestrial ecosystems reported an average fine root turnover rate of 0.52 year^{-1} and ranged from 0.02 year^{-1} to 2.64 year^{-1} (Gill & Jackson 2000). The estimates of fine root turnover also fall within the global range and the ranges reported for coniferous forests (0.28 year^{-1}–1.80 year^{-1}) (Majdi & Andersson, 2005; Brunner *et al*., 2009; Hertel *et al*., 2013), and coniferous forests in temperate ecosystems (0.5 year^{-1}–0.7 year^{-1}) (Nadelhoffer *et al*., 1985; Burke & Raynal, 1994; Ruess *et al*., 1996; An *et al*., 2017). The mean annual fine root turnover of kauri fine roots and non-kauri fine roots was 0.17 year^{-1} ± 0.08 year^{-1} and 5.84 year^{-1} ± 1.79 year^{-1}, respectively. Non-kauri fine root turnover was significantly greater than kauri fine root turnover (P = 0.03). A larger proportion of fine roots of non-dominant species has been reported in conifer-dominated forest stands (An *et al*., 2017). In a Norway spruce–dominated forest stand in northern Sweden, Norway spruce fine root turnover (0.5 year^{-1}) was lower than the turnover rate of the understorey vegetation (0.9 year^{-1}–1.1 year^{-1}) (Majdi & Andersson, 2005). Low turnover of kauri roots may be an adaptive strategy employed by more stress tolerant trees (Fogel, 1983), such as by kauri trees to help retain nutrients in the shallower O horizons as part of influence on the surrounding soil conditions. The greater turnover of non-kauri fine roots may be explained as the result of natural differences in species fine root turnover rates (Yuan *et al*., 2010). Sun *et al*., (2016) found perennial herbaceous species had more rapid fine root turnover than woody species due

to having less persistent belowground tissue and lowered fine root lifespans. The large difference in turnover between kauri and non-kauri fine roots may also be, in part, a consequence of PA infection causing fine root loss in kauri given the typical impact of root loss found in *Phytophthora* species (Rhoades *et al*., 2003; Corcobado *et al*., 2013 Jung *et al*., 2013) (see Section 4.4.).

Comparison of fine root turnover rate with other studies may be confounded by differences in defining the size of fine roots. Gill & Jackson (2000) found that global fine root turnover rates decrease with root size: in the smallest size class (0 mm–1 mm diameter) fine roots had a turnover rate of 1.2 $year^{-1}$, and this rate reduced to 0.10 $year^{-1}$ in the 0 mm–10 mm diameter size class. The considerable reduction in fine root turnover rates with increasing root diameter size suggests that even a small difference in the size definition of fine roots can drastically influence reported values of fine root turnover rates.

The majority of fine root studies report standing fine roots by biomass (g m^{-2}) rather than by density (g m^{-3}). Estimates vary considerably between units (Vogt *et al*., 1995) hence comparison of results with other studies is difficult. Furthermore, the standing fine root density and fine root production estimates in this study includes both living and dead roots whereas other studies generally only include living roots (Bauhus & Messier, 1999; Finér *et al*., 2007; Finér *et al*., 2017). Fine roots tend to experience rapid turnover (Hendrick & Pregitzer, 1993). Thus, the estimates of standing fine root density and fine root production in this study may be overestimated.

4.3. Factors influencing fine root characteristics

Standing fine root density, fine root production and fine root turnover were significantly correlated with fine root-, soil-, and tree-related variables (Table 6; Table A2). The most commonly reported influencers on fine roots are soil temperature, soil pH, soil fertility (nutrient availability), climate and tree age (King *et al*., 2002; Alvarez-Uria & Körner, 2007; Finér *et al*., 2011; Abramoff & Finzi, 2015; Förster *et al*., 2021).

Total standing fine root density and kauri standing fine root density were positively correlated with Oh temperature ($P < 0.05$). An increase in fine roots with soil temperature has been well documented (Gill & Jackson, 2000; Alvarez-Uria & Körner, 2007; Abramoff & Finzi, 2015; Wang *et al*., 2018). Warmer soil temperatures are typically associated with higher rates of root respiration and metabolic activity (Pregitzer *et al*., 2000; Lee & Jose, 2003) resulting in greater root growth. Pregitzer *et al*. (2000) suggests the increase in temperate forest may be due to increased N mineralisation, influencing N availability. Changes in soil temperature alongside changes in other essential resources due to increased temperature, such as nitrogen availability, could explain the increase observed in total and kauri standing fine root density with Oh temperature.

There were no significant correlations between soil moisture and fine root characteristics. The responses of fine roots to soil moisture have been typically associated with the alleviation of drought, and an increase in water has been documented to increase plant productivity and root longevity, reducing fine root turnover (Meier & Leuschner, 2008; McCormack & Guo, 2014). While the Waitakere ranges can be affected by drought (Awasthi, 2018), the kauri trees in this study were not water-limited. Thus, the findings in this study are consistent with the observations of Fukuzawa *et al*. (2013) in that soil moisture was not a key driver of fine root growth in temperate forests in the absence of severe drought.

Soil pH was not a key factor influencing fine root characteristics in this study. The soil pH of kauri trees in this study ranged from 3.6 to 5.4, which is more acidic than the pH range observed by Lee & Jose (2003) (6.0 ± 0.4) in conifer plantations but lies within what has previously been observed in kauri-dominated forests (Silvester, 2000; Wyse, 2012, Wyse & Burns, 2014). Acidic soils are generally associated with reduced root growth and lowered metabolic processes (Marschner, 1989; Vanguelova *et al*., 2004; Helmisaari *et al*., 2009). However, fine roots of kauri and other species within the vicinity of kauri are likely to be adapted to the acidic soil conditions formed by kauri trees, while these conditions act as barriers to less tolerant species. Therefore, soil pH is unlikely to have a major influence on fine root density, particularly in mature stands with well-developed soil organic layers.

Total fine root production was significantly positively correlated with kauri root C concentration and kauri root C/N ratio. Non-kauri fine root production was only significantly

correlated with an increase in kauri C/N ratio (Figure 13B; Table 7). Kauri standing fine root density was negatively correlated with kauri C/N ratio (Table 6). These results suggest that increased carbon allocation to, or uptake by, kauri fine roots is associated with an increase in total fine root production and non-kauri fine root production, and a decrease in kauri standing fine root density. Kauri C/N ratio was greater, although no significant, in trees where PA had been detected suggesting trees may have greater fine root kauri C/N ratios as a potential impact of PA presence impeding fine root functioning, creating the need for greater C allocation to fine roots. This could explain the increase in non-kauri fine root production with an increase in kauri C/N ratio.

In this study, kauri fine root production, total fine root turnover and non-kauri fine root turnover were positively correlated with Oh depth (Table 7). Typically, an increase in soil organic matter improves nutrient availability (Persson, 2012) and is associated with an increase in fine root biomass (Schenk & Jackson, 2002; Zielonka *et al*., 2021). The reverse is observed in kauri fine roots, and this may be a product of the unique properties of the soil organic layer beneath kauri trees, inhibiting plant growth of competing neighbouring species and lowering root competition (Verkaik & Braakhekke 2007; Wyse, 2012). The litter layer and soil layers beneath kauri are often increasingly N limited with depth (Silvester & Orchard, 1999; Silvester, 2000). Therefore more fine roots may be required to access the small amount of available N. This could explain why kauri fine root production increases with Oh depth. Non-kauri standing fine root density was negatively correlated with Oh depth (Figure 13A), forest floor depth and soil N (Table 6). Litter and soil beneath the canopy of kauri trees become increasingly N-limited with depth (Silvester & Orchard, 1999; Padamsee *et al*., 2016). Thus, the finding of a decline in non-kauri standing fine root density with greater Oh depth is consistent with other studies on soil N availability as a limiting factor to fine root growth (Nadelhoffer, 2000; Majdi & Andersson, 2005; Li *et al*., 2021a).

The increase in fine root turnover with Oh depth is consistent with findings by Baddeley & Watson (2005) who suggest that root turnover is faster with shallower soil depth. This may be due to the role of fine roots as the sites of resource uptake in forest ecosystems. Newer fine roots are more metabolically active that older roots (Emmet *et al*., 2014). Baddeley & Watson (2005) suggest that at shallower soil depths (< 10 cm) fine roots are exposed to greater environmental fluctuations and stressors than deeper roots, which encourages faster turnover.

An increase in total- and non-kauri fine root turnover was significantly correlated with an increase in tree height and DBH. These are measurements of tree size and also indicators of tree maturity. This finding is consistent with other studies on tree maturity (Baddeley & Watson, 2005), DBH (Cai *et al*., 2019), and tree size (McCormack *et al*., 2012) as factors influencing fine root longevity and turnover rates.

The significant correlation between fine root turnover and tree height and DBH could be explained as result of the physiological change in fine root distribution. Studies have observed an increase of more wide spreading fine roots with tree size and maturity, this has been found to positively affect root turnover (Day *et al*., 2001; Grulke & Retzlaff, 2001; Baddeley & Watson, 2005). Changes in fine root distribution with maturity have been observed in kauri trees, Steward & Beveridge (2010) reported that the root system of kauri shifts as the tree matures, from a well-developed tap root to widely branching lateral roots and deep peg roots. More widely branching roots may promote greater fine root production and mortality. Kauri trees with greater height and DBH likely exert a wider influence on their surrounding soil chemistry supporting a wider diversity of species dependant on the presence of kauri (Wyse *et al*., 2014). More diverse species assemblages have been found to increase fine root turnover rates due to differences in fine root longevity between species and high fine root competition intensity in species rich sites (Jacob *et al*., 2014; Williams *et al*., 2017; Ma & Chen, 2018), potentially explaining some of the difference in fine root turnover with tree height and DBH.

The results of this study suggest that kauri fine root C and N content, Oh depth and tree size are related to fine root characteristics. As multiple factors have been identified, this suggests that differences in fine roots are the result of the interactions between multiple variables. This is supported by Kramer-Walter & Laughlin (2017) who suggest no one driver is dominant in influencing fine root density, but rather fine root density is the outcome of multiple drivers that could change at any given time.

4.3. Impacts of *Phytophthora agathidicida* infection on fine roots

Kauri standing fine root density was significantly greater at trees where PA was not detected ($P = 0.01$) and in control plots ($P < 0.01$), in comparison to trees where PA was detected and

to symptomatic plots, respectively (Table 3). Kauri and non-kauri standing fine root density did not differ significantly between PA detection statuses nor plot type. As most *Phytophthora* species cause fine root loss (Erwin & Ribeiro, 1996; Jung *et al*., 2000, Fleischmann *et al*., 2004; Sena *et al*., 2018; Mora-Sala *et al*., 2019), it was hypothesised that standing fine root density of kauri trees would be lower in symptomatic plots and at trees where PA has been detected (hypothesis 1). The results of this study support this hypothesis. The lack of a difference in non-kauri standing fine root density between trees where PA has and has not been detected suggests that PA presence is mainly affecting kauri fine roots.

Fine root production differed significantly with pathogen presence. Total fine root production was greater at trees where PA has been detected compared to trees where PA has not been detected ($P = 0.03$), suggesting PA may be promoting total fine root production. Fine root production and turnover in the non-kauri root group was significantly greater than what was found in production ($P = 0.03$) and turnover ($P < 0.01$) in the kauri root group. It was hypothesised that non-kauri standing fine root density and non-kauri fine root production would be greater in symptomatic plots and at trees where PA has been detected (hypothesis 2), the results partially support this hypothesis. Non-kauri standing fine root density was not greater at trees detected with PA, but non-kauri fine root production was greater. The lower fine root production and turnover in the kauri root group suggests that the increase in total fine root production is driven by an increase in non-kauri fine root production and rapid turnover. The results indicate that PA presence is beneficial to non-kauri root growth.

The greater non-kauri fine root production and turnover observed at trees where PA has been detected suggests the loss in kauri fine roots is replaced by non-kauri fine roots. A shift in fine root abundance will affect species functioning given that fine roots are an important component in maintaining aboveground productivity (Bowen, 1985) and plant performance (Casper & Jackson, 1997). The rate and severity of *Phytophthora* species on fine root loss varies greatly between species (Mora-Sala *et al*., 2019; Scott & Williams, 2019). PA is likely associated with progressive loss rather than aggressive rapid root necrosis in kauri fine roots since tree mortality occurs over a long period of time (Bradshaw *et al*., 2020). Progressive fine root loss will affect physiological resilience to environmental stressors as fine root functioning declines (D'Souza *et al*., 2021). Thus, the increase in non-kauri fine roots in sites where PA has been

detected may indirectly reduce kauri resistance to PA through the increase in belowground interspecific competition (Casper & Jackson, 1997).

A shift to a greater fine root dominance of non-kauri species may have future consequences for forest biodiversity. Kauri-dominated forests are characterised by the considerable influence of kauri on its surrounding environment (Wyse, 2012). As a foundational species, kauri play a significant role in supporting distinctive plant species assemblages in its vicinity (Wyse *et al*., 2014). This study suggests kauri trees experience root loss in the presence of PA, therefore adversely affecting kauri plant performance. Fine roots and the associated mycorrhizal fungi are essential for resource uptake in the nitrogen limited soils produced by kauri trees (Padamsee *et al*., 2016). The role of fine roots in supporting aboveground productivity and plant performance has been well documented (Bowen, 1985; Casper & Jackson, 1997; Finér *et al*., 2007). A loss in kauri fine roots may cause affect aboveground biomass and productivity of kauri. The influence of kauri on the surrounding soil conditions is largely maintained by litter and the already developed organic layer. A decline in aboveground productivity would affect the amount of litter produced by kauri trees, thereby over time, reducing the influence of kauri as the soil conditions can no longer be maintained. Fine root turnover is an important source of C and organic matter to the soil (Fogel, 1983) and influence soil CO_2 efflux in kauri-dominated forest systems (Schwendenmann & Macinnis-Ng, 2016). Kauri fine root necromass may also play a role in maintaining the influence of kauri on soil conditions given the withdrawal of essential nutrients prior to root death (Fogel, 1983). As non-kauri turnover is heighted with PA presence, the addition of non-kauri organic matter will alter the composition of the soil layers maintained by kauri litter and kauri fine root decomposition. Flow-on effects from this could include a decline or weakened influence of kauri on its surrounding environment, potentially affecting the survival of species dependent on the environmental conditions created by kauri. This is supported by Landers *et al*. (2018) and Bishop *et al*. (2013) who found kauri dieback acted as a negative driver in forest biodiversity in the Waitākere Ranges Regional Park.

There were no significant differences in non-kauri fine roots between pathogen detection statuses, sites and plots (Table A3). Non-kauri standing fine root density, fine root production and turnover was similar in trees where PA has and has not been detected, suggesting the impact of PA presence on non-kauri species in the vicinity of the measured trees is negligible. The host range of PA is wider than kauri, and apart from kauri, several plant species native to

New Zealand —e.g. rewarewa (*Knightia excelsa*), mingimingi (*Leucopogon fasciculatus*), and tānekaha (*Phyllocladus trichomanoides*)— have the potential to be carriers or hosts of PA (Ryker, 2016). Thus, the impact of PA presence and infection can have some adverse effects on non-kauri fine roots. However, kauri fine roots appear to be more susceptible to infection and fine root loss.

Chapter 5. Recommendations for future research

This study found that fine roots are an important component in understanding the impacts of PA on kauri. Here, several knowledge gaps for future research are identified to further our understanding of the role of fine roots in kauri-dominated forest ecosystems.

Comparison of estimates of standing fine root density and fine root production with other fine root studies was limited due to two key challenges: the inclusion of both living and dead roots in the total estimates, and the calculation of estimates by *volume* rather than by *area*. Roots were not able to be separated due to difficulty in distinguishing live from dead post-freezing. Freezing of samples was necessary due to time constraints arising from the need to install ingrowth cores within the same time period. Root necromass generally makes up a sizeable portion of fine root biomass (Makkonen & Helmisaari, 1999; Scott & Williams, 2019), so the inclusion of dead roots within the estimates inflates standing fine root density and fine root production.

Fine roots in this study were calculated by volume as the Oh layer was highly variable between sites. The majority of past fine root studies calculate fine roots by unit *area* (Bauhus & Messier, 1999; Finér *et al*., 2017; Förster *et al*., 2021). Thus, comparison between the units is difficult because values vary considerably. The results of this study found a difference in fine root characteristics with maturity (tree size, DBH). Therefore, it would be beneficial to evaluate fine root characteristics of stands of similar maturity to increase understanding of how fine root productivity of kauri-dominated forests differs between stands. This would also allow for the more standard calculation by *area* for comparisons with global studies.

This study measured standing fine root density, fine root production and turnover using ingrowth cores that had been buried for 6 months in the spring-summer growing season. Values were then doubled to estimate annual density, production, and turnover. However, fine root growth differs with seasonality (Konôpka *et al*., 2005). Ingrowth core methods have been found to retard root colonisation in the first year of burial (An *et al*., 2017) therefore fine roots studies on kauri forests would benefit from longer term (≥ 2 years) approaches.

This study identified an increase in non-kauri fine root dominance in trees where PA had been detected which may have adverse effects on species biodiversity. Quantification of roots and

grouped at the species level would be useful in informing whether a loss in kauri fine roots affects surrounding species composition and, in particular, how the diversity of kauri dependent species may be affected.

A direction this study did not explore was the root trait variation of fine roots in kauri-dominated forests affected by PA. Fine root morphological traits such as specific root length, root diameter and root tip frequency, are important indicators of a species' strategy to cope with environmental change (Freschet *et al*., 2021; Förster *et al*., 2021). Root responses to changing environments appear to be species-specific (Finér *et al*., 2011; Fuchs *et al*., 2020), so generalisations are difficult. Further research into how functional traits of fine roots in kauri-dominated forest change in the presence and absence of PA will be crucial in understanding kauri resistance and resilience to PA and overall impacts of PA on kauri forest ecosystem functioning.

Chapter 6. Conclusions

The aim of this study was to increase understanding of belowground systems and, in particular, of fine roots in kauri-dominated forests and the potential impacts of *P. agathidicida*. This was done by:

i) quantifying the standing fine root density, fine root production and fine root turnover of kauri trees affected by the pathogen *P. agathidicida* in three sites in the Waitākere Ranges Regional Park using soil core and ingrowth core methods. Standing fine root density was generally greater than what has been reported in other studies on fine root properties. However, estimates fit within the range for the kauri forests in the Waitākere Ranges Regional Park (van der Westhuizen, 2014). Estimates of fine root production and turnover largely fall within global estimates, but typically had greater variability.

ii) determining what variables were influencing differences in standing fine root density, fine root production and fine root turnover at the three sites. The main variables influencing fine root characteristics in the kauri trees measured in this study were soil temperature, kauri C and C/N ratio, Oh depth, tree height, and DBH. Consistent with global patterns, temperature was strongly influencing standing fine root density. Non-kauri root production increased by higher levels of kauri C and C/N ratio, perhaps as an indirect effect of PA presence affecting kauri fine root strategies such as carbon allocation. Oh depth was strongly positively correlated with fine root production, turnover and negatively with non-kauri standing density. Fine root turnover appears to increase with tree maturity and size, following shifts in kauri root systems to enhance fine root activity, and potentially due to, in part, the unique species communities associated with more mature kauri stands enhancing turnover. The identification of multiple influences on fine roots suggests kauri-dominated forest root stock and turnover is the outcome of the interaction of a variety of variables.

iii) evaluating the impact of *P. agathidicida* on fine roots and applying this knowledge to predict long-term impacts on kauri-dominated forests in response pathogen pressure. The results of this study found that kauri fine roots were more susceptible to root loss than non-kauri fine roots. PA infection appears to be positively affecting non-kauri fine roots by directly causing kauri fine root loss, and also indirectly by reducing kauri fine root resilience to stressors, thus facilitating greater dominance of non-kauri fine roots and consequently non-kauri species in

kauri-dominated forests. This switch in dominance will potentially cause a loss in biodiversity associated with kauri. A reduction in kauri dominance will lead to the slow decline in the function of kauri as a foundational species in kauri-dominated forests.

This study has contributed towards New Zealand's root ecology and kauri dieback research by broadening understanding on the environmental influences affecting fine root characteristics in kauri-dominated forests. *P. agathidicida* infection has been demonstrated to potentially result in severe consequences for kauri forest function stemming from changes in fine root activity. Therefore, further research into fine root plasticity and the role of fine roots in mediating belowground processes are essential to predict ecosystem impacts of pathogen presence and other environmental stressors.

Appendix

Table A1. The 5-scale canopy health score used to quantify the severity of kauri dieback symptoms in a tree's canopy, based on Dick & Bellgard (2010) and modifications by Froud *et al.* (2022).

Health score	Canopy symptoms
1	Healthy crown with no loss in foliage, tree shows no signs of dieback
2	Some canopy or foliage thinning
3	Canopy thinning with some branch dieback
4	Severe loss in canopy, severe dieback symptoms
5	Severe symptoms of dieback, tree is dead

Table A2. List of variables used in the correlation analyses (Table 6; Table 7)

Fine root estimates	**Fine root properties**
Total standing fine root density	Kauri N
Kauri standing fine root density	Kauri C
Non-kauri standing fine root density	Kauri C/N
Fine root production	Non-kauri N
Kauri fine root production	Non-kauri C
Non-kauri fine root production	Non-kauri C/N
Fine root turnover	
Kauri fine root turnover	
Non-kauri fine root turnover	

Soil properties	**Tree properties**
Soil moisture	Height
Oh layer temperature	Diameter at breast height (DBH)
Oh depth	Canopy cover
Forest floor depth	Height
Slope	Canopy healthscore
pH	
Soil C	
Soil N	
Soil C/N	
Soil bulk density	

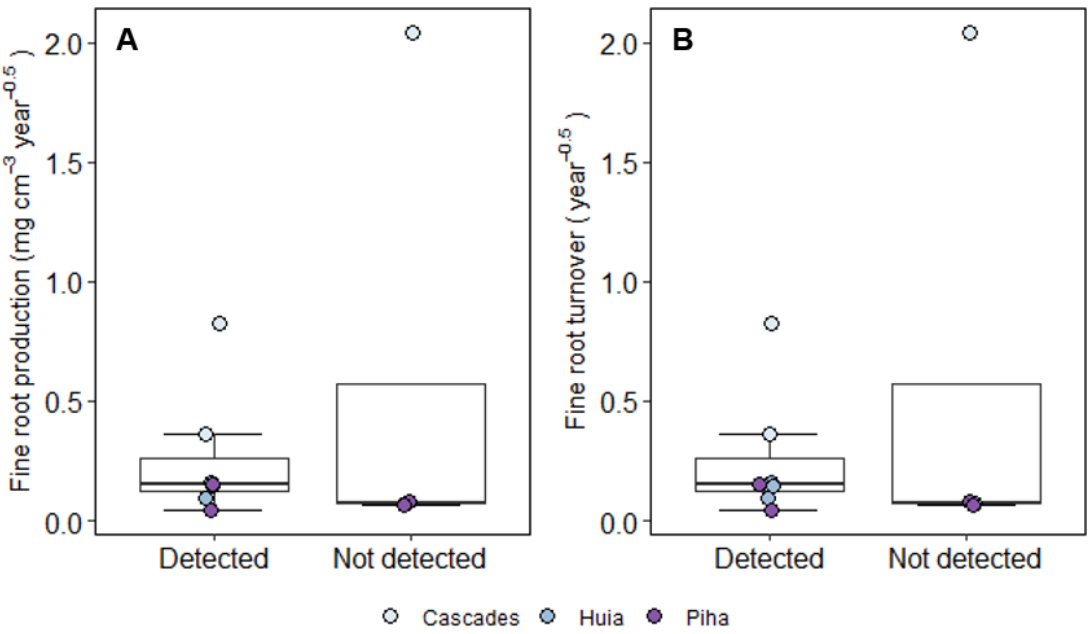

Figure A1. A) Fine root production (mg cm^{-3} year$^{-0.5}$) and B) fine root turnover (year$^{-0.5}$) grouped by pathogen (PA) detection status for N = 12 kauri trees.

Table A3. Summary of *P*-values of the Kruskal–Wallis and Pairwise Wilcoxon Rank Sum tests performed for estimates of root characteristics grouped by site, plot type and PA detection.

(* denotes $P \leq 0.05$).

	Standing fine root density (mg cm^{-3})			**Fine root production** (mg cm^{-3} $year^{-0.5}$)			**Fine root turnover** ($year^{-0.5}$)		
	Total	Kauri	Non-kauri	Total	Kauri	Non-kauri	Total	Kauri	Non-kauri
Site	<0.01*	0.45	0.08	0.37	0.38	0.47	0.09	0.29	0.09
Cascades-Huia	0.03*	0.69	0.07	0.51	0.80	0.73	0.09	0.80	0.09
Cascades-Piha	<0.01*	0.72	0.06	0.51	0.80	0.73	0.09	0.60	0.09
Huia-Piha	0.234	0.72	0.08	0.69	0.80	0.89	0.34	0.80	0.34
PA detection	0.06	0.01*	0.79	0.03*	0.22	0.37	0.45	0.08	0.85
Plot type	0.29	<0.01	0.31	0.11	0.81	0.63	0.79	0.07	0.58

Table A4. Fine root biomass (g m^{-2}) and density (mg cm^{-3}) values found in the literature. Reported values are underlined, and conversions from biomass to density were made using the calculation in Section 2.4.2. All values are the mean.

Forest type	**Country**	**Soil layer**	**Fine root biomass** (g m^{-2})	**Fine root density** (mg cm^{-3})	**Reference**
Agathis australis dominated forest	New Zealand	organic		16.9	
Agathis australis dominated forest	New Zealand	organic + mineral	800		Schwendenmann & Macinnis-Ng (2016)
Temperate mixed forest	Poland	organic	9.6	0.04	Finér *et al*. (2017)
Temperate mixed forest	Germany	organic	14.6	0.06	Finér *et al*. (2017)
Temperate mixed forest	Romania	organic	22.0	0.09	Finér *et al*. (2017)
Cunninghamia lanceolata plantation	China	organic		1.80	Liao *et al*. (2014)
Temperate mixed forest	Germany	organic + mineral	212		Lei *et al*. (2012)
Populus deltoides plantation	United States	organic + mineral	221	59.02	Lee & Jose (2003)
Pinus taeda plantation	United States	organic + mineral	144	38.46	Lee & Jose (2003)
Fagus sylvatica dominated forest	Italy	organic + mineral	160	53.43	Kwatcho Kengdo *et al*. (2022)
Pinus sylvestris dominated forest	Finland	mineral + forest floor	140		Makkonen & Helmisaari (1999)
Fagus sylvatica dominated forest			389		Finér *et al*. (2007)
Picea abies dominated forest			281		Finér *et al*. (2007)
Pinus sylvestris dominated forest			377		Finér *et al*. (2007)
Temperate mixed forest	Poland	mineral	146	58.4	Finér *et al*. (2017)
Temperate mixed forest	Germany	mineral	142	109.2	Finér *et al*. (2017)
Temperate mixed forest	Romania	mineral	93.6	42.7	Finér *et al*. (2017)

Fine root production estimates were converted into biomass using the equation:

$$fine\ root\ production\ = \frac{dry\ fine\ root\ mass\ (mg)}{\pi\ \times\ 2.25^2\ (cm) \times\ time\ buried\ (year^{-0.5}\ )}$$

In this calculation dry fine root mass (mg) was divided by the area of the ingrowth core (diameter 4.5 cm) and multiplied by the incubation time (6 months). Depth was not standardized for the ingrowth cores and varied between 5 cm and 10 cm.

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