

Physicochemical Characterisation of Soil from Dieback Kauri Forest

Trupti Mohini

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Abstract

Kauri (*Agathis australis*) is an ecologically and culturally significant conifer, endemic to the northern North Island of Aotearoa New Zealand. Kauri trees are designated as foundation species due to their substantial effect on the configuration of distinct surrounding plant communities and significant impact on overall species diversity in kauri forests. Kauri greatly influence the soil conditions underneath their crowns by lowering soil pH, impeding nitrogen cycle, and occasionally creating podzols. In kauri forests, soil has significant influence on the health of the ecosystem by anchoring roots, storing water and nutrients, and providing a habitat for a variety of invertebrates and microorganisms. However, these ancient and iconic kauri trees are threatened with extinction as a result of dieback disease caused by the highly pathogenic and intrusive oomycetes, *Phytophthora agathidicida*. This novel soil and waterborne pathogen has the ability to disturb above and below ground species composition and biogeochemical processes.

This study utilised soil samples from kauri forests located in the Waitākere Ranges Regional Park in Auckland, and Tairua and Whangapoua in Coromandel, to investigate physical and chemical characteristics of soil from beneath healthy kauri trees as well as kauri trees that display dieback disease symptoms. These soil characteristics were compared using two-sample unpaired t-tests and Wilcoxon tests to investigate whether there are differences in the physicochemical characteristics of kauri soil within and between healthy and unhealthy trees.

In both the Auckland and Coromandel regions, unhealthy kauri soil demonstrated significantly higher moisture factor ($p = 0.0481$ in Waitākere and $p = 0.00239$ in Coromandel) and water holding capacity ($p = 0.0224$, $p = 0.0347$) than healthy soil, which may indicate that wetter soil provides more favourable conditions for growth and proliferation of *Phytophthora agathidicida*. Moreover, unhealthy kauri soil in both regions also exhibited significantly higher total carbon ($p = 0.000559$, $p = 0.0235$), total nitrogen ($p = 4.621 \times 10^{-5}$, $p = 0.0318$), and total hydrogen ($p = 0.00953$, $p = 0.0265$) in comparison to healthy kauri soil. The root cause of the elevated content of these elements is likely to be thinning of kauri canopies and defoliation, both symptoms of dieback which add to the acidic, tannin-rich litter. The association with litter was confirmed by using Kendall rank coefficient test to find significant negative correlations between pH and total carbon ($p = 2.58 \times 10^{-5}$) as well as total nitrogen ($p = 0.00762$) in unhealthy kauri soil. Hence, these elements may be useful indicators of the presence of dieback, and thus could help map the spread of the disease.

The findings of this study contribute towards presenting more comprehensive insight into the link between soil physicochemical characteristics and kauri dieback in the Auckland and Coromandel regions. The current study also contributes to the ongoing research into the detection and prevention of dieback disease, and ultimately in the preservation of the remaining kauri stands in Aotearoa New Zealand.

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Attestation of authorship

I hereby declare that this submission is my own work and that, to the best of my knowledge and belief, it contains no material previously published or written by another person (except where explicitly defined in the acknowledgements), nor material which to a substantial extent has been submitted for the award of any other degree or diploma of a university or other institution of higher learning.

Trupti Mohini

Chapter 1: Introduction



Bendle (2019)

1.1 New Zealand forest – historical and environmental factors

Aotearoa New Zealand features very distinctive flora (Salmon, 1996). According to biogeographic theory, the origins and diversity of New Zealand's biota can be traced back to the Mesozoic fragmentation of Gondwana during the Cretaceous period (136-65 million years ago), during which clusters of islands (which included New Zealand) became isolated from the rest of Gondwana due to continental drift by the Great Southern Ocean (Biffin et al., 2010; McGlone et al., 2010; Setoguchi et al., 1998; Stöckler et al., 2002). In the modern age, New Zealand's seclusion from other continental mainland in the southern South Pacific, and its warm, temperate oceanic climate are responsible for the uniqueness of the distribution and ecology of New Zealand flora (McGlone et al., 2010).

Today, the New Zealand archipelago has a large variety of trees (614 species), and displays much greater relative species diversity and abundance than regions with similar temperate climate such as southern Australia, Tasmania, Europe, and northern North America (Leathwick, 2001; McGlone et al., 2010). Even though the land area of the country is not large, its temperate climate and wide latitudinal range create favourable conditions for its high arborescent richness and primary production (Adams & Woodward, 1989; Leathwick, 2001).

Therefore, New Zealand's evergreen forests are categorised as 'oceanic temperate forest', which exhibit much similarity to forests in southern South America and southeast Australia, with respect to both oceanic influences as well as dominant taxonomic groups such as Araucariaceae, Nothofagaceae, Podocarpaceae, and Winteraceae (Adams & Woodward, 1989; Leathwick, 2001; Salmon, 1996). The indigenous forests of New Zealand are largely divided into two main categories: conifer-hardwood forests and beech forests (Salmon, 1996). The evergreen conifer-hardwood forests, dominated by Araucariaceae, occupy the warmer, more fertile terrain in the northern region while cooler, drier, and less fertile areas of southern regions are covered with beech forest, dominated by Nothofagaceae (Leathwick, 1995; McGlone et al., 2010).

1.2 New Zealand kauri ngahere

Fossil records show that by the middle of the Cretaceous period (110-80 million years ago), Araucariaceae (the primitive ancestors of kauri) along with other species of Podocarpaceae such as rimu, kahikatea, miro, mataī, and tōtara initiated the formation of modern forests of New Zealand (Halkett & Sale, 1986). In the present day, Araucariaceae is a relictual family, consisting of only 41 species from three genera – *Agathis*, *Araucaria*, and *Wollemia* – which display low species diversity (Kershaw & Wagstaff, 2001; Miller, 1977). Through molecular phylogenetic analyses, (Stöckler et al., 2002) illustrated that all species of the three genera form a monophyletic group (Figure 1.1). These southern conifers are constrained to South America, Southeast Asia, and Pacific Islands in the southern hemisphere, indicating disjunct distribution on the globe as an evolutionary response (Kershaw & Wagstaff, 2001; McGlone et al., 2010). The genus *Agathis*

exists explicitly in the south-west Pacific region (Halkett & Sale, 1986; Miller, 1977). The most renowned member of the genus, *Agathis australis*, commonly known as kauri, is the sole indigenous member of the *Araucariaceae* family, and is confined to the northern region (north of 38°07'S) of Aotearoa New Zealand (Ecroyd, 1982; Halkett & Sale, 1986).

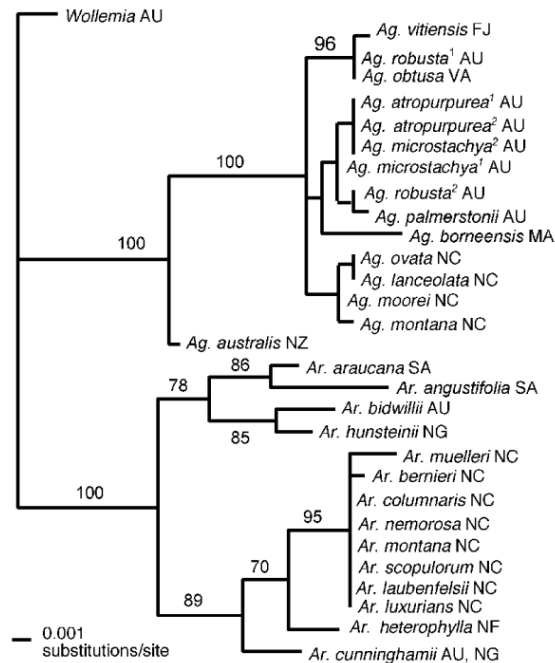


Figure 1.1: Phylogenetic tree showing *A. australis* as the earliest diverging extant lineage in *Agathis*. AU-Australia; FJ-Fiji; MA-Melanesian region; NC-New Caledonia; NG-New Guinea; NF-Norfolk Islands; NZ-New Zealand; SA-South America; VA-Vanuatu (Stöckler et al., 2002).

1.3 *Agathis australis* – Kauri

The evergreen *Agathis australis* are well-known for their incredible size. Like other conifer species, narrow pyramid-shaped young kauri develop from fertilised seeds, which transform into cone-bearing young trees called ‘rickers’ (Ecroyd, 1982; Halkett & Sale, 1986). Upon maturity, kauri attain heights up to 60 m, develop column-like trunks with diameters ranging between 3-5 m, and can survive beyond 1500 years depending on the site and other environmental conditions (Bradshaw et al., 2020). The crowns of these forest giants dominate the coexisting plant community by reaching above the forest canopy and extending whorls of lateral branches (Orwin, 2007b). Because of their enormity and longevity, as well as a unique blend of spiritual and biological magnitude, kauri have gained an important position of ‘rākau rangatira’, meaning ‘a canopy tree of significance’ (Paine et al., 2021; Wyse & Burns, 2013).

1.4 Kauri as a foundation species

Foundation species are species that play a major role in structuring the surrounding ecosystem influencing important ecosystem dynamics and biodiversity of coexisting species. In addition, foundation species may also hold cultural significance (Ellison, 2019).

Kauri forests are categorised as complex kauri-podocarp-hardwood forests that are dominated by kauri, which mostly cover northern parts of the North Island (Salmon, 1996). A mature kauri stand displays distinct vegetation patterns that encompass emergent kauri, a discontinuous secondary canopy tier comprising of smaller conifers, a lower tier of broadleaved trees alongside other indigenous plants, and epiphytes scattered underneath in its vicinity. The open space under these multilayer canopies mainly includes endemic arborescent flora with ground cover predominantly containing kauri grass (Wyse et al., 2014; Wyse et al., 2018). Thus, kauri plays a major role in shaping the surrounding plant community and so is considered as a foundation species (Wyse et al., 2014).

In the 19th century, dense kauri forest covered large regions (1.2 million hectares) of North Auckland and Coromandel Peninsula extending from sea level to elevation of 600m (Salmon, 1996). However, as the heartwood of kauri was renowned for its finest quality, heavy kauri logging caused extensive exploitation of the kauri forest with the arrival of Europeans during the 19th century (Halkett & Sale, 1986; Salmon, 1986). Although kauri timber trade and kauri gum industry have contributed significantly to Aotearoa New Zealand's economy (Bradshaw et al., 2020; Steward & Beveridge, 2010), their adverse effects have left a significant and long bearing impact on forest ecology, leaving behind only 5% of the original kauri forests at present (Steward & Beveridge, 2010).

1.5 Impact of kauri on soil

As a foundation species, kauri trees not only support ecologically distinct species but also have a great impact on the soil environment. Kauri forests are categorised as the most carbon rich ecosystems in the world in terms of both living and dead mass (Macinnis-Ng & Schwendenmann, 2015). As much as 546 tonnes/ha of litter can be deposited on the forest floor, mainly in the form of woody material (Bielecki, 1979; Silvester & Orchard, 1999). Additionally, records indicate that up to 6.54 tonnes/ha of nitrogen have been stored deep within the organic layers in kauri forest floors, which is four times the forest floor nitrogen content measured in any other forest (Silvester, 2000; Wyse et al., 2014; Wyse, 2012). Despite abundant nitrogen present in the organic litter, it does not exist in plant-available forms and therefore kauri forests are believed to experience nitrogen deficiency, restricting the growth of kauri trees in spite of their enormous size (Ecroyd, 1982; Enright & Ogden, 1987; Schwendenmann & Michalzik, 2019; Silvester, 1978; Silvester, 2000). The accumulation of large volume of poorly-decomposable organic matter, the release of leachates from the litter under the canopy, and the protracted life of kauri which elicits continuous addition to the litter content, all are the main contributing factors to the impact that kauri trees have on the surrounding soil (Jongkind & Buurman, 2006).

The leaching of high amount of phenolic compounds from the woody material and the tannins from kauri leaves, into the deeper layer of soil, makes the soil under the canopy very

acidic (Silvester & Orchard, 1999; Wyse et al., 2014), with pH ranging between 4.8 - 6 (MPI, 2023). The high acidity causes immobilisation of nitrogen by inhibiting nitrification (mineralisation) process and thus impact the nitrogen dynamics of the soil underneath the tree (Persson & Wirén, 1995). Moreover, the acidic condition reduces the availability of other nutrients such as phosphorous by affecting their solubility (Kidd & Proctor, 2001). On the other hand, the solubility of compounds such as aluminium increases as the pH plummets, which intensifies the concentration of aluminium in the soil to a toxic level (Kidd & Proctor, 2001). Thus, the organic soil formed under the kauri trees is remarkably acidic, with increased amount of total carbon, total nitrogen, and ammonium (NH₄-N), but low nitrate nitrogen (NO₃-N) content (Wyse et al., 2014).

This effect of kauri on the abiotic environment has created a direct influence on the biotic component of the kauri forest, whereby alteration in composition of plants species surrounding mature kauri stands has been observed (Wyse et al., 2014). Despite the infertility and possible toxic conditions of the soil, kauri forests encompass more diverse species than other forest types in Aotearoa New Zealand (Ogden, 1995; Wardle, 1991). Approximately 90 species of insects, reptiles, birds, minor flora, and trees have been identified as tohu, or indicators that are integral components of kauri forests (Chetham & Shortland, 2013). The majority of these coexisting plant species are endemic to Aotearoa and have positive relationship with kauri (Ogden, 1995). Therefore, they reflect the whakapapa (ancestral lineage/genealogy) of the species inhabiting on, and in close proximity of kauri (Chetham & Shortland, 2013).

1.6 Soil and forest health

Soil, as a unit of the entire terrestrial ecosystem, comprises of abiotic and biotic components that nurture a myriad of interdependent organisms and play a vital role in maintaining global chemistry by cycling of the elements (Falkowski & Jelen, 2013; Osman, 2012). Biogeochemical cycles are imperative for sustenance of life as well as ecosystem functionality (Brusseau, 2019). Microorganisms connect the living and non-living world by maintaining several biogeochemical processes (Falkowski & Jelen, 2013). Soil is regarded as a living system and it is crucial to preserve soil health in order to enhance its various functions such as sustaining biological productivity, maintaining the quality of air and water environments, and promoting plant, animal, and human health (Doran et al., 1996; Janvier et al., 2007; Samaddar et al., 2021; Stevenson et al., 2022). More importantly, soil performs a prime role in forest health in maintaining the energy flow amongst all flora and fauna of the ecosystem, by providing water and nutrients (Burger, 2004). In fact, all biogeochemical cycles operating at a global scale rely on forest ecosystems. Therefore, it is essential that forest health is preserved (FAO, 2020a).

Even though the concept of soil health differs with the usage of the land, the aim of maintaining the soil function to support the biological productivity remains the focal point

(Brevik, 2010). Efficient nutrient cycling, soil fertility, soil structure, water interactions, and comprehensive microbial activities are considered as health indicators to evaluate the soil health (Manaaki Whenua – Landcare Research, 1996; Samaddar et al., 2021; Stevenson et al., 2022). Larson and Pierce (1991) were the first to suggest the implementation of a universal minimum data set (MDS) for evaluating soil health through standardised methodologies and procedures (Doran & Parkin, 1994). Some of the selected soil quality indicators of physical, chemical, and biological characteristics and the pertinent examination methods from the MDS proposed by Larson and Pierce (1991) includes nutrient availability, total organic carbon, labile organic carbon, particle size, plant-available water capacity, maximum rooting depth, soil structure, soil strength, pH, and electrical conductivity (Doran & Parkin, 1994). These properties are inter-reliant and interconnected in such a way that a shift in one physicochemical (abiotic) property can have a direct bearing on the biological attributes of the soil (Samaddar et al., 2021).

1.7 Te Ao Māori perspective on soil and forest health

Aotearoa New Zealand Māori are strongly connected to soil through their whakapapa, and core Māori values have been embedded while considering the soil health (Chetham & Shortland, 2013; Stevenson et al., 2022; Stronge et al., 2020). Like many other indigenous cultures, Te Ao Māori have a holistic approach to maintain and strengthen the vitality of the soil through kaitiakitanga (cultural and environmental guardianship) (Stronge et al., 2020). In the same manner, Māori consider it a hereditary obligation to protect and preserve their forests with the help of Mātauranga (indigenous knowledge) (Lyver et al., 2018). According to Māori beliefs, all trees have arrived from the spiritual world and have been gifted to the mortal world of humans by their spiritual ancestors (MPI, 2023). Indigenous ecological knowledge offers valued perception and understanding correlated to the status of the biological, physical, and spiritual environments. Cross-cultural environmental monitoring systems provide information from combined perspective of both scientific and Mātauranga Māori viewpoints, to understand the state of forests and preserve or restore them accordingly (Lyver et al., 2018).

1.8 Cultural significance of kauri

Kauri has cultural and spiritual significance and is considered a taonga (treasure) by Māori and non-Māori alike. Māori regard the health of kauri as an indicator of general well-being of the ngahere (forest) and the people (MPI, 2023). As a part of kaitiakitanga, a methodological framework for monitoring kauri health indicators has been established, which provides parameters based on the holistic kauri ecosystem approach (Chetham & Shortland, 2013). The principle objective for establishing these indicators is based on the Māori philosophy of “whangaia te mauri/hau o te kauri”, which means “reciprocal protection or care for the life force or breath of life of the kauri”. This indicates the reciprocal relationship of tangata whenua with the forest (Chetham & Shortland, 2013). Everything in the world has a mauri (life force), which deteriorates when proper care is not available (MPI, 2023).

1.9 Kauri dieback programme

Kauri dieback was officially recognised by Landcare Research in the Waitākere Ranges Regional Park in 2008 after alteration in health status of kauri trees was observed. This led to the identification of the causal agent *Phytophthora agathidicida* in 2015, earlier tentatively named *Phytophthora* ‘taxon *Agathis*’ (PTA) (Waipara et al., 2013; Weir et al., 2015). Beever et al. (2009) confirmed that despite its high pathogenicity towards kauri, no other species was found vulnerable to PTA, suggesting species-specific pathogenicity. In recent years, *P. agathidicida* has caused biotic disruption and posed a serious threat to the existence of kauri forests (Schwendenmann & Michalzik, 2021). Any such natural intrusion can have significant repercussions on ecosystem processes and associated functions, subsequently affecting the feedback from the ecosystem (Rouault et al., 2006; Thom & Seidl, 2016). Even though pathogens are an inherent part of forest dynamics, they are leading biological disturbance agents and can majorly disturb structure, composition, and function of the ecosystem at both stand and landscape level (Burdon & Laine, 2019; Dale et al., 2001; Flower & Gonzalez-Meler, 2015; Kautz et al., 2017; Seidl et al., 2017).

According to some research, this novel water and soil borne pathogen has prevailed in Aotearoa New Zealand for a minimum period of 40 years (Beever et al., 2009; Bellgard et al., 2013; Chetham & Shortland, 2013; Gadgil, 1974). In fact, Winkworth et al. (2021) used mitochondrial genome sequencing to suggest that the pathogen could have arrived several thousand years ago, and diversified more recently into its detected form, resulting in change in the relationship between the pathogen, host, and environment, leading to the emergence of kauri dieback.

The zoospores of *P. agathidicida* enter through fine root necrosis, cause impairment of vascular tissues, and disrupt the transport of water and nutrients. The disease severely affects kauri trees irrespective of their age, and displays visual symptoms such as lesions, basal bleed or gummosis, chlorosis of leaves, defoliation leaving ‘stag head’ branches, and eventual death (Beever et al., 2009; Bradshaw et al., 2020). Numerous infected sites have been discovered throughout the Northland and Auckland regions, particularly Waitākere, Trounson Park, Waipoua Forest, and Aotea (Great Barrier Island) (Chetham & Shortland, 2013).

A kauri dieback programme has been implemented since 2009 as a joint response from the Department of Conservation, the Ministry of Agriculture and Forestry, Biosecurity New Zealand, Northland Regional Council, Environment Bay of Plenty, Auckland Regional Council, Environment Waikato, and tangata whenua (Chetham & Shortland, 2013). Scientific methodologies accompanied by kauri cultural indicators (KCI) have been implemented for investigating and scrutinising kauri dieback, alongside the evaluation of kauri health and building resilience to disease (Chetham & Shortland, 2013). As a part of this programme, permanent quadrant plots were created at several locations in the Northland, Coromandel, and Auckland

regions for long term surveillance of kauri dieback (Bellgard et al., 2013; Chetham & Shortland, 2013).

In 2014, the Ministry for Business, Innovation and Employment (MBIE) issued eleven National Science Challenges to address Aotearoa New Zealand's major scientific issues, one of which was New Zealand's Biological Heritage (Ngā Koiora Tuku Iho). The BioHeritage challenge aims to restore the nation's biological heritage by preserving native biodiversity, enhancing biosecurity, and increasing resistance to pests and pathogens (MBIE, 2014). Within the BioHeritage challenge, the Ngā Rākau Taketake (NRT) programme was launched in 2018 to work with local iwi including Te Kawerau ā Maki of the Auckland region, to tackle the issue of kauri dieback (Biological Heritage, 2023). The present study is part of the NRT programme, and investigates the possible link between kauri dieback and soil by using soil samples from five different kauri forest sites in the Waitākere region, established between 2011-2015 by Bruce Burns and George Perry from the University of Auckland. Each of these five sites are comprised of two plots, one with trees showing symptoms of kauri dieback and the other as a control, with asymptomatic kauri (Froud et al., 2022). Kauri soil samples from an asymptomatic and symptomatic location from the Coromandel region, collected in a separate project, have also been used in this study.

1.10 Significance of the study

Despite intensive research for over a decade on the occurrence of kauri dieback, there are still gaps in the knowledge regarding the cause of the susceptibility of kauri towards *P. agathidicida*. The physical and chemical properties of the soil from kauri forest have been determined by many researchers (Byers, Waipara, et al., 2020; Jongkind et al., 2007; Lewis et al., 2019; Yang, 2022). All of these studies compared the soil characteristics of *A. australis* with either other podocarps or angiosperms. Some of these studies investigate only a few soil characteristics, or target specific kauri age groups, and most utilise a very limited number of soil samples. This study investigates a range of physicochemical characteristics of kauri soil. Moreover, it is the first study to utilise comprehensive sampling from the symptomatic and asymptomatic sites of all three locations in Waitākere Ranges Regional Park since they were established between 2011-2015. Additionally, samples from symptomatic and asymptomatic locations in the Coromandel region were also used in this study. The findings presented here will support ongoing studies related to the NRT project and Waikato Council projects.

With the passage of time, trees from the asymptomatic sites began showing symptoms of *P. agathidicida* infection, hence the designation of the asymptomatic control sites was no longer accurate. Similarly, the symptomatic sites also contained several trees that showed no symptoms of kauri dieback. This study represents the soil physicochemical characteristics first according to the site designation (asymptomatic or symptomatic), then on the basis of presence or absence of

symptoms on individual trees, using symptom data collected as part of another study, to distinguish each soil sample as healthy (no visual dieback symptoms) or unhealthy (dieback symptoms visible). Analysis of the results, including comparison and correlation, is also performed based on both site designation as well as true health status of the trees. Hence, this study attempts to paint an accurate picture of kauri soil physicochemical characteristics in the Waitākere and Coromandel regions.

1.11 Research objectives

This study aims to provide a small piece of the larger puzzle and contribute towards New Zealand's kauri dieback response. The research objectives of this study are as follows:

1. Measure physical and chemical characteristics of soil from kauri forest that is asymptomatic (healthy) and symptomatic (unhealthy) of dieback disease.
2. Determine whether there are differences in the physical and chemical characteristics of kauri soil from asymptomatic (healthy) vs. symptomatic (unhealthy) kauri forest.

Chapter 2: Literature review



Priestly (2023)

2.1 Introduction to kauri

2.1.1 Ecology – distribution and habitat

Agathis australis, more commonly known as ‘kauri’ in te reo Māori, is the most eminent conifer species and the only member of the family *Araucariaceae* that is native to Aotearoa New Zealand, growing naturally in warm temperate forests north of 38°07'S in the North Island (Te Ika-a-Māui) (Ogden et al., 1992; Steward & Beveridge, 2010; Steward et al., 2014). Aotearoa New Zealand kauri forests, as shown in Figure 2.1, are dispersed in the area with the boundary that stretches out from Kawhia Harbour, Raglan in the west, passing through Hamilton, to the Kaimai Ranges located just below Tauranga in the east in Coromandel peninsula (Te Tara-o-te-ika a Māui or Te Paeroa-a-Toi) (Orwin, 2007b; Salmon, 1996). Apart from the Northland (Te Tai Tokerau), the present day range of kauri growth also extends to offshore islands, which includes Great Barrier Island (Aotea) and Little Barrier Island (Te Hauturu-o-Toi) (Ecroyd, 1982).



Figure 2.1: Remaining kauri forest in Northland and Coromandel regions, shown in green (Orwin, 2007a).

Kauri play a very substantial role in the forest ecology within Aotearoa New Zealand, not only creating profound influence on the soil beneath the canopies but also providing unique environment for diverse, coexisting species of plants, animals, and microorganisms for their survival (Wyse et al., 2014). According to Ellison (2019), foundation species have a key position in structuring the surrounding ecosystem by governing important ecosystem dynamics and the biodiversity of coexisting species. This definition justifies kauri being referred to as a foundation species. Being a prominent species, forest containing kauri is generally known as kauri forest,

even though kauri may not be the most predominant tree (Wyse et al., 2014). Their coexistence with diverse conifers such as totara (*Podocarpus totara*), rimu (*Dacrydium cupressinum*), and miro (*Pectinopitys ferruginea*), along with broad-leaved trees such as kohekohe (*Didymocheton spectabilis*), taraire (*Beilschmiedia taraire*), and mangeao (*Litsea calicaris*), forms a complex community (Allan, 1961; New Zealand Plant Conservation Network, 2023; Orwin, 2004; Wassilieff, 2007).

Various distinct plant species of the kauri forest are endemic to the “Kauri region” (Ecroyd, 1982; Halkett & Sale, 1986; Waipara et al., 2013). These plant families and genera represent a typical mature kauri forest with a combination of subtropical and tropical Pacific natives (Orwin, 2004). The defoliated open area underneath the canopy formed by giant kauri is usually spotted with Shiny Karamū (*Coprosma lucida*), neinei (*Dracophyllum latifolium*), Mingimingi (*Leucopogon fasciculatus*), and Mapou (*Myrsine australis*), various species of tree ferns like Silver tree fern (*Cythea dealbata*) and Brown tree fern (*Dicksonia squarrosa*), as well as kauri grass *Astelia trinervia* (Dawson & Lucas, 2011; Jongkind & Burman, 2006). In addition, Taraire (*Beilschmiedia tarairi*), Rewarewa (*Knightia excelsa*), Celery pine (*Phyllocladus trichomanoides*), Tawheowheo (*Quintinia serrata*), and *Toronia toru* are included under the canopy (Wyse et al., 2018; Wyse & Burns, 2013). *A. australis* creates a specific soil environment with a deep organic layer and intense acidic condition in its vicinity, which is reflected in the structure of the surrounding plant population (Wyse, 2012; Wyse & Burns, 2013). This gives rise to a kauri region with stress-tolerant plant communities which is structurally and configurationally unique from the adjacent conifer-angiosperm forest community, portraying kauri as a foundation species (Wyse et al., 2014). They can be found in varied elevation from lowlands to 600 m in the mountains (The Gymnosperm Database, 1997).

2.1.2 Nomenclature

The scientific nomenclature of ‘*Agathis*’ (meaning ball of thread) is acquired from Greek origin and is associated to the appearance of the strobiles (Eagle, 2006; Gledhill, 2008; Orwin, 2007b), while the species name ‘*australis*’ (meaning southern) originates from Latin (Eagle, 2006). The species name specifies that *Agathis australis* is the southern-most species out of the 20 species in the *Agathis* genus that are located in the Southern Hemisphere (Gledhill, 2008; Orwin, 2007b; Salmon, 1996). Franco (1949) initially depicted the appropriate nomenclature for kauri as “*Agathis australis* (D.Don) Lindl.”. Commonly known as Southern Kauri or New Zealand Kauri, it has been cited by different scientific names such as *Dammara australis* by Don (1824) and *Podocarpus zamiaefolius* by Richard (1832) (Steward & Beveridge, 2010).

2.1.3 Life cycle

Kauri is a monoecious tree, bearing both male and female cones (Allan, 1961; The Gymnosperm Database, 1997). Kauri initiates its life from a winged seed, which is a result of

fertilisation of an ovule of a female cone by the pollen produced by a male cone during early autumn (Ecroyd, 1982; Halkett & Sale, 1986; Owens et al., 1997; Waipara et al., 2013). The seed disperses and lands into a place away from the parent tree in conducive soil, normally under manuka (*Leptospermum scoparium*) and kanuka (*Kunzea ericoides*) shrubbery (Halkett & Sale, 1986; Ogden et al., 1987; Orwin, 2004). After germination, it appears as a slender sapling which evolves from a monopodial into a tapered trunk conical adolescent called a “ricker,” comparable to other conifers (Ecroyd, 1982; Halkett & Sale, 1986). This immature kauri pole advances upwards and transforms into a cone-bearing young tree. Upon maturity at a height of 30-40 m, the lower angular branches are shed (in a process called abscission), the trunk becomes clean and columnar, and a flat-top crown with lateral whorls of massive branches emerges above the coexisting forest canopy (Halkett & Sale, 1986).

2.1.4 Tree morphology

These evergreen conifers are renowned for their incredible size, with the basal trunk diameter ranging between 3-5 m and heights up to 60 m, and have life-spans beyond 1500 years (Bradshaw et al., 2020). A distinctive amalgamation of spiritual, biological, and genetics empowers kauri to be a ‘rākau rangatira’, a canopy tree of significance (Paine et al., 2021). The enormity and longevity of *A. australis* is unmatched among the prevalent tree species in Aotearoa New Zealand (Wyse & Burns, 2013).

During the life span, regular self-pruning of the branches occurs (cladoptosis), however the trunk is free of knots due to the abscission process. Unlike other species of the *Araucariaceae* family, the trunks (or boles) of kauri do not taper with height, but have uniform girth, appearing like vast, smooth pillars, as seen in Figure 2.2(a) (Halkett & Sale, 1986). Wilson et al. (1998) identified four types of kauri branches: early ricker branches, late ricker branches, adult support branches, and adult foliage branches. The branches of young conical kauri are long, upwards-pointing, and frail but enduring. Foliage branches on matured trees have the shortest life span of all four branch types (Wilson et al., 1998).

The bark of the mature kauri tree is typically bluish grey to silvery grey with a distinct ‘hammered’ appearance visible in Figure 2.2(b), and differs from the bark of the young kauri trees (Dawson & Lucas, 2011). The bark regularly decorticates in large thick flakes, which deter the growth of epiphytes and parasite damage (Allan, 1961; Dawson & Lucas, 2011). According to Māori legend, it represents kauri wearing a cloak of whale skin – a treasured gift given by the whale (Parāoa) at their separation during the primeval era of the world (Stewart, 2008).

Kauri gum (resin) is produced during flaking of the bark. It is also secreted from other parts of the tree such as cones, branches, and base of the leaves (Eames, 1913; Salmon, 1996). As shown in Figure 2.2(c), the resin is also exuded during cladoptosis (Halkett & Sale, 1986). Hence,

kauri are also classified as ‘resiniferous’, like some other conifers (Ecroyd, 1982). Additionally, large amount of gum is released if the trunk is wounded (Eames, 1913).

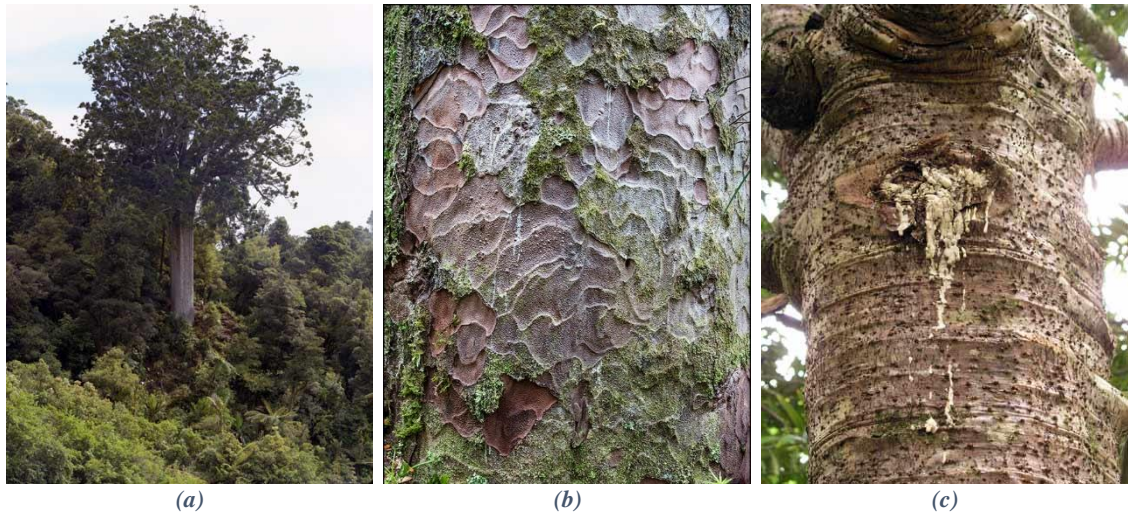


Figure 2.2: Kauri morphology showing (a) kauri tree (Orwin, 2007a), (b) kauri bark (Shwartzman, 2017), (c) kauri gum leaking from abscess after cladoptosis (Walrond, 2007).

The juvenile and transitional forms of the leaves are reddish-green to glaucous-green with tapered, lanceolate shape which transform to mature leaf forms that are bright green, oblong, and feature an obtuse apex, parallel veins, and a short petiole, visible in Figure 2.3(a) (Allan, 1961; Dawson & Lucas, 2011).

Being monoecious plant, both male and female cones are produced on the same tree. The male cones are cylindrical, around 2-5 cm long, protruding from leaf axils (Figure 2.3(b)). They are nearly black in colour and produce pollens (Allan, 1961; Dawson & Lucas, 2011). The female cones, or strobiles, are globular with spiral scales (like a ball of thread), around 6cm in diameter, and emerge from short peduncles. They are bright green and bear seeds (Figure 2.3(c)). It is the shape and appearance of the female cones that depicted the genus name *Agathis* (Allan, 1961; Dawson & Lucas, 2011). The fertilisation of the seeds may occur by wind pollination from a pollen (male) cone of the same or a different tree. The reproductive cycle ranges over 19-20 months from pollination to seed maturity (Eames, 1913; Owens et al., 1997).

Two types of root systems are found in matured kauri trees, visible in Figure 2.3(d). One is a shallow tap root system that forms a plate surrounding the tree and extends beyond the dripline (Ecroyd, 1982; Halkett & Sale, 1986). They absorb nutrients from its own litter with the aid of symbiotic mycorrhiza. The other is a deep root system made of large ‘peg roots’ that penetrate up to 5 meters into the soil to secure the tree (Halkett & Sale, 1986). Recent investigation by Bader and Leuzinger (2019) demonstrated below ground intraspecific root grafting between kauri trees for hydraulic coupling as an adaptive, beneficial feature. This physiological interaction through extended root network was presumed to support hydraulic systems among conspecific trees and possibly for the exchange of carbon and other nutrients (Bader & Leuzinger, 2019).



Figure 2.3 Kauri botanical features; (a) kauri leaves (Byrom, 2020), (b) male cone (black) and female cone (green) (Foster, 2014), (c) kauri seeds inside female cone (The Living Tree Company, 2023), (d) scale model of kauri tree and root system (Tantau & Preece, 2022).

2.1.5 Tree litter

Kauri usually grows in infertile ridgetop soils. The thick layers of dead leaves, bark flakes, branches, and cones accumulate under the canopy of the mature kauri tree and are slow to decompose, thereby releasing less nutrients (Ecroyd, 1982; Halkett & Sale, 1986). The weak decomposability of this litter results in the build-up of a large layer of partially decomposed bark and other vegetative matter, known as mor formation (“pukahukahu” in te reo Māori), which can be found up to 2 m in depth (Chetham & Shortland, 2013; Jongkind et al., 2007; Sando, 1936). Over a period, the built-up acidic litter liberates similar acidic compounds that leach into the surrounding soil, further impoverishing it by leaving the soil acidic and depleted of nutrients, especially nitrogen and phosphorous. This process is known as “podzolisation” and converts the soil to dull grey colour (Halkett & Sale, 1986; Wyse & Burns, 2013). This infertile soil deprives other competing plant species; however, kauri is efficient in thriving at a low water and nutrient level (Ecroyd, 1982; Steward & Beveridge, 2010). With this soil transformation, kauri competes with the fast-growing angiosperms creating niche partitioning with various coexisting species (Thompson et al., 2015).

Kauri seedlings are well-adapted to germinate beneath mature kauri trees, in soil with low water and nutrient availability which is not favourable for seedlings of angiosperms. However,

winged seeds also strategically disperse away from the parent tree and neighbouring broad-leaved competitors into more favourable light and soil conditions. These seeds give rise to a stand of similarly aged, young kauri trees, especially in the shrubland of myrtacean tea trees ascendancy (Ecroyd, 1982; Halkett & Sale, 1986; Ogden et al., 1987). This is described by Ogden et al. (1987) as the cohort regeneration model, where spatially distributed patches (or cohorts) of discrete kauri stands establish within the forest. Hence, kauri excels at both survival strategies of patch distribution and competition by influencing soil properties.

2.1.6 Large living legends

While considering characteristic features such as age, size, girth, and quality and quantity of timber, kauri giants possess impressive attributes when compared with other giant species in the world (Adams, 1973). Among several living kauri giants in Aotearoa New Zealand, Tāne Mahuta, located in Waipoua forest, tops the table with its exceptional height of 51.5 m, girth of 13.78 m, and an estimated age of 1500-2000 years. Meanwhile, within the same Waipoua forest, Te Matua Ngahere, also known as “Father of the forest” displays its supremacy with its massive girth of 16.41 m (Halkett & Sale, 1986). On the other hand, Kairaru in Tutamoe Mountains, which was destroyed by a fire, was about 4000 years old and was recorded to have a girth of 25 m and height of 30 m to the first branch, claiming the title of largest kauri of all time (Halkett & Sale, 1986; Orwin, 2004).

2.1.7 Economical aspect

The heartwood of the full-grown kauri possesses an iconic status for being the finest wood in the world (Bradshaw et al., 2020; Steward & Beveridge, 2010). Because of its innate characteristics of resistance to decay under humid environment and consistent dimension of the trunk, kauri timber contributed enormously to the growth of Aotearoa New Zealand’s economy between 1830-1900 (Roche, 1990; Steward et al., 2014). In addition, due to the usefulness of kauri gum in paints, polishes, varnishes, and jewellery, the digging of fossilised gum and the export of finished Kauri gum dominated between 1850-1960, and exceeded any other industry during this period (Adams, 1973). For this reason, kauri gum industry along with kauri timber trade have contributed significantly to Aotearoa New Zealand’s economy (Bradshaw et al., 2020; Steward & Beveridge, 2010).

2.1.8 Cultural significance

New Zealand kauri trees are not only important ecologically and economically, but they are of immense cultural, social, and historical prominence to both Māori and non-Māori Aotearoa New Zealanders (D'Souza et al., 2021). For indigenous Māori tribes, many cultural and spiritual beliefs are focused around the kauri tree, and it is considered ‘taonga’ (treasured or sacred). The health of kauri forests is intricately connected to the health of the reliant ecosystem as well as the health of the tribe. A failure to protect kauri reflects on their inherent responsibilities as ‘kaitiaki’

(guardians) of these trees (Bradshaw et al., 2020; Lambert et al., 2018). According to ancient Māori legend, Tāne Mahuta (God of the forest), separated Ranginui (Sky father) and Papatuanuku (Earth mother) with the thrust of his strong legs to let light in and allow life to commence, shown in Figure 2.4 (Orwin, 2004; Paine et al., 2021; Samoa, 2021).



Figure 2.4: Tāne Mahuta separating Ranginui (Sky father) and Papatuanuku (Earth mother) (Samoa, 2021).

2.1.9 History

Kauri belongs to an ancient lineage – its existence is linked 200 million years before prehistorical detachment of Aotearoa New Zealand from Gondwana (Coles, 2005; Orwin, 2007b; Stewart, 2008). Tāne Mahuta has witnessed human history right from the arrival of the first canoes of Polynesian voyagers as Aotearoa New Zealand’s earliest inhabitants, till today (Orwin, 2004). Present day kauri shows much similarity to Araucarian ancestors that existed during the Cretaceous period (Halkett & Sale, 1986; Stewart & Beveridge, 2010). Molecular sequence data reveals that *Agathis* is the oldest living genus of the family *Araucariaceae*, even surviving the Oligocene epoch, and so it is rightly considered ‘tipuna’ (ancestor) of conifers (Coles, 2005; Orwin, 2007b; Stewart, 2008; Stöckler et al., 2002).

2.2 Kauri dieback

Like any other plant, kauri interacts with several beneficial and antagonistic organisms including plants, insects and microorganisms, both above and below the ground (Pieterse & Dicke, 2007). One of the reasons that kauri have survived for millions of years is their ability to comprehend interactions with other organisms and to react with defensive response if required (Orwin, 2004). However, in spite of its natural resilience and the health condition, the kauri forests are vulnerable to a disease known as ‘kauri dieback’ which is caused by oomycetes *Phytophthora agathidicida* (Lambert et al., 2018). The occurrence of kauri dieback disease across the upper North Island is shown in Figure 2.5 below. The cases of kauri fatality were initially registered between 2005-2006 in Maungaroa Ridge in the Waitākere Ranges Regional Park and Waipoua

Forest leading to the research and identification of the cause (Beever et al., 2009; Waipara et al., 2013).

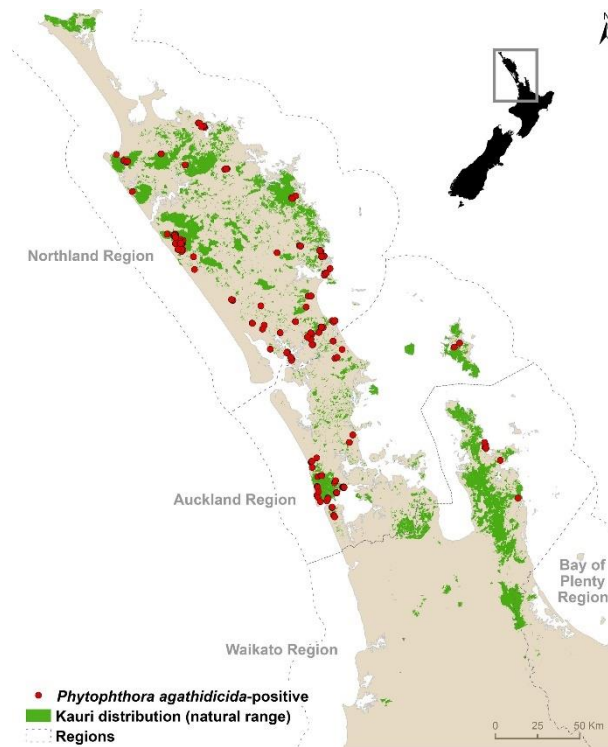


Figure 2.5: Distribution of *Phytophthora agathidicida* across the upper North Island (Bradshaw et al., 2020).

The pathogen originates the infection from the fine roots and progresses to the outer vascular tissue, revealing symptoms like root rot, collar rot causing large basal lesions which bleed profuse amounts of resin (gummosis or hyper-resinosis, visible in Figure 2.6(a)), severe chlorosis, defoliation and thinning of canopy (Figure 2.6(b)), and eventual tree mortality several years after the onset of the infection (Figure 2.6(c)) (Bradshaw et al., 2020; Seyfullah et al., 2018). The potency of this pathogen affects the trees irrespective of their age and so is a huge threat to kauri – this demonstrates the magnitude of virulence of the organism (Beever et al., 2009).

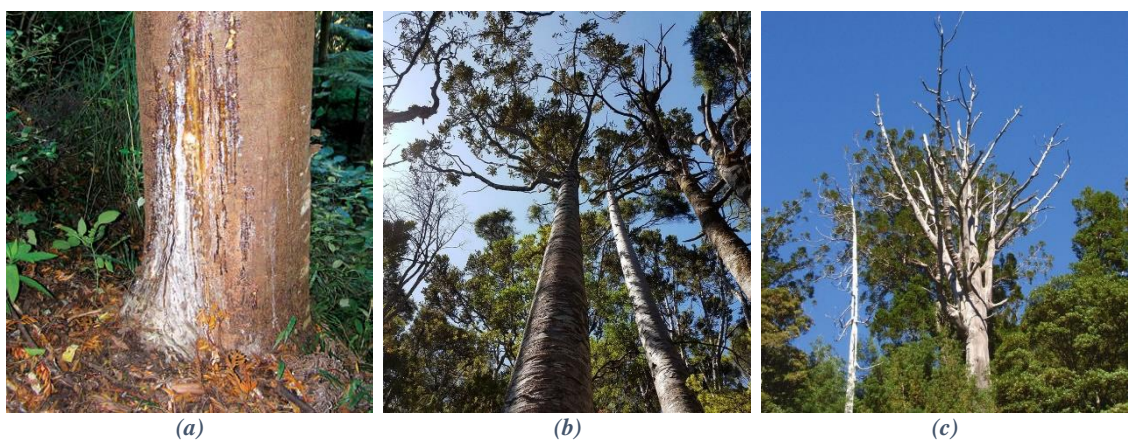


Figure 2.6: Symptoms of kauri dieback such as (a) gummosis (Auckland Council, 2023), (b) thinning foliage (Jakobsson, 2021), and (c) tree mortality (Lambert et al., 2018).

In spite of resemblance in distribution and life cycle of different *Phytophthora* species, their impact on forest ecosystems varies, subject to the host specificity of the pathogen, mechanism of infection leading to host dieback, host ecological attributes, and configuration of the respective forest ecosystem (Hansen, 2008). The mechanisms involving carbon deficiency as well as flow of water and nutrients have been observed to be the cause of death of the host (Davison, 2011). For example, *Phytophthora cinnamomi* and *Phytophthora quercina* cause fine root necrosis hindering water and nutrient uptake following chlorosis, defoliation, and eventual tree death (Davison, 2011). The other mechanisms involve impairment due to toxins and the damage of xylem and phloem tissues resulting in hydraulic failure and carbon starvation respectively, as causal factors of the death of the host species (Davison, 2011). Symptoms associated with kauri dieback include chlorosis, defoliation, loss of canopy, and gummosis, which indicate high probability of presence of mechanisms involving fine root necrosis and/or phloem invasion. However, the mechanisms triggering kauri dieback subsequent to *P. agathidicida* infection remain unknown (Waipara et al., 2013).

According to the projection model of Bellgard et al. (2013) in the report generated for Ministry for Primary Industries (MPI Contract 11927), the ill-effect of *P. agathidicida* will not only be limited to the keystone species but it will potentially have a cascading and dispersing effect on forest species composition and associated ecosystems, shown in Figure 2.7. Further to the prediction, the alteration in the distribution of the host species (kauri) could possibly bring transformation in accessibility for *P. agathidicida* to the host and perhaps to the strength of the pathogen as well (Bellgard et al., 2013).

For instance, alteration of forest species composition was observed subsequent to the disappearance of the key species of enormous trees of tanoak (*Notholithocarpus densiflorus*) caused by *Phytophthora ramorum* (Metz et al., 2012). Species with increased dominance following loss of tanoak play a different role in the coastal forest ecosystem, especially with regards to litter chemistry and nutrient cycling (Metz et al., 2012). Hence, *Phytophthora ramorum* was shown to have both short-term and long-term effect on forest species composition and ecosystem functioning.



Figure 2.7: Triangle of potential cascading impacts caused by *P. agathidicida* (PTA) (Bellgard et al., 2013).

2.2.1 *Phytophthora* and its species

Phytophthora agathidicida, formally known as *Phytophthora* taxon *Agathis* (PTA), is a water and soil-borne pathogen. The word *Phytophthora* originates from Greek word meaning ‘plant destroyer’, and the species name *agathidicida* means "kauri killer”, derived from Latin origin (agathid meaning stem of *Agathis*, cida meaning killer) (Weir et al., 2015). This causal agent for kauri dieback was found in kauri forest in several locations in Aotearoa New Zealand by 2010 and carries risk for long-term subsistence of kauri (Beever et al., 2009; Waipara et al., 2013). PTA was detected from the soil collected from vicinity of infected kauri, as well as from cambium vascular tissues and bleeding lesions on the kauri (Beever et al., 2009; Waipara et al., 2013). Several other species such as *P. cinnamomi*, *P. cryptogea*, *P. kernoviae*, *P. nicotianae*, and *P. ultimum* associated to kauri were identified, but the origin – whether introduced or indigenous – is not clear (Beever et al., 2009). Horner and Hough (2014) demonstrated in laboratory conditions that *P. agathidicida* is an antagonistic pathogen and exhibits more virulence towards kauri than the three other species of *Phytophthora*.

2.2.2 Lifecycle of *Phytophthora agathidicida*

The life cycle begins, as shown in Figure 2.8, with the transfer of oospores (dormant stage) into kauri forest through anthropological activities as well as through feral pigs (Bellgard et al., 2016; Lambert et al., 2018). *P. agathidicida*, being homothallic, reproduces asexually by producing motile zoospores (Figure 2.9(a)) as well as sexually by producing oospores (Figure 2.9(b)) (Bellgard et al., 2016; Weir et al., 2015).

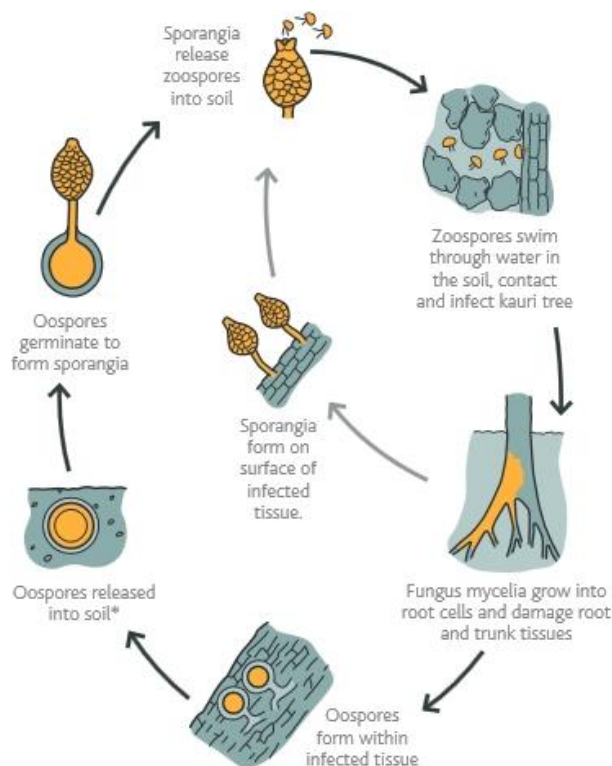


Figure 2.8: Life cycle of *Phytophthora agathidicida* (LEARNZ, 2020).

The oospores can survive in the environment for long periods and can resist changes to temperature (Bellgard et al., 2013; Horner & Hough, 2014). The oospores germinate under wet conditions to form sporangia from which bi-flagellated zoospores are released. The motile zoospores recognise and get attracted to the plant chemicals that are secreted from the fine tips of the kauri roots. The zoospores make their way through the water in the pores of the soil towards the host (Bellgard et al., 2013; Bradshaw et al., 2020).



Figure 2.9: *Phytophthora agathidicida* (a) sporangia and germinating zoospores (Weir et al., 2015), (b) oospore (Paine et al., 2021).

Upon reaching the root interface, the zoospores encyst and produce hyphae that pierce through to inhabit within the root (Bellgard et al., 2013; Bradshaw et al., 2020). The *P. agathidicida* propagates to the vascular tissues and form cluster of hyphae and produce more oospores. These oospores are dispersed in nature through water and soil or alternatively transmitted through humans and animals. The oospores remain dormant and serve as propagules, producing zoospores, upon acquaintance with new host and favourable conditions (Bradshaw et al., 2020).

Bellgard et al. (2013), in the Landcare Report (MPI Contract 11927) produced for Ministry for Primary Industries has pointed out three major factors that contributes to the intensity of dieback disease. These mediating factors are: (a) the environmental severity, (b) the presence as well as highly infectious nature of *P. agathidicida*, and (c) the vulnerability of the host to the pathogen. All these parameters are interconnected and critical to the kauri dieback issue (Bellgard et al., 2013; Horner & Hough, 2014).

2.3 Forest ecosystem

Forest ecosystems are the most prevalent terrestrial ecosystems spread over nearly one-third of the world's total land area (FAO, 2020b). Forest ecosystems support both terrestrial and aquatic biodiversity, and are imperative to the sustenance of life cycles by nurturing and sheltering copious inhabitants (Jenkins & Schaap, 2018). For instance, moist tropical forests harbour 50%

of the world's species, making it the most species-diverse habitat (Dirzo & Raven, 2003; Jenkins & Schaap, 2018). Moreover, forests are key elements in modifying the course of climate change by carbon sequestration, soaking up a net of 7.6 billion metric tonnes of CO₂ per annum through biomass accumulation globally (Harris et al., 2021).

Forests play an important role in soil conservation and prevention of land degradation and desertification. The nutrients utilised by plants for biomass accumulation are returned to the soil through mineralisation of organic matter. Additionally, the roots of trees enhance the forest floor-bearing ability, alleviate the soil, and prevent soil erosion (Cofie, 2001; Cohen & Schwarz, 2017). Roots holding the soil prevent the soil particles and constrained nutrients from being swept away into the watercourses, combatting threats to water quality and preventing leaching of the nutrients (Jenkins & Schaap, 2018). Thus, forests are crucial habitats for biodiversity that promote the functionality of forest ecosystems, reduce anthropogenic bearing on environment, and provide comprehensive ecosystem services such as climate management, biomass production, water refinement, pollination, and facilitating habitats for a myriad of species (Brockerhoff et al., 2017).

2.3.1 Forest biodiversity

Species diversity is essential for the sustainability of ecosystems and facilitation of ecosystem services. Forest biological diversity includes all species co-existing within a forest ecosystem, performing diverse ecological functions (CBD, 2016). Biologically diverse forests comprise of a huge congregation of plants, animals, and microorganisms associating and interacting at different levels, encompassing the ecosystem, landscape, population, species, and genetics. Multifaceted interactions take place within and between these levels, allowing life forms to adapt to the everchanging ecological conditions and retain ecological functions (CBD, 2016). Conservation measures such as sustainable forest management, arresting biodiversity loss, and preventing desertification and land degradation are focused in international agreements such as the Convention on Biological diversity (CBD) and the FAO Sustainable Development Goals (SDG 15) (FAO, 2020b).

2.3.2 Forest health

Forest health attributes define the overall fitness of the forest. A healthy forest is reasonably unhampered by insect invasions, ailments, unusual weeds, and air pollution, and is able to endure the negative influence of acute insect attacks, disease outbreaks, fire, wind, and flooding, and able to recover from these distresses to resume growth and development (Burger, 2004). Soil plays a vital role in forest health by securing the tree roots firmly, synchronising energy flow among the inhabitants of the ecosystem, and by regulating water and nutrient accessibility for the benefit of the entire forest ecosystem (Burger, 2004). Additionally, according to the holobiont concept, introduced by German theoretical biologist Adolf Meyer-Abich in 1943, plant-associated endophytes, epiphytes, and symbiotic microbes are crucial for the health and

productivity of the host tree (Hassani et al., 2018). Ecosystem indicators such as habitat quality, community structure, and soil fertility are used to evaluate forest health (Trumbore et al., 2015). Forest health is crucial as global nutrient cycles are reliant on forests and trees. Thus, ensuring the health and progression of the forests are vital (FAO, 2020a).

At present, the health of forests is threatened by the imminent change in growth conditions triggered by climate change and invasive pathogens and pests (Woods et al., 2010). Additionally, invasive pathogens now present a greater risk than before due to climate change (Woods et al., 2010). The forest as well as forest soil serve as potential means to mitigate the cause of climate change, for the reason that they function together as major carbon sinks and storages (Asiegbu, 2020). However, tree pathogens are the causal agent of decline of forests, which in turn controls their economical, ecological, and social significance (Pautasso et al., 2015). Global warming allows the proliferation of pathogens to extended geographical locations which were previously less favourable (Woods et al., 2010). Introduced pathogens generate a greater threat than native pathogens due to lack of resistance of the host plant (Ferreira et al., 2006).

2.3.3 Epidemiology of forest tree

Microbes play a prime role in enhancing the tree health in forest ecosystem by increasing productivity and viability, some microbes cause adverse effect resulting in plant disease (Asiegbu, 2020). An occurrence of a disease in a tree is referred to as critical and lethal disturbance in its physiology, caused by a microorganism (pathogen) (Asiegbu & Kovalchuk, 2022). Various pathogens cause interferences at all cellular and morphological components of a tree and hinder growth and physiological and metabolic functions such as reproduction, nutrient transfer, storage of food reserve and process of photosynthesis (Bell, 2019; Tainter & Baker, 1996). Both biotic as well as abiotic factors can be the causal agent for diseases and disruptions (Bell, 2019; Burger, 2004). However, diseases are considered an innate part of forest dynamics, causing disruptions on which numerous insect and plant species are reliant. A dead tree harbours diverse saproxylic species through all stages of decomposition, correlating to high biodiversity (Hassani et al., 2018).

A crucial foundation of epidemiology is the notion that disease and other health issues do not occur randomly in a population (CDC, 2012). The traditional model for disease causation, called the epidemiologic triad or triangle, projects that plant disease is a consequence of the bilateral interactions between susceptible plants and pathogenic agents in favourable environmental conditions that allow transmission of the agent from a source to that host. (Bischoff et al., 2021; CDC, 2012). Different equilibria and interactions of these three elements are prerequisite for different diseases to occur (CDC, 2012). The model is depicted in two ways (Figure 2.10).

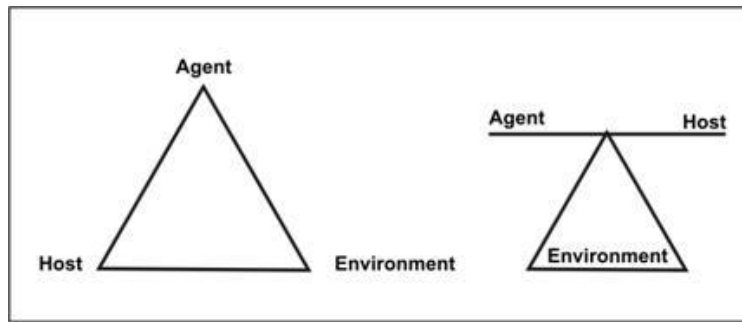


Figure 2.10: Epidemiologic triad and the balance between its three components (CDC, 2012).

The following three components must be congregated for a disease to occur (Asiegbu & Kovalchuk, 2022; Bell, 2019; Bischoff et al., 2021; Moore et al., 2020):

1. The species of host plant must be susceptible and at the right stage of development.
2. The pathogen must be of a virulent strain and must be exist in sufficient numbers (inoculum potential). At times, the presence of suitable vectors or other agents of dispersal may also be required.
3. The environmental conditions must be favourable for disease to develop. These include climatic conditions, plant health and nutritional status, and soil health (biotic and abiotic factors).

Figure 2.11 illustrates the concept of the epidemiologic triangle, where the three components must exist simultaneously for a disease to occur (Bell, 2019; Bischoff et al., 2021; Moore et al., 2020).

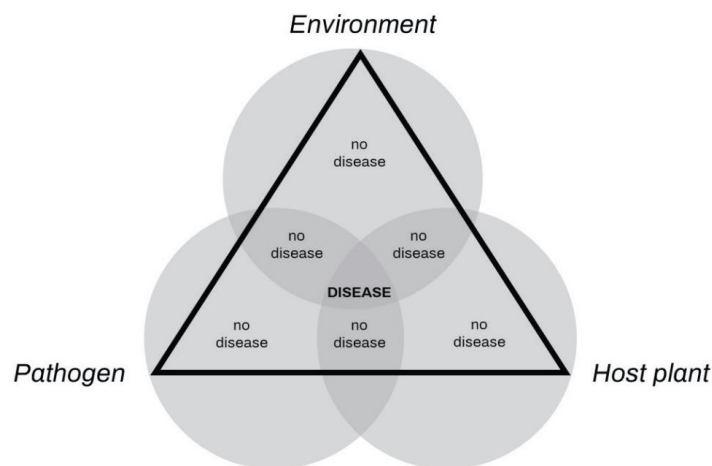


Figure 2.11: Plant disease triangle (Moore et al., 2020).

Figure 2.12 represents the bilateral relationships between the three components and human influence as an additional parameter (Asiegbu & Kovalchuk, 2022).

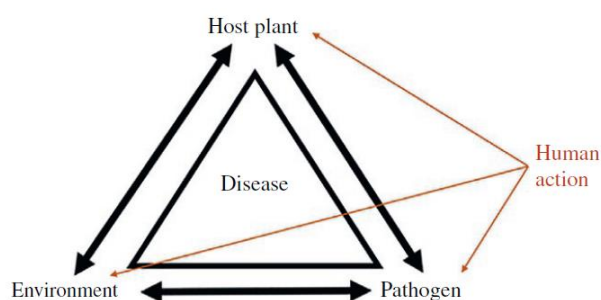


Figure 2.12: The disease triad incorporating human influence (Asiegbu & Kovalchuk, 2022).

2.3.4 Epidemiological viewpoint to kauri dieback

A strong correlation has been established between kauri dieback and pathogenicity of *P. agathidicida* – the existence of *P. agathidicida* is required to cause kauri dieback (Bellgard et al., 2016). However, according to the epidemiological triad concept, other two components required for disease to develop must be present, such as a vulnerable host and environmental conditions that favour the pathogen while increasing host susceptibility. In the Waitākere Report 2021, Froud et al. (2022) proposed that the causal agent of kauri dieback could be soil biotic or abiotic factors which may affect host susceptibility as well as disease severity.

2.3.5 Environmental severity

As stated above, one potential factor relating to kauri dieback disease is the severity of the environmental conditions in kauri forest (Bellgard et al., 2013). Environmental stress either directly or ambiguously causes most plant growth-related issues, which in turn depress the plant immune system and increase propensity to diseases (Bell, 2019; Froud et al., 2022). The environmental factors include weather, topography, soil health, and nutrients derived from the soil (Chetham & Williams, 2022). The role environmental factors play on proliferation and establishment of pathogens as well as disease expression and severity are directly reflected in plant health through various symptoms (Chetham & Williams, 2022; Froud et al., 2022). Hence, any change in plant growth or susceptibility is the result of plant interactions with climatic factors and the soil system, which makes the plants vulnerable to the pathogen, according to the epidemiologic triad concept (Chetham & Williams, 2022; Froud et al., 2022).

2.4 Soil health

The Soil Science Society of America (SSSA) has recently defined soil as “the layer(s) of generally loose mineral and/or organic material that are affected by physical, chemical, and/or biological processes at or near the planetary surface and usually hold liquids, gases, and biota and support plants” (Karlen et al., 1997; van Es, 2017).

Soil is a major element of the environment and is regarded as a living system (Janvier et al., 2007; Kirschenmann et al., 2000). Originally, in the 1990s, the Soil Science Society of America conceptualised the idea of soil quality, which was associated with soil function, and

related only to the purpose it serves. However, later on the concept of ‘soil health’ was introduced, which specifies the condition or state of the soil irrespective of its use (Janvier et al., 2007).

Soil health is described as “the continued capacity of soil to function as a vital living system, within ecosystem and land-use boundaries, to sustain biological productivity, maintain the quality of air and water environments, and promote plant, animal, and human health” (Doran et al., 1996; Janvier et al., 2007; Samaddar et al., 2021; Stevenson et al., 2022).

Soil health emphasises and pursues the preservation of soil as a limited but dynamic living resource, and the enhancement of performance of its various functions (Doran et al., 1996; Janvier et al., 2007; Stevenson et al., 2022). In a report focused on soil health, FAO (2008) have also placed stress on the two components of the soil health definition that differentiate it from the definition of soil quality. These are, first, “the continued capacity of” i.e. addition of time component, which emphasises the ability of the soil to function over time, and second, identifying the soil “as a vital living system” which highlights the prominent relationship of soil biology to soil function (FAO, 2008). To ensure the performance of the various soil functions, it is important to address the biological, physical, and chemical components of the soil, shown in Figure 2.13. Soil organic carbon (SOC) was considered a subset of the biological component, but it is now regarded as a separate component due to its growing prominence (Stevenson et al., 2022). The soil functions comprise of maintenance of nutrient cycles, climate regulation, and encouraging biodiversity as well as production of food for all living beings (Janvier et al., 2007; Stevenson et al., 2022).

Various theories of soil health are formed based on the usage of the soil. In general, the concept of soil health is associated with plant growth. The concept of soil health is dependent on location and land use (Brevik, 2010). Therefore, the capacity of the soil to function differs according to the contiguous environment. This implies that ‘normal’ soil function in an urban location is distinct to that of the ‘normal’ function in any other location such as agriculture, forest, or wetlands (Brevik, 2010). Hence, Brevik (2010) in his work published by UNESCO-EOLSS, describes soil productivity as the capacity of a soil, in its normal environment, to support plant growth. This relates directly to the section within the soil health definition which states the requirement of a soil to support biological productivity (Brevik, 2010; Doran & Parkin, 1994). Thus, soil productivity is concurrent to the concept of soil health (Brevik, 2010).

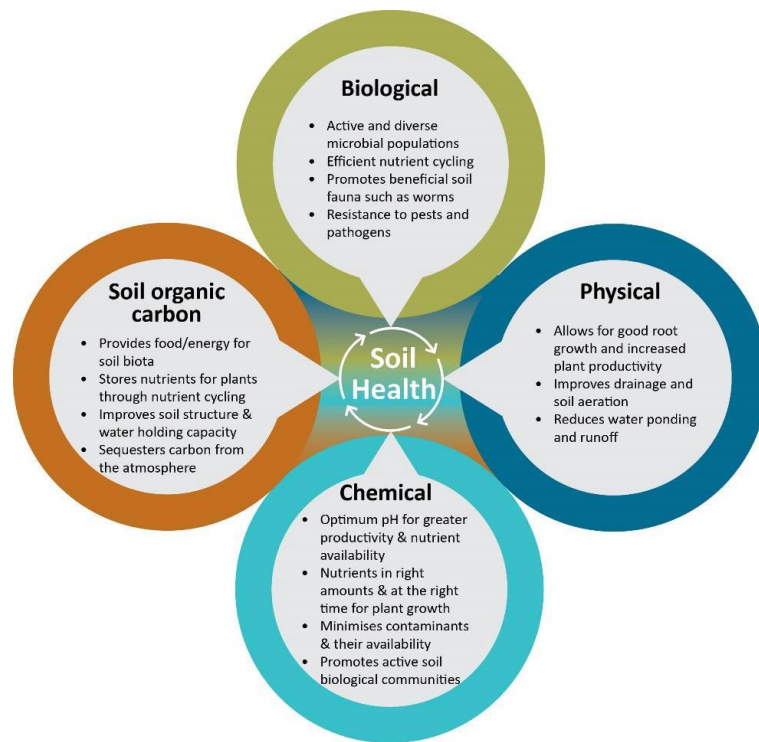


Figure 2.13: Biological (including SOC), physical, and chemical components affecting soil health (Stevenson et al., 2022).

Soil health is evaluated based on soil health indicators such as (Manaaki Whenua – Landcare Research, 1996; Samaddar et al., 2021; Stevenson et al., 2022):

- effective nutrient cycling
- soil organic matter – provides soil fertility
- soil structure – aids aeration and root growth
- water interactions – regulate the water cycle and reduce soil erosion
- overall microbial activities.

Larson and Pierce (1991) suggested for the first time the implementation of a minimum data set (MDS) for evaluating global soil health, and that the verification of any changes in soil attributes should be measured through standardised methodologies and procedures (Doran & Parkin, 1994). Of many elementary indicators of soil physical, chemical, and biological characteristics proposed by Larson and Pierce (1991), some of the soil quality indicators and the respective assessing methods were shortlisted as a minimum data set for soil examination (Doran & Parkin, 1994). These indicators include:

- Nutrient availability
- Total organic C
- Labile organic C
- Particle size
- Plant-available water capacity
- Soil structure

- Soil strength
- Maximum rooting depth
- pH
- Electrical conductivity

The health of soil is determined by these physical, chemical, and biological indicators. These properties are interconnected and interdependent and require attention to maintain healthy soil (Manaaki Whenua – Landcare Research, 1996). A shift in soil physicochemical characteristics (or abiotic factors) influence the biological aspect (or biotic factor) considerably (Samaddar et al., 2021). For example, soil health plays a major role throughout the lifecycle of both kauri and *P. agathidicida*. Therefore, the characteristics and overall health of the soil can have a major influence on the growth of kauri as well as proliferation of *P. agathidicida* (Halkett & Sale, 1986; Lambert et al., 2018).

2.4.1 Significance of soil health to Te Ao Māori

Aotearoa New Zealand Māori are firmly affiliated with soil through their whakapapa (ancestry). The concept of healthy soil has evolved and is based around the following Māori core values principles, shown in Figure 2.14 (Chetham & Shortland, 2013; Stevenson et al., 2022; Stronge et al., 2020):

- mauri (life force or energy)
- whakapapa (ancestry)
- wairua (spiritual connection)
- taonga tuku iho (treasured ancestral lineage)
- māra kai/mahinga kai (ability of soil to provide healthy food)
- oranga (ability of well-functioning soil to ensure health and wellbeing of plants, animals, and humans)
- kaitiakitanga (cultural and environmental guardianship).
- mana (power, prestige, and authority)

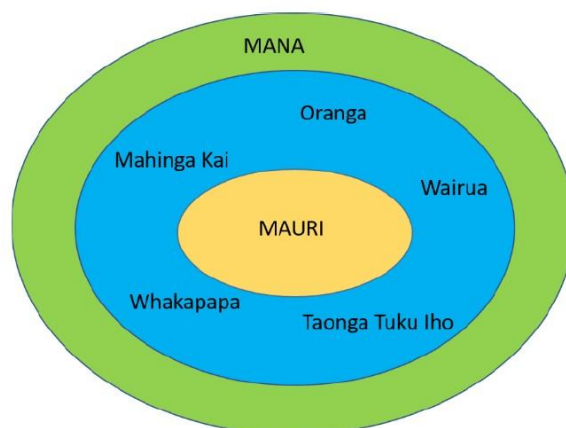


Figure 2.14: Māori key values and principles related to maintaining soil health (Stevenson et al., 2022).

“Soil health and resilience: oneone ora, tangata ora” is a project based on conventional science in conjunction with indigenous knowledge (mātauranga Māori), and is targeted toward the development of an integrated framework for soil health based on a “well-being” approach. This approach, which focuses on diversity and inclusion, can improve the management of soil and other land resources throughout Aotearoa New Zealand (Manaaki Whenua – Landcare Research, 1996; Stevenson et al., 2022).

2.5 Soil characteristics

Soil is a unit of whole terrestrial ecosystem. At the same time, soil is an ecosystem by itself, nurturing a myriad of organisms that are not only interdependent amongst each other but also with the encompassing physical and chemical soil environment (Osman, 2012). Figure 2.15 below depicts the abiotic and biotic components of a typical soil ecosystem that are inter-reliant on each other (Osman, 2012).

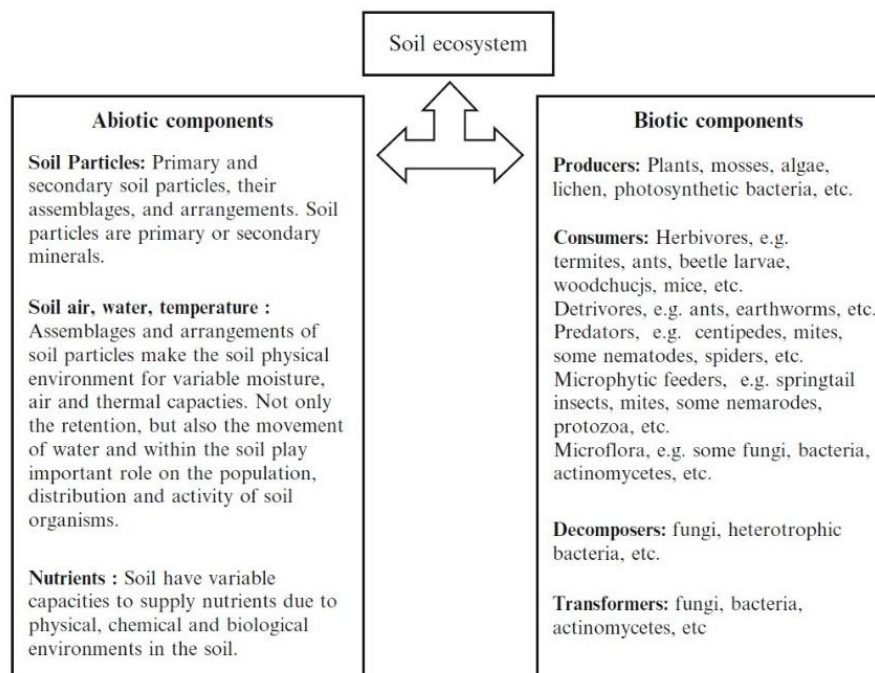


Figure 2.15: Constituents of a typical soil ecosystem (Osman, 2012).

The relationships between biotic and abiotic systems support life and maintain global biochemistry by cycling of the elements (Falkowski & Jelen, 2013). The elemental circulation between living and non-living domains of the earth’s reservoirs (the atmosphere, terrestrial biosphere, hydrosphere, and geosphere) governed by chemical, physical, geological, and biological interactions is referred to as biogeochemical cycles (Krapivin, 2008). The six most universal elements, namely carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulphur, serve as components of the chief building blocks of organic molecules in living entities (Brusseau, 2019; Falkowski & Jelen, 2013). Biogeochemical cycles are crucial for sustenance of life as well as ecosystem functionality through transformation of energy and matter (Brusseau, 2019).

Microbial communities play a significant role in maintaining several biogeochemical processes (Falkowski & Jelen, 2013). At the interface of the living and non-living world, the microorganisms play a pivotal role through enzymatic reactions in all environmental processes as demonstrated in Figure 2.16. These biogeochemical processes are very intricate, involving the cycling of basic building blocks (or nutrients) as well as by electron transfer pathways using solar energy as a primary source of energy (Falkowski & Jelen, 2013).

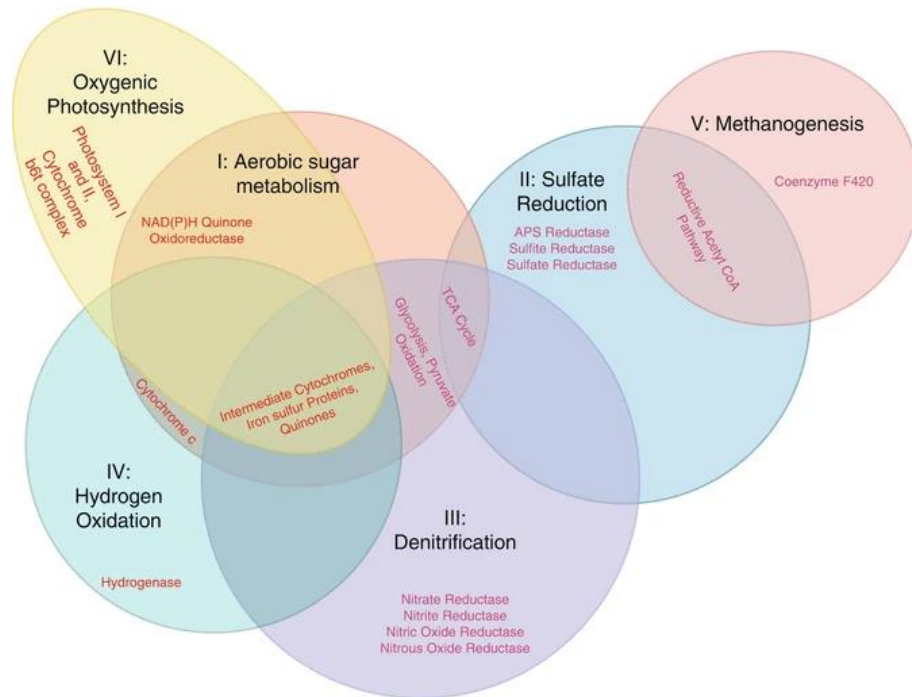


Figure 2.16: Venn diagram illustrating the interconnected biogeochemical processes (Falkowski & Jelen, 2013).

2.5.1 Biological characteristics

Microorganisms are the most important biotic component of soil and play a major role in the ecosystem, dictating numerous functions (Gałązka et al., 2017; Sofo et al., 2014). There can be considerable variations in microbial composition over space and time depending on the type of soil (Xue et al., 2018). Any changes in relative abundance, structure, and complexity of microbial communities are directly reflected in the soil condition. Thus, microbial communities act as the biological indicator of the health status of the soil (Gałązka et al., 2017; Shao et al., 2020).

The distribution of the microbial community is driven by the (abiotic) physical and chemical conditions as well as the biological processes (biotic) in each environment. Concurrently, the microbial activity reciprocates the status of the soil, forming a complex yet self-managing soil-microbe system (König et al., 2020). Soil microbial communities have a remarkable impact on various soil ecological and physiological functions including decomposition of soil organic matter, regulation of different cycles of soil nutrients, nitrogen fixation, and carbon storage (Sofa et al., 2014; Xue et al., 2018).

By influencing several processes, the microbes enhance the physicochemical characteristics of the soil, thereby facilitating plant habitability (Sofo et al., 2014). They promote plant growth via production of biologically active substances as well as mycorrhiza formation (Sofo et al., 2014; Xue et al., 2018). According to Bardgett and Wardle (2010), the microbial communities below the ground have a direct influence on the biotic communities above the ground, which not only affects the diversity of microbes on the surface of the ground but also the richness, distribution, and productivity of the plant species. On the other hand, the structure and diversity of the microbial community is significantly influenced by the variation of plant species above ground (Zak et al., 2003). This synergistic plant-microbe correlation forms a fundamental component of the functionality of the ecosystem (Zak et al., 2003).

In forest ecosystems, nutrient cycling occurs through the uptake of nutrients from soil by plants and returning these nutrients back to the forest floor in the form of dead leaves, branches, roots, and even dead trees (Morris, 2004). The availability of plant nutrients through microbial decomposition is a focal point of the biogeochemical nutrient cycle (Falkowski & Jelen, 2013). This process of conversion of organic matter to mineral forms, described as mineralisation, plays a significant role to source nutrients for forest evolution (Morris, 2004). In the case of kauri forest, kauri greatly affects the condition of the soil beneath the canopy by altering nutrient and moisture levels (Verkaik & Braakhekke, 2007; Wyse & Burns, 2013). The study conducted by Byers, Waipara, et al. (2020) found a considerable change in the soil microbiota of the kauri forest when compared to neighbouring pine forest.

The relationship between microorganisms in a soil ecosystem can be either beneficial (symbiosis, mutualism, or commensalism) or antagonistic (competitive, parasitic, or predatory) and is represented by the existence of the soil microorganisms and the effect created by them (Samaddar et al., 2021). Heterogeneity in soil microbiota means there are more beneficial microorganisms, which creates an antagonistic or competitive effect by suppressing the detrimental and invasive pathogens (Samaddar et al., 2021; Yang et al., 2017). This important aspect of suppression of pathogens was proposed by Janvier et al. (2007) and more recently by Lehmann et al. (2020), and has been included in the latest version of soil health indicators (Samaddar et al., 2021). Soil which innately contains microorganisms that deter harmful organisms by lowering the endurance and impact of the pathogens is known as disease-suppressive soil (Schlatter et al., 2017).

The presence of *P. agathidicida* in soil has been found to have a significant impact on the soil microbial community. Byers, Condron, et al. (2020) and Byers et al. (2021) found a notable change in the diversity and composition of both fungal and bacterial population. The soil with *P. agathidicida* displayed a higher relative abundance of taxa such as *Penicillium*, *Trichoderma*,

Enterobacteriaceae, and *Pseudomonas*, which are known to have disease-suppressing ability (Byers, Condron, et al., 2020; Byers et al., 2021).

The diversified species of microbes as well as their abundance and configuration play an important role in controlling several ecological functions. Thus, it is vital to identify the physicochemical factors and soil properties which contribute to the distribution and composition of microbes in soil (Tian et al., 2017).

2.5.2 Physical characteristics

Soil is heterogenous system that is polyphase, diffused, and permeable. Figure 2.17 shows that soil consists of four phases – solid (mineral matter and organic matter), liquid, and gaseous – which hold key positions in the formation of the soil and its physical properties (Gliński, 2011). Several physical properties of soil have been identified by pedologists which play vital roles in supporting plants and microbes alike (König et al., 2020; Osman, 2013c). Several physical factors influence plant health. According to Indoria et al. (2017) the physical condition of the soil supports root proliferation, assists water and nutrient uptake, and provides firm attachment for optimum plant growth. Some physical factors that influence plant health comprise of colour, texture, structure, porosity, bulk density, consistency, and temperature (Osman, 2013c). The distribution of microbes is primarily controlled by the texture and the structure of the soil (König et al., 2020).

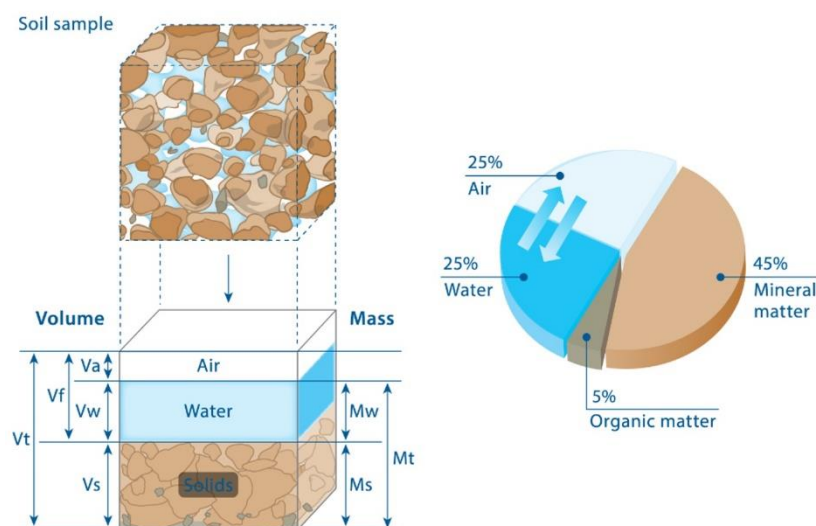


Figure 2.17: Soil phases and their relative proportions (Selker & Or, 2023).

2.5.2.1 Soil texture and structure

Soil texture is the most important physical property as several physical and chemical properties are contingent on soil texture. It is defined as the relative proportion of sand, silt, and clay present in the soil (Karlen et al., 1997; McKenzie et al., 2011). Soil structure is characterised by the composition of these mineral constituents with soil organic matter (McKenzie et al., 2011).

Beneficial mineral soil usually contains (physically by weight) 5% organic matter and 95% inorganic material whereas, chemically, mineral soil is formed with various combinations of organic and inorganic components (McCalla, 1950). Soil texture remains unaltered and is usually a stable characteristic, while the soil structure can be readily modified to superior or inferior quality by factors such as tillage and compaction (Osman, 2013c).

Normally, mineral soil is comprised of equal parts soil particles and pores by volume. (van Es & Magdoff, 2009). There are 12 textural classes of soil determined by the relative percentage of sand (0.05-2 mm particle size), silt (0.002-0.05 mm), and clay (less than 0.002 mm), as depicted in Figure 2.18. Particles with size 2 mm in diameter or larger fall under the category of rock fragments (gravel, pebbles, etc.) and are not included in the textural classification (van Es & Magdoff, 2009). A textural triangle is referred to define the textural class of the soil. The percentage of sand, silt, and clay is determined through sieve analysis in the laboratory (University of Hawai'i, 2023; van Es & Magdoff, 2009).

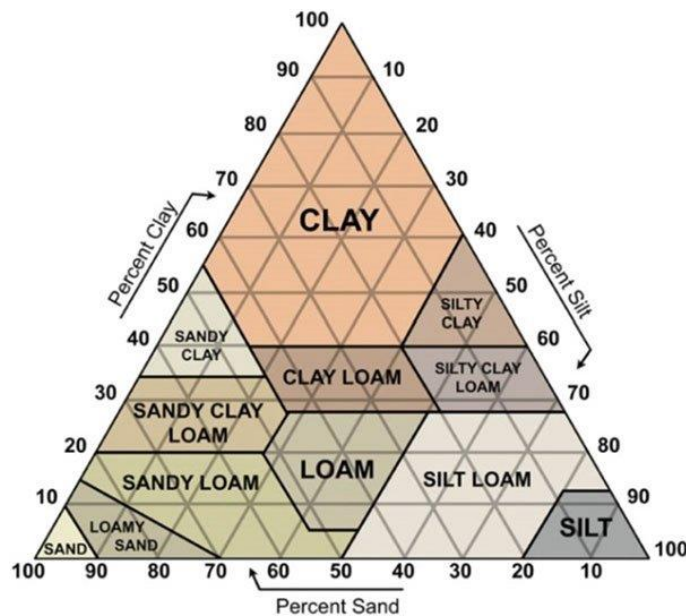


Figure 2.18: Soil textural classes (University of Nebraska-Lincoln, 2023a).

Soil particles are distributed throughout a diverse range of sizes, from large stones and rocks measuring above 0.25 m in diameter to minute clay particles that are less than 1 μm in diameter (Gee & Or, 2002; Grossman & Reinsch, 2018). Various approaches for classification of soil particle size have been adopted to outline the array of particle sizes of the soil. Soil particles smaller than 2 mm are parted into three major categories known as soil separates, namely, sands, silts, and clays. The soil separates are further divided into classes with smaller particle sizes. These particles are separated using sieves with graded pore diameters of varied range (Gee & Or, 2002; Grossman & Reinsch, 2018). The particle size, dimensions of sieve pores, and distinct size class for structured classification implemented by the U.S. Department of Agriculture (USDA), the Canadian Soil Survey Committee (CSSC), the International Soil Science Society (ISSS), and

the American Society for Testing and Materials (ASTM) are represented in Figure 2.19. According to USDA classification, sand particles range between 50 μm -2 mm, silt particles vary between 2 μm -50 μm , and particles less than 2 μm are classified as clay particles.

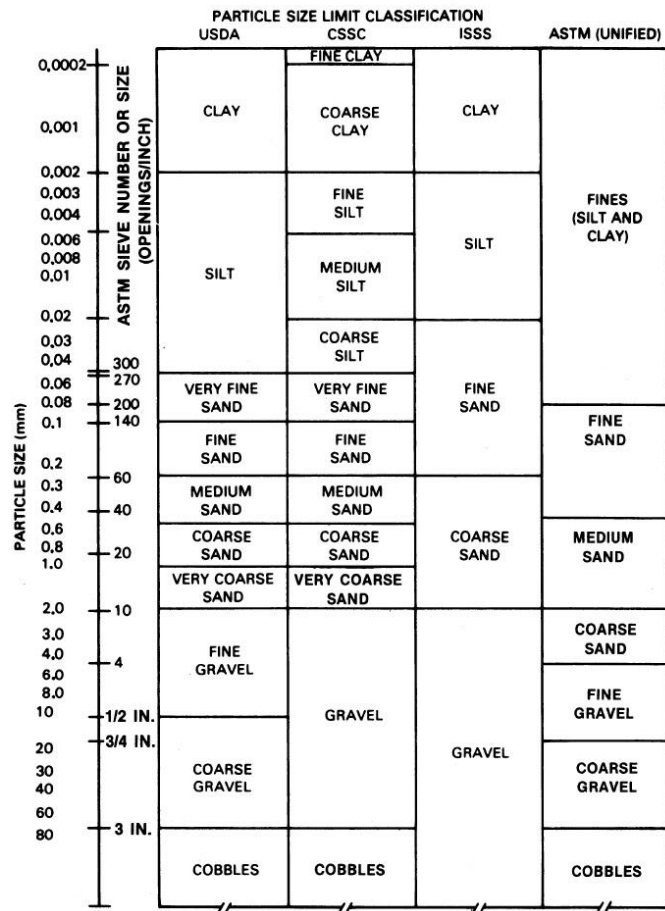


Figure 2.19: Particle size limits according to a number of current classification schemes (Gee & Or, 2002; Grossman & Reinsch, 2018).

The void space in between the different sized particles is known as pore space. This pore space or porosity varies amounts of sand, silt, and clay in a soil as well as the amount of aggregation. Pore with the relative space allows the movement of water and air in between the particles. Soil texture is crucial as it affects water and nutrient-holding capacity, drainage, and aeration (University of Nebraska-Lincoln, 2023a; van Es & Magdoff, 2009).

The organisation of the soil particles held together is referred to as soil structure. The clustered particles are known as aggregates which are formed due to the binding effect of organic materials and humic acid (University of Hawai'i, 2023; University of Nebraska-Lincoln, 2023a). Soil structure is characterised by the size, form, and strength of the aggregates (Pierret & Moran, 2011). Stable structure of the soil with well-distributed pore spaces between the aggregates allows soil drainage and provides adequate aeration, permitting favourable microbial activity and root penetration, thus improving plant health (McCalla, 1950; Pierret & Moran, 2011). In turn, the biological activity of the living world, such as decomposition, provides soil structure and fertility

to the soil. According to Osman (2013c), “Soil structure is the key to soil fertility”. Hence, soil structure plays a principal role in connecting the mineral world to the myriad of life forms at all tropic levels of the biosphere (Pierret & Moran, 2011).

Thus, the combination of soil structure, texture, and geomorphology governs the physical quality of the soil and correlates with the ability of the soil to perform its intended function (McKenzie et al., 2011).

2.5.2.2 Soil bulk density

Bulk density (BD) is described as the dry weight or mass of soil per unit volume of soil (Brown & Wherrett, 2022; Indoria et al., 2020). Of the total volume of the upper layer of the soil, the solid portion contributes towards merely 50%, which is comprised of 45% soil particles and 5% organic matter. The remaining 50% is pore space that is filled with air and water (USDA-NRCS, 2014). It reflects on the type of soil and compactness, which is a result of management practise (Indoria et al., 2020; Krzic M. et al., 2010). Usually, the BD of mineral soils ranges between 1.0-1.8 g/cm³ (Brown & Wherrett, 2022; Krzic M. et al., 2010).

The determination of BD is usually performed by drying and weighing soil of a known volume (core method), or by determining the volume at a later stage (clod or excavation method). Recently, a novel in situ method known as computerised tomography (CT) has been developed, which involves transmission of gamma radiation to determine the BD of a given soil mass (Blake & Hartge, 1986; Hao et al., 2008). Another procedure known as time domain reflectometry (TDR) is also employed, however, water content and air-filled porosity are measured simultaneously with BD (Hao et al., 2008). Several factors such as pore space, texture, soil water content, organic matter, and soil depth can impact the BD of the soil (Barbosa et al., 2018). Other external aspects involving environmental factors, for instance climatic influence and topography of the soil as well as management practise, can have a bearing on the BD of the soil (Feng et al., 2022).

Soil pore space is a prime component associated with BD, as any factor that affects pore space will likewise influence BD of the soil (Weil & Brady, 2017a). The type of pores (micropores and macropores) and the quantity of pores are both equally important when considering any soil property (Figure 2.20) (Hao et al., 2008). Soils with higher amount of pore space will have lower BD than soils with fewer pores (Weil & Brady, 2017a). BD increases with both compaction and depth of the soil, as well as reduced organic matter content, lesser aggregation, and fewer biopores (Brown & Wherrett, 2022; Weil & Brady, 2017a).

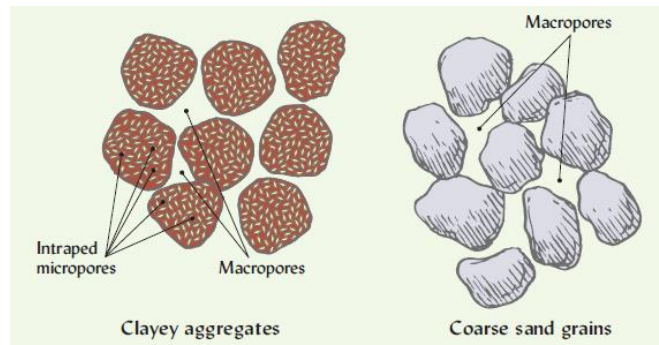


Figure 2.20: A comparison of the macropores and micropores in clayey and sandy soils (Weil & Brady, 2017a).

Soil organic matter plays an integral part in imparting porosity and thereby influencing the BD of any textured soil (Kay & VandenBygaart, 2002). Fine textured soil such as silt loam, clay, and clay loam forms aggregates with sufficient organic matter, materialising into higher amount of pores both within and in between the aggregates, imparting lower BD (Weil & Brady, 2017a). Contrarily, coarse textured soil such as sandy soil contains less organic matter causing less aggregation and lower porosity, and thereby has high BD (Weil & Brady, 2017a). The scarce amount of pores within aggregates makes coarse soil denser than fine soil (Franzluebbers, 2002). Even though the BD of sandy soil is high, the particle size and particle heterogeneity both can affect the BD of the soil (Huang et al., 2013). Similar size particles (well sorted sand) lower the BD, while mixed grain size sand (well graded sand) tends to have higher BD (Weil & Brady, 2017a).

With all factors considered, soil BD in turn controls important soil functions and characteristics like infiltration, available water capacity, soil porosity, nutrient availability, soil microorganism activity, root proliferation as well as rooting depth or restriction (Indoria et al., 2020).

Dec et al. (2008) demonstrated that BD has a direct impact on pore diameter and pore distribution, and their changes are in turn reflected onto the hydraulic properties of the soil. Tanveera et al. (2016) and Brown and Wherrett (2022) also displayed a direct positive relationship was found between BD and sand content. On the other hand, Tanveera et al. (2016) found an intensely negative correlation between BD and soil organic matter (organic carbon), clay content, and porosity. The decrease in organic matter means higher BD, which leads to more compacted soil (Indoria et al., 2020). In addition Brown and Wherrett (2022) found that soil BD greater than 1.6 g/cm^3 hinders root growth.

All in all, soil BD controls important soil functions and characteristics like infiltration, available water capacity, soil porosity, nutrient availability, soil microorganism activity, root proliferation as well as rooting depth or restriction (Indoria et al., 2020).

2.5.2.3 Soil moisture factor

Soil moisture factor is defined as the quantity of water present in the unit mass or volume of unsaturated soil (Brouwer et al., 1985; Campbell & Campbell, 2013; Heddam, 2021). Soil water is described as soil solution that contains dissolved nutrients in both organic and inorganic form, available for plant roots to absorb (University of Hawai'i, 2023). The porosity, structure, and texture of the soil dictates the soil water content (University of Nebraska-Lincoln, 2023a). Water and soil are fundamentals for all lives associated with soil and control geological, ecological, hydrological, and bio-organic processes of the soil (Umasankareswari et al., 2022).

Soil water content has a prominent effect on root proliferation, in both dry and wet conditions. It affects photosynthesis and eventually the obtainability of carbohydrates (Lynch et al., 2012). The amount of moisture present is crucial as it regulates soil temperature, determines yield of crops, and also aids weathering processes and soil formation (American Geosciences Institute, 2023; University of Nebraska-Lincoln, 2023a). Excess water content fills up pore spaces causing anaerobic conditions, resulting in shortage of oxygen. Inadequate aeration reduces root as well as microbial respiration and encourages anaerobic microorganisms (Luo & Zhou, 2006). Lack of soil water causes negative impact such as water stress in plants (Dawson & Ehleringer, 1998). Therefore, it is essential for soil to have appropriate moisture levels.

2.5.2.4 Water holding capacity

Water holding capacity (WHC), also known as volumetric water content (VWC) indicates the amount of gravitational water that soil holds (Reynolds & Topp, 1993). Alternatively, it refers to the total volume of water retained in the soil at field capacity. Soil exhibits sponge-like absorbance and can soak up water within the pores (University of Nebraska-Lincoln, 2023a). The experiment to determine water holding capacity was first tried for Millville loam soil by Widtsoe and McLaughlin in 1902-1903 at the Experiment Station Farm, Utah (Israelsen & West, 1922). Of the many prevalent methods, the 'soak and drain' method is one used commonly in a laboratory (Reynolds & Topp, 1993). The WHC of the soil relies on several other soil properties, namely soil texture, organic matter content, amount of salts, and presence of carbonates and rock fragments. These elements govern the soil for storage and release of water (U.S. Department of agriculture, 2013).

When soil becomes saturated with water, all pores are filled with water. However, after gravitational water is drained out of macropores through percolation, the quantity of water that is left behind within the capillary pores (mesopores and micropores) due to capillary tension is known as the field capacity of the soil. Field capacity denotes the soil water content retained against gravity by the capillary tension of -0.033 MPa in mesopores and micropores (O'Geen, 2013). To extract the capillary water from the pores, plants must surpass this capillary tension (U.S. Department of agriculture, 2013). Initially, plants can readily absorb this water by exceeding

the capillary tension, however, as the soil becomes drier, water extraction from the micropores becomes difficult for the plants and further extraction is not possible. The water content at this stage is said to have reached permanent wilting point. The amount of water held between the field capacity and the wilting point, is known as the water holding capacity of the soil (O'Geen, 2013; Oregon State University, 2023). Figure 2.21 below depicts the wilting point, field capacity, and saturation point of soil. Only a portion of water from the WHC of soil is absorbed by the plants (University of Nebraska-Lincoln, 2023a). Plant available water is the fraction of the WHC that plants are able to absorb without being stressed. Generally, plant available water is assumed to be 50% of the WHC (Rogers et al., 2014).

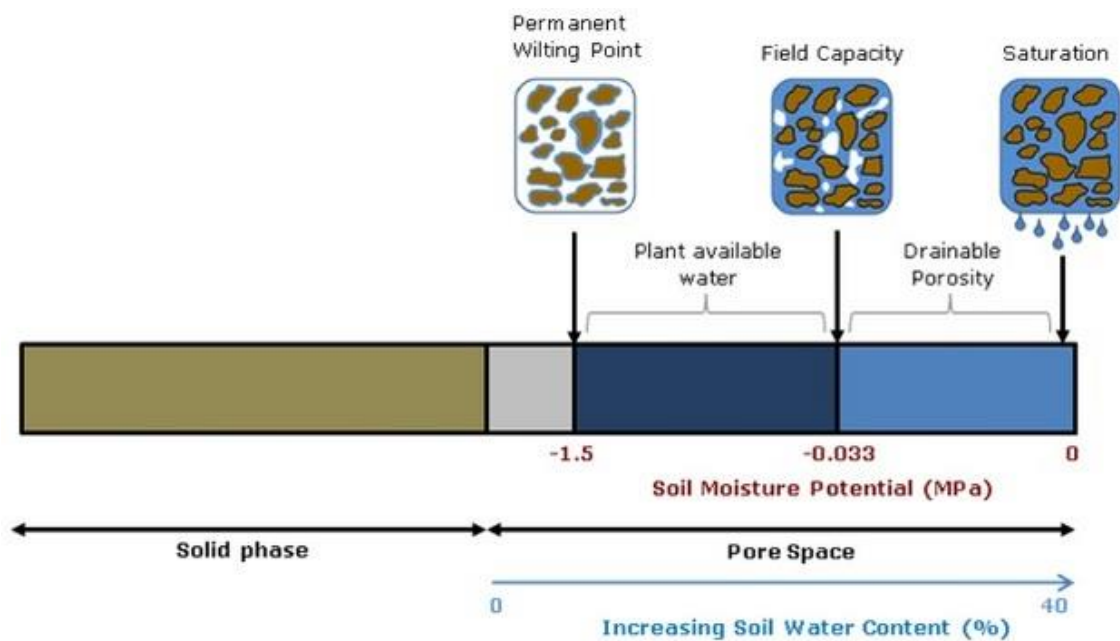


Figure 2.21: The relationship between water content and water potential of soil at permanent wilting point, field capacity, and saturation (O'Geen, 2013).

Soil texture has a key role in determining WHC as every soil has a distinctive combination of particle sizes. Additionally, soil consists of numerous layers, or horizons, each consisting of a different texture and exhibiting varying physical characteristics which control the WHC as well as the amount of water available to the plants (Clark, 2023; Oregon State University, 2023). The WHC of a particular soil texture is reduced by poor structure, low organic matter content, low carbonate levels as well as the amount of stones present (Oregon State University, 2023). Figure 2.22 below displays the WHC with the shaded area between the field capacity and permanent wilting point for soils of different texture.

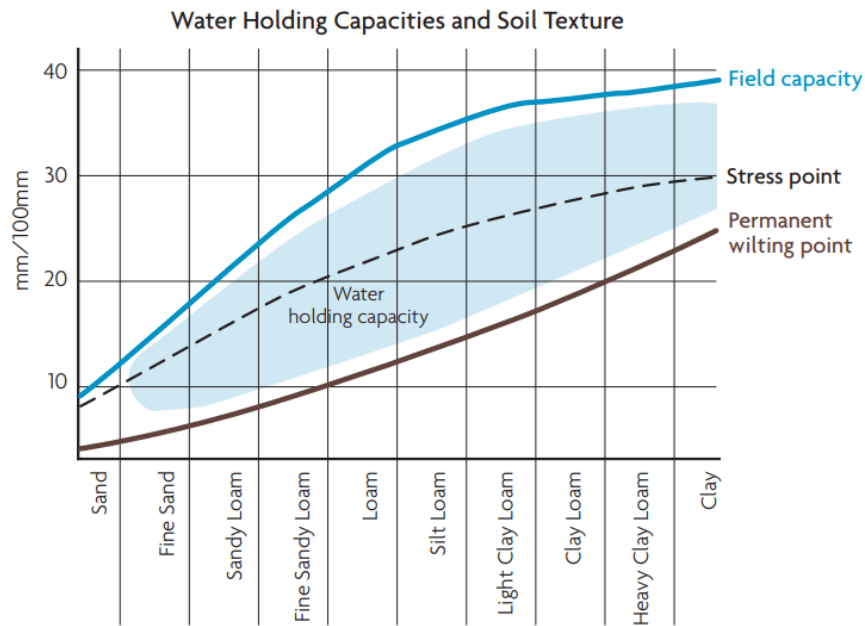


Figure 2.22: The field capacity, WHC, stress point, and wilting point for soils of different textures (Irrigation New Zealand, 1973).

Organic matter, the other predominant factor that contributes to WHC, has the potential to store larger volumes of water than mineral matter due to its capability to attract water naturally (Clark, 2023). Secondly, organic matter boosts soil structure which consequently improves infiltration and increases WHC through water retention. It also aids aggregation creating pore space for water storage (Clark, 2023). Hence, soil organic matter contributes directly and indirectly to increase of WHC, and thereby soil water availability for plant uptake (Weil & Brady, 2017c).

Individual pores of sandy soil are large (macropores), imparting more permeability for the water to drain away, exhibiting low water retention ability. Likewise, sandy soils exert low capillary tension on the retained water. Conversely, clayey soils have innumerable tiny pores (micropores) in the fine textured soil which hold moisture tightly by capillary tension, retaining more water (University of Hawai'i, 2023; University of Nebraska-Lincoln, 2023a).

2.5.3 Chemical characteristics

Osman (2012) describes soil as a “chemical entity”. The chemical properties of soil monitor the quantity and availability of nutrients for plant growth, reveal the amount of toxic components, control microbial composition and distribution, and regulate biogeochemical cycles (Manaaki Whenua Landcare Research, 2022; University of Nebraska-Lincoln, 2023a). Common chemical properties of soil include pH, electrical conductivity, total carbon, total hydrogen, total nitrogen, and carbon:nitrogen ratio.

2.5.3.1 Soil pH

Soil pH, also known as soil reaction, determines the acidity or alkalinity of the soil (FAO, 2021). Sorenson (1909) was the first to define pH as the negative logarithm of the hydrogen ion concentration in equivalents per litre. The unit of hydrogen ion concentration is stated as moles per litre (mol/L).

$$pH = -\log H^+$$

Soil pH is the most crucial chemical characteristic of the soil as it stimulates other soil characteristics and impacts several biological phenomena (Gentili et al., 2018; University of Nebraska-Lincoln, 2023c), and so it is rightly regarded as the “master soil variable” (Neina, 2019; Rekwar et al., 2021). Soil pH is reliant on the anion and cation exchange capacity (AEC & CEC) between the soil and the soil solution (Gentili et al., 2018).

Although pH does not act as a growth factor, it has a significant impact on a myriad of soil biogeochemical processes, as shown in Figure 2.23 (Neina, 2019; Schjonning et al., 2018). The nutrient absorption of plants is very species-specific and relies on the soil reaction (Gentili et al., 2018). Soil pH controls the solubility of individual elements and compounds in soil, eventually directing the availability of nutrients to the plants (Schjonning et al., 2018; University of Hawai‘i, 2023). Extreme acidity or alkalinity results in either mineral deficiency or metal toxicity (König et al., 2020; Lončarić et al., 2008).

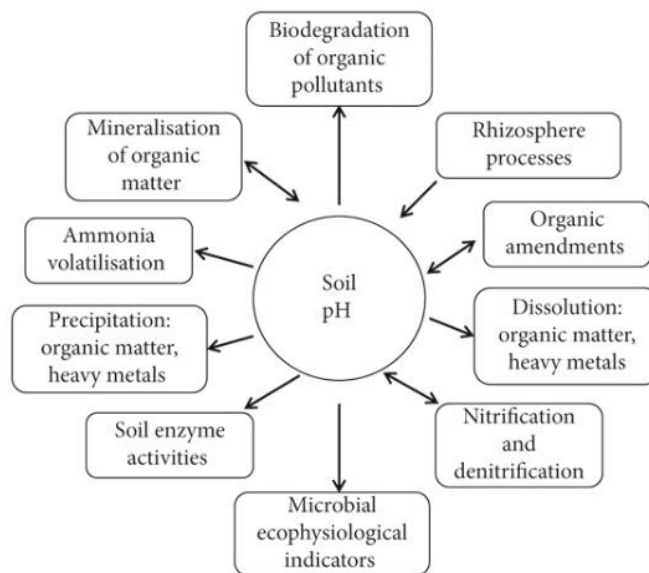


Figure 2.23: Relationship between soil pH and biogeochemical processes. (Neina, 2019).

Furthermore, soil pH controls the abundance of soil microorganisms (University of Hawai‘i, 2023). Soil pH also dictates the relationship between the soil microorganisms and other abiotic factors (Gentili et al., 2018). It manipulates plant growth by influencing the activity of both the beneficial microorganisms at the soil-root interface that are involved in decomposition

of organic matter and releasing nutrients, as well as the activity of organisms causing plant diseases (Tisdale et al., 1985; University of Nebraska-Lincoln, 2023c). Alkaline condition of the soil disrupts aggregation and thereby soil structure, while acidic condition reduces the biological transformation of ammonium to nitrate (University of Hawai'i, 2023). Thus, soil pH is a key variable supporting a multitude of functions.

2.5.3.2 Electrical conductivity

Electrical conductivity (EC) determines the ability of the salt solution to conduct an electrical current at any specific temperature (FAO/GSP, 2020). Alternatively, it is an indicator of electrolyte concentration or salinity of the soil (Ding et al., 2018). Soil contains cations (Ca^{2+} , Mg^{2+} , K^+ , Na^+ , and NH_4^+) and anions (SO_4^{2-} , Cl^- , NO_3^- , and HCO_3^-) in dissolved form that contribute to the salinity of the soil. The ions may be present innately from the parent material, or could be introduced to the soil, so there is variation in concentration in different soils (Bernstein, 1975; USDA & NRCS, 2014).

Factors such as dissolved CO_2 , the type of different ions present, their relative concentrations, valence, mobility as well as temperature have direct bearing on the measurement of EC (Csuros, 1994; FAO/GSP, 2020). It acts as an indicator of availability and deficiency of nutrients, soil moisture, and available water capacity (USDA & NRCS, 2014). It gives an indirect reference to many physical conditions of the soil such as soil texture, porosity, soil thickness, water holding capacity, and drainage conditions (South Dakota Soil Health Coalition, 2023).

Optimum EC is plant specific, and any variation is reflected in plant health. Low EC indicates nutrient deficiency which impedes plant growth. On the other hand, high EC causes salinity stress to the plants by elevating osmotic pressure of nutrient solution and obstructing nutrient uptake (Ding et al., 2018). Increase in EC also deters microbial activities which consequently has negative implications on some vital soil processes such as respiration, residue decomposition, nitrification, and denitrification (USDA & NRCS, 2014). This implies that EC is an important indicator not only of plant health but also soil condition.

2.5.3.3 Total carbon

In soil, carbon occurs in three different chemical forms (Pluske et al., 2023):

- a. Soil organic carbon (SOC) – a component that makes up to 45-60% of soil organic matter and comprises of residues of plants and animals that exist in several decomposition phases (Weil & Brady, 2017b). The resultant product of decay constitutes molecules of organic compounds that contain carbon, oxygen, nitrogen, and hydrogen (Lal, 2016; Pluske et al., 2023). It also consists of the microbial biomass and their derivatives (Lal, 2016). It is a heterogeneous mixture of complex organic compounds, carbohydrates, simple sugars, and some pyrogenic and inert

materials (Lal, 2016). Total organic carbon, soil organic carbon and organic carbon are other synonymic terminologies and can be referred alternatively (Pluske et al., 2023).

- b. Soil inorganic carbon (SIC) – usually exists in form of calcitic and silicatic carbonates and bicarbonates, however, majority of bicarbonates are leached into groundwaters (Lal, 2016; Pluske et al., 2023).
- c. Elemental carbon – this form is negligible in most soil types (Pluske et al., 2023).

2.5.3.4 Total organic carbon

In terrestrial ecosystems, litter decomposition plays a pivotal role for nutrient rejuvenation and determination of the structure of the ecosystem. The process of decomposition has a strong connection to microbial activity, which aids in production, organisation, and stabilisation of soil organic matter (SOM) as well as controlling the carbon and nitrogen cycles (Baumann et al., 2013; Zeng et al., 2017). SOM is commonly used interchangeably with the term total organic carbon (TOC). However, SOM contains not only carbon, but is a reservoir of many plant nutrients including nitrogen, phosphorous, sulphur, potassium, and many other micronutrients (Rice et al., 2021; University of Nebraska-Lincoln, 2023b). TOC is a measure of the carbon content of the SOM. Because organic matter is difficult to measure via a laboratory procedure, TOC is measured instead and a conversion factor of 1.72 is applied to convert TOC to SOM (Pluske et al., 2023). Major environmental factors that control the amount of organic matter accumulation in soil are temperature, moisture, and soil texture (Weil & Brady, 2017b).

$$SOM (\%) = 1.72 \times TOC (\%)$$

Soil organic matter comprises of a combination of intricate and diverse organic constituents (Rice et al., 2021). The soil organic matter is an everchanging element and contributes to only 5% of the total soil composition, however it profoundly impacts several soil physical, chemical, and biological properties as well as the soil function, thus, it is rightly termed as a ‘soil health indicator’ (Rice et al., 2021; Weil & Brady, 2017b). Larson and Pierce (1994) categorised SOM as one of five essential determinants of soil condition, alongside soil cation exchange capacity (CEC), bulk density (BD), water retention, and aeration. SOM is vulnerable to other soil traits, meteorological conditions, and agronomics (Feng et al., 2022).

SOM is a source of numerous pedogenic processes, shown in Figure 2.24, because of its highly reactive nature. It combines with clay and mineral particles of the soil to form organo-mineral complexes because of a high surface area and charge density (Lal, 2016). SOM acts as a binding agent and serves as a key factor in the formation and stabilisation of soil aggregates, and thereby directly influences soil structure (University of Nebraska-Lincoln, 2023b; Weil & Brady, 2017b). Formations of macro- and micro-aggregates stimulates physical properties related to

water and aeration such as porosity, water holding capacity, water infiltration, and bulk density (Pluske et al., 2023; Rice et al., 2021). Micro-aggregates form a rigid and complex network of pores, providing space for air, water and microbes (Hoffland et al., 2020).

In addition, SOM greatly impacts the nutrient holding capacity, thereby reflecting on throughput and rotation of nutrients (Pluske et al., 2023). Mineralisation of nutrient compounds containing nitrogen, phosphorous, sulphur, and other elements present in the SOM is a crucial phase of biogeochemical cycles (Rice et al., 2021). These specific organic compounds act as growth-stimulators promoting plant growth (Weil & Brady, 2017b). It also supports the soil organisms during nutrient cycling by acting as a storehouse for the energy-providing components (Rice et al., 2021). Moreover, SOM sequesters biochemically recalcitrant soil organic carbon (SOC) fractions and acts as a carbon sink (Lorenz et al., 2009). The amount of SOC present in soil is twice that in the atmosphere, and thrice that in vegetation (Rice et al., 2021; Zhao et al., 2021). All the above-mentioned reasons justify that the quality and the quantity of the SOM is paramount for soil quality (Rice et al., 2021; Weil & Brady, 2017b). By contributing in several physical processes through aggregation and providing a conducive environment for biogeochemical cycles, SOM promotes soil microbial community as well as plant health, eventually improving primary production (Hoffland et al., 2020).

Moreover, SOM acts as a reactive surface by retaining harmful toxic heavy metals and organic pollutants, preventing their dispersal into ground and surface water reservoirs, thereby restricting their bioavailability and disease dissemination. This process of water purification through chelating and enriching heavy metals, pesticides, and other organic pollutants is a key soil function of SOM (Hoffland et al., 2020; Pluske et al., 2023). SOM also enhances chemical properties by buffering pH and binding cations (Hoffland et al., 2020; Pluske et al., 2023).

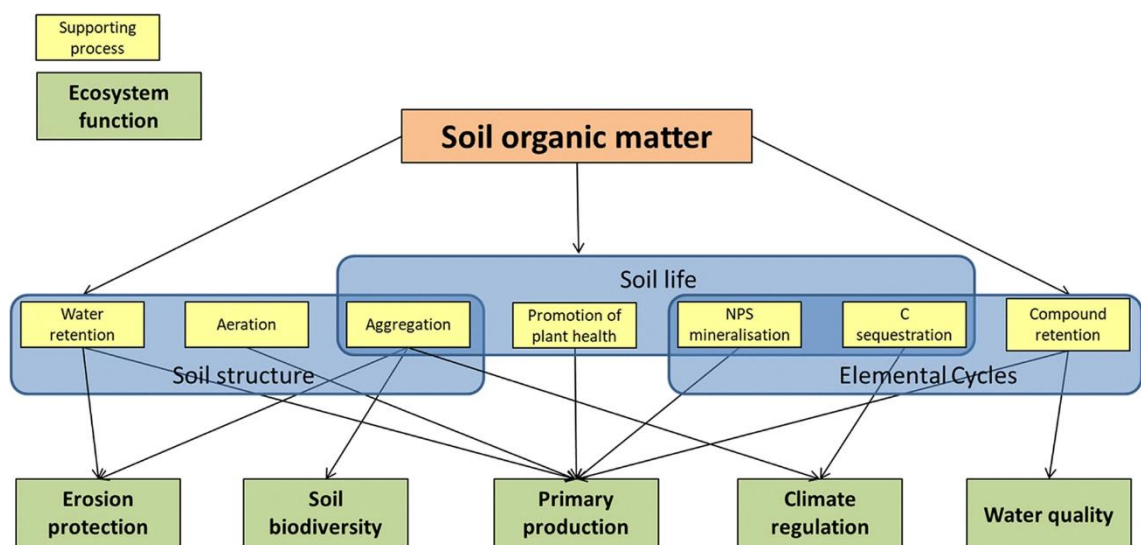


Figure 2.24 Overall ecosystem functions of soil organic matter and their supporting processes (Hoffland et al., 2020).

Thus, by playing a vital sustaining role in soil functions in multiple traits such as protection against soil erosion, provision of a habitat for biodiversity, and promoting primary production, climate regulation, and compound retention, SOM/TOC supports processes associated with soil structure (physical), soil life (biological) and elemental cycles (chemical), which are summarised in Figure 2.25 below.

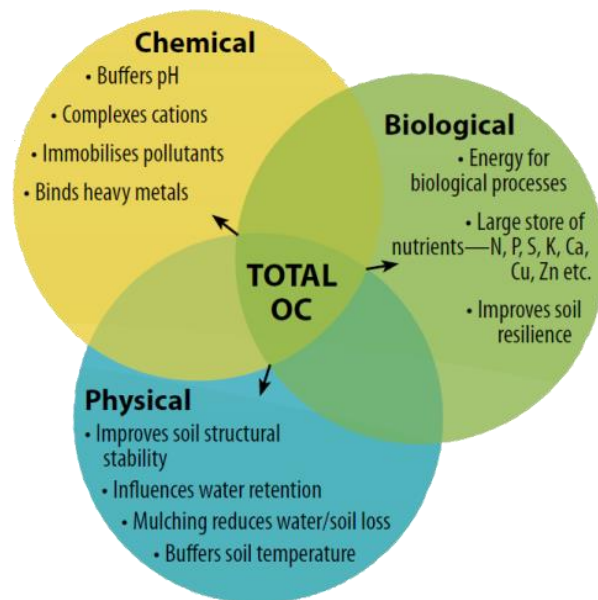


Figure 2.25: Beneficial contributions made by TOC to various physical, chemical, and biological processes (Pluske et al., 2023).

As far as forest ecosystems are considered, TOC is a prime factor in maintaining forest production. The geographic location, type of the forest, as well as the type of soil dictate the distribution of TOC (Liu et al., 2016). Additionally, the rate at which TOC is accumulated and decomposed poses direct bearing not only on the carbon storage of the terrestrial ecosystem but also on the global carbon balance (Liu et al., 2016; Weil & Brady, 2017b). Furthermore, there is 4-6 times more carbon in the SOM in the world's soil than there is in the whole world's vegetation (Weil & Brady, 2017b). Thus, TOC has a crucial role in soils and ecosystems globally.

2.5.3.5 Total nitrogen

As mentioned earlier, soil organic matter is a pool of many plant nutrients. It contributes to more than 90% of total nitrogen present in the soil, which is released by soil microorganisms (University of Nebraska-Lincoln, 2023b). Alongside photosynthesis, biological nitrogen fixation is a crucial biochemical phenomenon for existence of life. The process of nitrogen fixation transforms ubiquitous but inert atmospheric nitrogen (N_2) to reactive forms, which are then available to other organisms through nitrogen cycle. Very specific species of bacteria such as *Rhizobium*, actinomycetes, and cyanobacteria are involved in this conversion process (Weil & Brady, 2017c). The organic nitrogen is mineralised and nitrified by nitrogen-fixing bacteria and nitrifying bacteria to produce ammonia and nitrates respectively (University of Nebraska-Lincoln, 2023d).

Normally, plants only use nitrogen in the ammonium (NH_4^+) and nitrate (NO_3^-) forms, which are the most prevalent inorganic forms of nitrogen in soils (University of Nebraska-Lincoln, 2023d). The presence of different nitrogen forms depicts the abundance and composition of the microbial communities regulating respective pathways involved in nitrogen cycle in the soil (Bru et al., 2011; Nelson et al., 2016). The pH of the rhizosphere soil is dictated by the form of nitrogen utilised by the plants. The pH drops with the absorption of ammonium, while it rises with the uptake of nitrate. The changes in the pH consequently impact the uptake of other minerals and micronutrients (Weil & Brady, 2017c).

Being a macro element, nitrogen has a vital role in plant growth and development. Optimal supply of nitrogen is exhibited in healthy plant foliage with deep green colour, root growth, and overall plant productivity (Weil & Brady, 2017c). Conversely, deficiency of nitrogen reduces the photosynthetic ability of the plants which is visible through plant growth and productivity (Mu & Chen, 2021). Sun et al. (2020) proposed that plants counteract nitrogen deficiency through adaptive measures such as root elongation. Similar results of root elongation were observed by Costa et al. (2002) during excess supply of nitrogen as well.

2.5.3.6 Carbon to nitrogen ratio

Carbon to nitrogen ratio, particularly for soil, represents the ratio of organic carbon to total nitrogen components. It is indicated by C:N or C/N and denoted by a single number with no unit (Brust, 2019; Flavel & Murphy, 2006; Osman, 2013a). This ratio has a direct implication on natural processes occurring in the soil such as decomposition of organic matter, mineralisation, ammonification, and nitrification (Osman, 2013a). In turn, the rate of decomposition as well as the release of nutrients relies on organic residues, the accessible decomposers, and the environment (Mafongoya et al., 1998; Swift et al., 1979). Several environmental elements such as climate, moisture, aeration, pH, and temperature contribute to the decomposition rate and thereby to the C:N ratio (Osman, 2013a; Weil & Brady, 2017b).

The C:N ratio for soil depends on the origins of organic matter, such as types of trees, various parts of plant materials, or animal materials (Weil & Brady, 2017b). The C:N ratio in plant residue varies according to the percentage of lignin, cellulose, and plant proteins and ranges from 8-30. On the other hand, the C:N ratio in microbes is low and constant, ranging between 5-10 (Weil & Brady, 2017b). A soil C:N ratio of 24 is preferable for microbes in order to maintain their C:N ratio (Brust, 2019).

With the addition of organic residues with high nitrogen content and therefore low C:N ratio (<20), decomposing microbes rapidly mineralise the nitrogen from the organic compounds and release it into the soil. This process enhances the nitrogen level of soil, making it available for plant uptake (Boyd, 2009; Brust, 2019; Weil & Brady, 2017b). Alongside this, there is a sharp

increase in microbial growth and the concentration of SOM (Boyd, 2009). However, no nitrate depression is noticed, as seen in Figure 2.26 (Weil & Brady, 2017b).

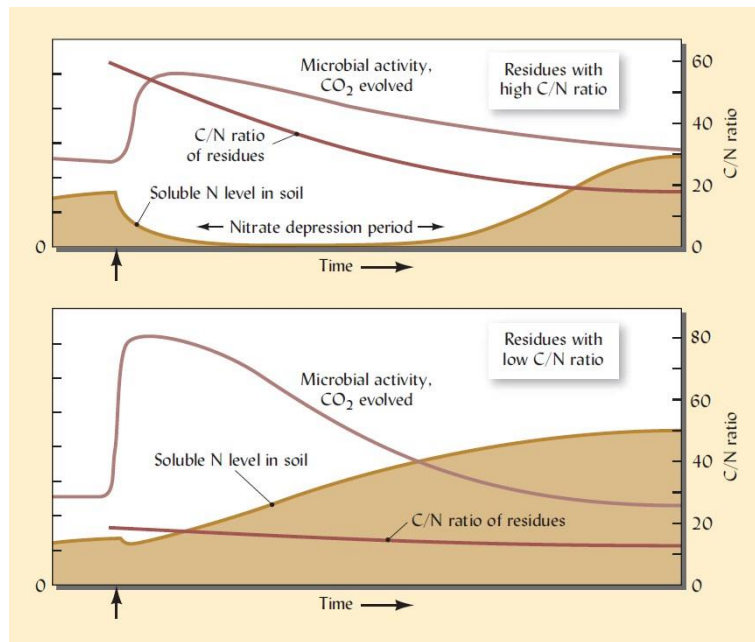


Figure 2.26: Effect of high and low C:N ratio on microbial activity, soluble nitrogen, and residual C:N ratio over time (Weil & Brady, 2017b)

Conversely, organic residues with lower nitrogen content and higher C:N ratio (>25) will attract heterotrophic microorganisms, which consume organic compounds that have higher carbon content. This results in microbial immobilisation of nitrogen, as seen in Figure 2.27, leaving little mineral nitrogen (NH_4^+ or NO_3^-) for plant uptake (Boyd, 2009; Brust, 2019; Weil & Brady, 2017b). This causes nitrate depression, no change in SOM concentration in the soil, and increased CO_2 production, as illustrated in Figure 2.26 (Boyd, 2009; Weil & Brady, 2017b). Figure 2.27 demonstrates that an equilibrium status is achieved between mineralisation and immobilisation at a C:N ratio of 20-30 (Brust, 2019). Thus, the C:N ratio of organic residue is linked to the rate of decomposition as well as SOM formation.

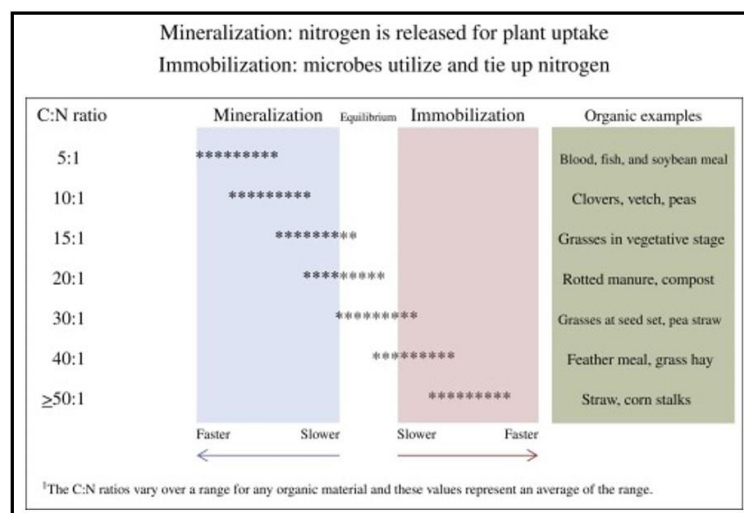


Figure 2.27: C:N ratio in relation to mineralisation and immobilisation rate (Brust, 2019).

Plant residues contain inconsistent amounts of lignin and polyphenols, which impact the rate of decomposition and mineralisation (Vanlauwe et al., 1997). Plant litter containing high lignin content with high C:N ratio has a minimal decomposition rate. Phenolic compounds act to further slow down the decomposition process (Cadisch & Giller, 1997). However, such plant residues releasing nitrogen at a slow rate are beneficial in forest ecosystems as they prevent loss of nitrogen (Vanlauwe et al., 1997). Dise et al. (1998) suggested C:N ratio is an indicator of nitrate leaching for conifer forests.

2.5.3.7 Total hydrogen

Hydrogen is the most prevalent element and is responsible for more than 75% of the mass of the universe (Li et al., 2018; Zeng et al., 2014). It is most abundant in human body composition. Even though it exists as the smallest, lightest, and structurally simplest gaseous molecule in nature, it has a significant role in most biological process involving animals, plants, and microbes alike (Li et al., 2018; Zeng et al., 2014). Most hydrogen exists in a stable diatomic molecular form (H_2). In contrast, the ionic form (H^+) is highly unstable and combustible (Jolly, 2023). It is very reactive and readily forms bonds with negatively charged oxygen to form water – which is the source of life. On the other hand, plants utilise hydrogen during the process of photosynthesis and release oxygen which is also crucial to all living beings. Thus, hydrogen plays a key role in spite of it being the simplest element on the periodic table (Jolly, 2023).

Due to the permeative nature of hydrogen, it is found in all subsurface environments and ubiquitously above the earth's upper mantle (Morita, 1999). In soil, hydrogen takes diverse positions in the molecular structure of various compounds. It exists in organic and inorganic forms, differing in its exchangeability with available hydrogen (Paul et al., 2016). In abiotic environments, the release of hydrogen is dependent on the bond strength and the energy required for exchange. When hydrogen is bound to nitrogen, sulphur, and oxygen, it is easily exchangeable. But when it is bound to carbon with strong covalent bonds, it stabilises and is non-exchangeable, which is the case at ecosystem level (Paul et al., 2016).

It has been hypothesised that the atmosphere around the earth during its formative period was mostly surrounded by hydrogen gas, which was the energy source for the primitive life forms (bacteria) (Morita, 1999; Piché-Choquette & Constant, 2019). Because of its ubiquity, hydrogen has been projected as the first electron donor for ATP synthesis. This is supported by the fact that hydrogen is readily diffusible through the membrane of microbial cells with very low activation energy (Piché-Choquette & Constant, 2019). In 1939, de Saussure stated there was a loss of hydrogen from the soil, which was later in 1982 inferred by Immerdrof to be a consequence of biological activity (D'Imperio, 2008; Morita, 1999).

Hydrogen is a potent energy source for microorganism that are spread through wide variety of archaea and bacteria in varying ecosystems (D'Imperio, 2008; Morita, 1999; Piché-Choquette & Constant, 2019). The presence of a unique group of enzymes called hydrogenases were noticed for hydrogen metabolism in hydrogen-oxidising organisms in both oxic and anoxic environments (D'Imperio, 2008; Piché-Choquette & Constant, 2019). Piché-Choquette and Constant (2019) signifies hydrogen-oxidising bacteria as a foundation species for the carbon cycle (Piché-Choquette & Constant, 2019). Similarly, there are hydrogen-producing bacteria found not only in anaerobic environments, liberating hydrogen gas through the process of fermentation, but also in aerobic environments releasing hydrogen gas by nitrogenase, a vital enzyme during nitrogen fixation in root nodules. The majority of hydrogen is produced through the latter process (Morita, 1999; Piché-Choquette & Constant, 2019). Hence, an equilibrium is maintained between the production and the consumption of hydrogen in soil (Morita, 1999).

The studies related to hydrogen production in plants have been promising. In plants, hydrogen is synthesised by two different pathways involving hydrogenase and nitrogenase enzymes (Li et al., 2018). Hydrogen has proven to be very influential during several plant growth processes such as seed germination, seedling growth, adventitious rooting, root elongation, and other functions such as stomatal closure and anthocyanin synthesis (Li et al., 2018). Hydrogen monitors the expression of responsive genes at some stages of adventitious roots formation and anthocyanin biosynthesis as well as the duration of abiotic stress. Hydrogen interacts with other molecules and serves as a signalling molecule (Li et al., 2018). Hydrogen has already been anticipated as a universal source of energy for growth and maintenance in plants, has been proposed to have a key role as a driver of biogeochemical processes, and may also safe-guard plant progression by antioxidative action (Li et al., 2018; Piché-Choquette & Constant, 2019).

2.5.4 Summary of literature review

Kauri (*Agathis australis*) is a unique conifer species native to Aotearoa New Zealand and found only in the northern North Island (Ogden et al., 1992; Steward & Beveridge, 2010; Steward et al., 2014). As a foundation species, kauri have an integral role in Aotearoa New Zealand forest ecology, providing a unique environment for many species of plants and animals, as well as above and below-ground microbial communities (Wyse et al., 2014). Furthermore, kauri also has significant historical, cultural, and economic impact for Aotearoa New Zealanders (D'Souza et al., 2021; Steward & Beveridge, 2010).

However, kauri is susceptible to a disease called kauri dieback, which is caused by the soil-borne oomycetes *Phytophthora agathidicida*. Kauri dieback originates in the roots and causes symptoms such as basal lesions, gummosis, chlorosis, defoliation, and eventually tree death (Bradshaw et al., 2020; Lambert et al., 2018). One of the major factors relating to kauri dieback

disease is the severity of the environment surrounding kauri trees, particularly the soil system (Bellgard et al., 2013).

Soil is a living system whose functions are associated with sustaining biological processes, maintaining contiguous air and water quality, and promoting the health of plants, humans, and animals (Doran et al., 1996; Janvier et al., 2007; Samaddar et al., 2021; Stevenson et al., 2022). In order to maintain and enhance these functions, it is important to evaluate soil health, which is determined by various biotic (biological) and abiotic (physical and chemical) indicators. These indicators are interconnected and interdependent, and may have a major influence on the growth of kauri as well as proliferation of *P. agathidicida* (Halkett & Sale, 1986; Lambert et al., 2018).

This literature review has discussed the abiotic factors of soil that are essential for determining soil health, and the techniques used to measure and quantify these factors. Physical soil characteristics include soil texture and structure, bulk density, moisture factor, and water holding capacity. Chemical characteristics include pH, electrical conductivity, total carbon, total nitrogen, carbon to nitrogen ratio, and total hydrogen content. The physical and chemical soil characteristics will be determined by following the current accepted methods in soil analysis, as shown in Table 2.1 below:

Table 2.1: Methodologies for measuring soil physical and chemical characteristics (C:N ratio will be calculated from the results obtained from determination of total carbon and total nitrogen).

Soil characteristic	Methodology	Source
Physical characteristics		
Particle size distribution	Sieve analysis	(Hossain et al., 2021a)
Bulk density	Reconstituted bulk density	(Dec et al., 2008)
Moisture factor	Gravimetric water content	(Rayment et al., 2011a)
Water holding capacity	Modified soak and drain method	(Harding & Ross, 1964)
Chemical characteristics		
Soil pH	pH meter (temperature-compensated)	(Blakemore et al., 1987)
Electrical conductivity	EC meter (temperature-compensated)	(Blakemore et al., 1987)
Total carbon	Dry combustion method with elemental analyser	(Dhaliwal et al., 2011; Jimenez & Ladha, 1993)
Total nitrogen	Dry combustion method with elemental analyser	(Dhaliwal et al., 2011; Jimenez & Ladha, 1993)
Total hydrogen	Dry combustion method with elemental analyser	

Chapter 3: Methods



Bendle (2019)

3.1 Location and soil sampling

The present study is a part of the Ngā Rākau Taketake Research Programme, and used soil samples from the Waitākere Ranges Regional Park in Auckland (three locations) and the Coromandel region in Waikato (two locations) (Figure 3.1), that were collected as part of two other postgraduate projects. In the Waitākere region, the samples were collected between June and October 2021 from three different sampling locations, namely Cascade, Huia, and Piha. These locations were established by Bruce Burns and George Perry from the University of Auckland between 2011-2015 for long term monitoring of composition and demography of kauri and other plant species (Froud et al., 2022). For each location, Burns and Perry created symptomatic and asymptomatic sites, based on the presence of visible kauri dieback symptoms. In the Coromandel region, the samples were collected from Tairua (an asymptomatic location) in December 2020 and Whangapoua (a symptomatic location) in April 2021.

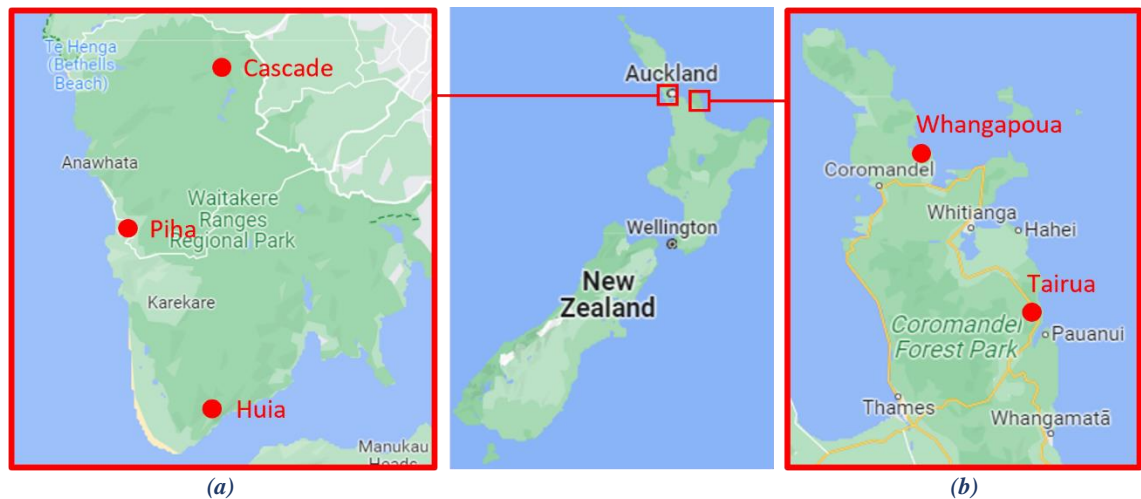


Figure 3.1: Distribution of sampling sites in the (a) Waitākere and (b) Coromandel regions.

The asymptomatic and symptomatic sites of the Cascade location contained many mature kauri trees with trunk diameter over 1 m, while the sites of the Huia location contained adolescent kauri trees, and sites of the Piha location were comprised mainly of young rickers. The symptomatic sites contained trees that presented with kauri dieback symptoms, specifically the presence of basal lesions and poor canopy health. The asymptomatic sites were established as a control and contained trees without visible symptoms of kauri dieback. However, the lack of symptoms does not guarantee the absence of infection by *P. agathidicida* (Froud et al., 2022).

From each symptomatic and asymptomatic site of the Waitākere region, systematic sampling design using either transects or grids was adapted for sample collection as part of another project (Pennock et al., 2008). Four kauri trees were randomly selected in each transect (four transects per site, for a total of 16 kauri trees) and ~200 g of soil was collected at four cardinal points of each tree at 10 cm depth, shown in Figure 3.2. The samples from the four cardinal points were homogenised and pooled into one sampling bag. In the Coromandel region, all kauri trees were selected using random sampling method (Pennock et al., 2008). From the

asymptomatic Tairua site, there were 15 randomly selected kauri trees with ~200 g of soil collected at each cardinal point. In the symptomatic Whangapoua site, 22 randomly selected kauri trees were sampled, but only a total of ~300 g of soil could be collected from all four cardinal points. There was insufficient amount of soil sample for individual tree for physicochemical analyses, therefore, samples in close proximity (GPS location within $\pm 0.005^\circ$) were pooled together. A total of eight pooled samples represented the Whangapoua location. All samples were stored at -20°C until processed.

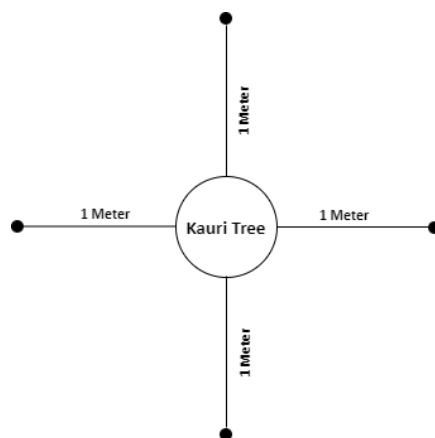


Figure 3.2: Soil sampling for each tree – each ● represents a cardinal point with 1 meter distance from the tree.

3.2 Physicochemical characterisation

Recently, report LC4166 prepared by Stevenson (2022) for the Ministry of Business, Innovation and Employment (New Zealand) updated the list of key soil quality indicators that make up the basic minimum data set for determining state of the environment (SOE). This was based on the findings of Larson and Pierce (1991) as well as Doran and Parkin (1994) as discussed previously in Section 2.4. These indicators characterise diverse soil quality/health aspects such as pH as an indicator of soil acidity; total carbon, total nitrogen, and mineralisable nitrogen to determine the organic status of the soil; Olsen phosphorus determination for soil fertility; and bulk density and macroporosity to gauge the soil physical status (Stevenson, 2022; Stevenson et al., 2022).

This study included analysis of the following physical characteristics: moisture factor (MF), bulk density (BD), and water holding capacity (WHC). Particle size distribution (PSD) was also determined, which consequently led to the verification of the type of the soil and the coefficient of uniformity (C_u). For the analysis of chemical characteristics, soil pH, soil electrical conductivity (EC), and determination of total carbon (TC), total nitrogen (TN), carbon to nitrogen ratio (C:N ratio) as well as total hydrogen (TH) were included.

3.3 Physical characteristics

3.3.1 Particle size distribution

Each soil sample was first dried at 105°C for 24 hrs and weighed (total weight of the soil sample, around 50 g for most samples). Using a sieve tower, a series of eight sieves with decreasing mesh size ranging from 4.75 to 0.075 mm (Figure 3.3(a)), and with a pan at the bottom. The soil sample was placed in the topmost sieve, and the sieve tower was shaken in a mechanical shaker (Endecott Test Sieve Shaker E.F.L.1 Mk11) for 10 mins (Figure 3.3(b)). The sieves and pan were then separated (Figure 3.4), and soil particles retained in each sieve were weighed. The sieves and pan were thoroughly cleaned before processing each soil sample.

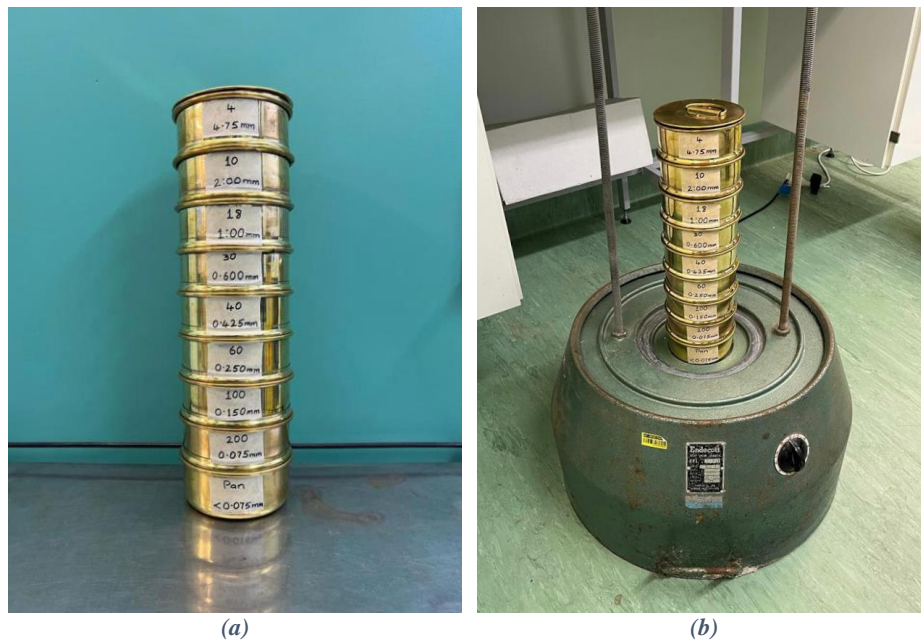


Figure 3.3: Setup for particle size determination; (a) series of sieves in order of decreasing mesh size from 4.75-0.075 mm, (b) sieve tower on shaker.

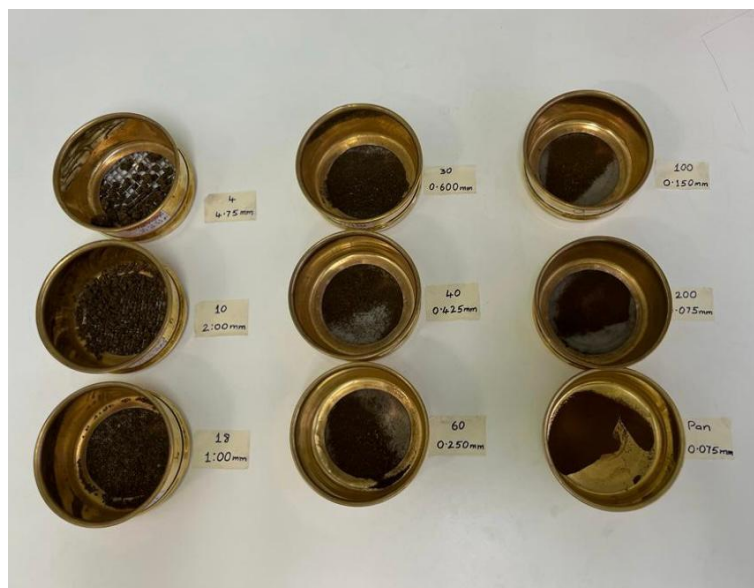


Figure 3.4: Distribution of the soil particles retained by each sieve as well as the pan.

The mass of soil passing through each sieve was able to be used to determine the particle fractions of each soil sample, namely the proportions of gravel, sand, and fines (silt and clay), based on soil classification by USCS (Geotechnical Engineering Bureau, 2015). Soil with particle size greater than 4.75 mm (mesh size of the largest sieve used) was classified as gravel, between 4.75-0.075 mm was classified as sand, and less than 0.075 mm (mesh size of the smallest sieve used, collected in the pan) was classified as fines (Appendix 3).

The uniformity coefficient (C_u), which is used to quantify the particle size distribution of soils, was also calculated. The formula for calculating C_u is:

$$C_u = \frac{D_{60}}{D_{10}}$$

where D_{10} is the diameter at which 10% of soil particles are finer and 90% of soil particles are coarser, while D_{60} is the diameter at which 60% of particles are finer and 40% of the particles are coarser. In other words, D_{10} and D_{60} are the theoretical sieve diameters through which only 10% and 60% of soil would pass, respectively. Soils with uniformity coefficient value greater than 4 are classified as well graded, whereas soils with uniformity coefficient value lower than 4 are classified as poorly or uniformly graded (Zekkos, 2002).

To calculate C_u , the percentage of soil passing through each sieve was required for each soil sample. Table 3.1 demonstrates the measurements and calculations carried out for a single soil sample (UC-A43 from the Asymptomatic Cascade site).

Table 3.1: An example of the measurements taken, and values calculated to determine particle size distribution for a single soil sample (UC-A43 from the Asymptomatic Cascade site).

ASTM Sieve #	Opening diameter (mm)	Mass of empty sieve (g)	Mass of sieve + soil retained (g)	Mass of soil retained (g)	Percentage retained (%)	Cumulative percentage retained (%)	Percentage passing (%)	
		A	B	C	D	E	F	
					$C_i = B_i - A_i$	$D_i = \frac{C_i}{Total\ mass}$	$E_i = C_i + E_{i-1}$	$F_i = 100 - E_i$
4	4.750	210.597	211.076	0.479	0.646	0.646	99.354	
10	2.000	219.042	239.796	20.754	27.984	28.630	71.370	
18	1.000	187.610	212.310	24.700	33.305	61.935	38.065	
30	0.600	177.137	190.602	13.465	18.156	80.091	19.909	
40	0.425	174.294	180.040	5.746	7.748	87.839	12.161	
60	0.250	162.670	167.336	4.666	6.292	94.131	5.869	
100	0.150	167.441	170.087	2.646	3.568	97.698	2.302	
200	0.075	165.124	166.161	1.037	1.398	99.097	0.903	
Pan	-	127.000	127.670	0.670	0.903	100.000	0.000	
Total mass				74.163				

The percentage passing values were plotted, and values of D_{10} and D_{60} were interpolated from the logarithmic graph (Figure 3.5). The values of D_{10} and D_{60} were then used to calculate C_u

for the soil sample as per the formula above. This entire procedure, including sieving, weighing, plotting logarithmic graph, and calculating C_u , was repeated for each soil sample.

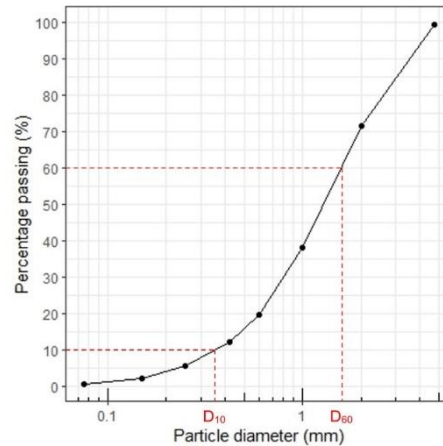


Figure 3.5: Logarithmic graph of Percentage passing vs. Particle diameter, used to find values of D_{10} and D_{60} for UC-A43 soil sample.

3.3.2 Bulk density

The soil samples were disturbed and not representative of their original state, therefore, the method for measuring bulk density of the pooled soil samples in laboratory conditions was adapted from Dec et al. (2008). The soil samples were filled to the capacity of the crucible (125 cm^3), dried in the oven at 105°C for 24 hrs, and weighed. The bulk density (g/cm^3) of each soil sample was calculated using the equation given below.

$$BD = \frac{\text{mass}_{\text{dried soil}}}{\text{volume}_{\text{crucible}}}$$

3.3.3 Moisture factor

The ratio of water mass lost to the mass of dried soil is known as gravimetric water content, ascribed by Topp et al. (1993). The method to measure moisture factor of soil, based on the thermogravimetric concept, is known to generate absolute results (Gardner, 1986; Topp et al., 1993). In order to determine the moisture factor or moisture content of the given kauri soil samples, the method was adapted from Manaaki Whenua Landcare Research (2021) and Rayment et al. (2011a).

The wet soil samples were placed in clean, dry, and tared crucibles and weighed by a pre-calibrated balance (Ohaus Explorer EX1103, 1 mg precision). The weight of each wet sample was recorded (Campbell & Campbell, 2013; Gardner, 1986; Hossain et al., 2021b). Plant organic matter, gravel, and stones were removed prior to weighing. The crucibles containing the soil samples were dried at 105°C for 24 hours.

Dried samples were cooled in the oven to avoid ambient exposure and immediately weighed and recorded. Moisture factor for each sample was calculated as a percentage using the following formula (Gardner, 1986; Topp & Ferre', 2002):

$$\text{Moisture factor (\%)} = \frac{\text{mass}_{\text{wet soil}} - \text{mass}_{\text{dry soil}}}{\text{mass}_{\text{dry soil}}} \times 100\%$$

3.3.4 Water holding capacity

Water holding capacity (WHC) is the quantity of water retained by the soil after it has been saturated and then allowed to drain overnight (Manaaki Whenua Landcare Research, 2021). This direct method of Harding and Ross (1964), which involves the removal of water from the saturated soil matrix, was used.

Glass funnels were set up as shown in Figure 3.6, with 25 g of soil samples, glass wool, and rubber stoppers. The soil samples were saturated by adding 50 mL of water in a 1:2 ratio between soil and water. After addition of water, the funnels were covered with parafilm to avoid water loss into the atmosphere, and placed in conical flasks to keep them upright. The soil samples were allowed to soak for 16 hours (Figure 3.7(a)).

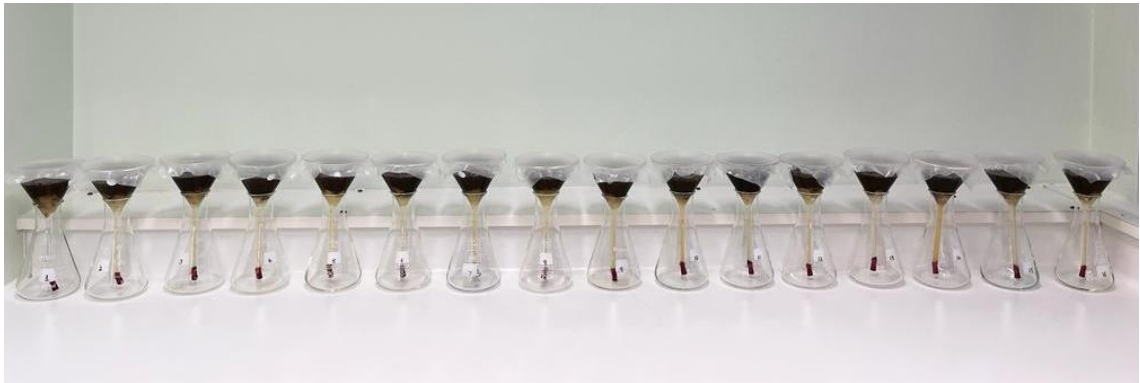


Figure 3.6: Setup for WHC experiment.

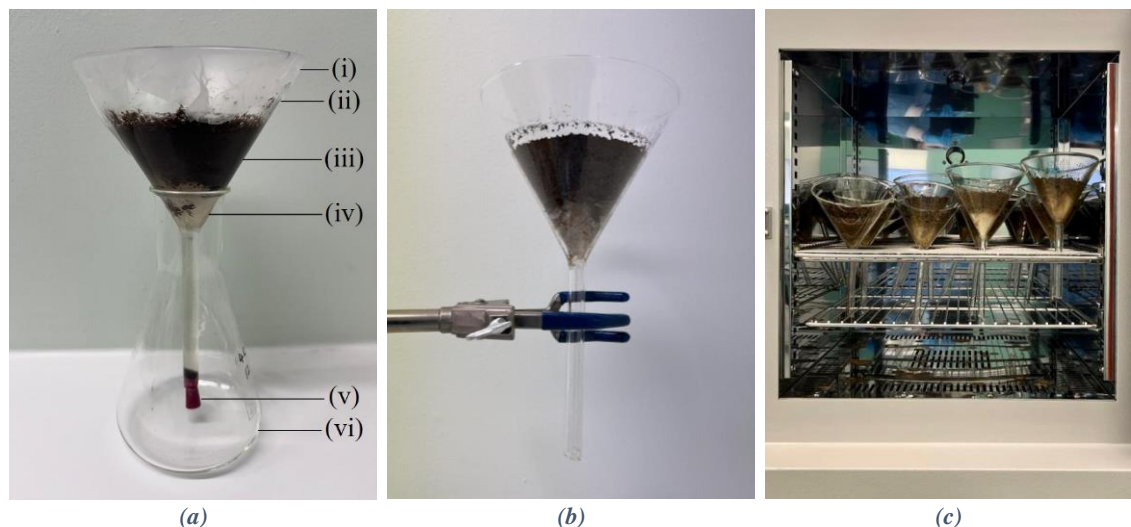


Figure 3.7: Stages of WHC procedure (a) soaking soil sample ((i) parafilm, (ii) funnel, (iii) soil, (iv) glass wool, (v) rubber stopper, (vi) conical flask), (b) draining soil sample, (c) dried soil samples in oven.

After 16 hrs, the rubber stoppers were removed and excess water was allowed to drain for 3 hrs, or until there was no more water dripping (Figure 3.7(b)). The saturated soil and glass wool were weighed before drying in the oven for 16 hrs at 105°C (Figure 3.7(c)). After cooling, the mass of dried soil and glass wool was measured.

The standard formula given by Harding and Ross (1964) for calculating WHC is:

$$WHC = \frac{mass_{saturated\ soil} - mass_{dried\ soil}}{mass_{saturated\ soil}} \times 100\%$$

This formula does not take into account the water retained by the glass wool. It was important to consider the water-retention capacity of glass wool for two reasons. Firstly, the porosity of glass wool enables the retention of substantial amounts of water. Secondly, due to limitation of funnel volume, very low mass of soil samples was used. Therefore, glass wool had a considerable effect on the WHC of the soil samples.

Furthermore, it was impossible to use an identical mass of glass wool for each funnel. Hence, an additional procedure was carried out to measure water retention of glass wool, and derive a linear relationship between mass of glass wool and mass of water retained (Appendix 1). The modified formula for calculating WHC of the kauri soil samples is shown below:

$$\begin{aligned} WHC &= \frac{mass_{total\ water\ loss} - mass_{water\ retained\ by\ glass\ wool}}{mass_{saturated\ soil}} \times 100\% \\ &= \frac{mass_{total\ water\ loss} - (7.7799mass_{glass\ wool} + 2.7018)}{mass_{saturated\ soil}} \times 100\% \end{aligned}$$

3.4 Chemical characteristics

3.4.1 Soil pH

The water extraction procedure for measuring soil pH was followed as described by Blakemore et al. (1987). The Oakton pH 700 bench meter was calibrated using calibrating solution or pH buffer 7.00 followed by pH buffer 4.01 prior to the pH measurement of the soil solution. For the preparation of soil solution, a suspension of 4 g of each soil sample with 20 mL millipore water (18.2 Ω) in a ratio of 1:5 was made in falcon tubes. The suspension was agitated in the shaking incubator for 30 mins at 200 rpm maintained at 25°C, and allowed to rest for 5 mins. pH was measured using the calibrated probe (Blakemore et al., 1987; Manaaki Whenua Landcare Research, 2021). All readings were taken in triplicates for each of the soil samples. The electrode was carefully washed with millipore water after every use. Millipore water was used as a negative control (Csuros, 1994), for which pH was in acceptable range of 7.0 ± 0.1.

3.4.2 Electrical conductivity

A benchtop Conductivity-TDS-mV-Temperature Instrument from labCHEM-CP containing platinum electrodes was used to measure the EC of all the soil samples. To calibrate the EC meter, 0.01 M potassium chloride solution (KCl) was used as a standard or reference solution, which has conductivity of 2760 $\mu\text{S}/\text{cm}$ at 25°C. The EC meter is also calibrated to compensate the reading at 25°C. A successful calibration is displayed with conductivity cell constant $k = 1.00$ (Csuros, 1994; MS-labCHEM-CP- TPS, 2003).

The method for EC measurement was adapted from Alam et al. (2020), Blakemore et al. (1987), and FAO/GSP (2020). For each soil sample, 20 mL of millipore water was added to 4 g of soil and agitated for 30 mins at 200 rpm, maintained at 25°C. After allowing the soil particles to settle for 5 mins, the soil solution was filtered through Membrane Solutions qualitative filter paper (125 mm, medium fast, 11 μm), and the filtrate was used to measure the electrical conductivity. All readings were taken in triplicates for each of the soil samples, and the glass electrode was washed with millipore water after each measurement (FAO/GSP, 2020). Millipore water was used as a negative control (Csuros, 1994), with EC ranging between 1.22-1.50 $\mu\text{S}/\text{cm}$.

3.4.3 Total carbon, total nitrogen, C:N ratio, and total hydrogen

3.4.3.1 Elemental analyser

To determine total carbon (TC), total nitrogen (TN), and total hydrogen (TH) content in the soil samples, the Exeter CE-440 Elemental Analyser was used. The elemental analyser simultaneously determines content of both organic and inorganic forms of carbon, nitrogen, and hydrogen in the sample (Exeter Analytical Limited, 2003). The total carbon and total nitrogen content were used to derive the carbon to nitrogen (C:N) ratio of each sample.

The results drawn from the elemental analyser are sensitive to the moisture factor, particle size, and quantity of soil samples analysed (Dhaliwal et al., 2011). These factors were standardised and optimised as per the procedures described in Appendix 2. After the standardisation process, the optimised variables were set as follows:

- A. drying temperature of 80°C,
- B. sample mass of 10 mg, and
- C. particle size of <0.25 mm.

3.4.3.2 Sample preparation

The soil samples from each site and location were prepared according to the optimised variables above. Initially, gravel as well as visible organic matter such as plant/animal materials and dead soil invertebrates were removed from the soil samples. The samples were dried at 80°C for 24 hours (Appendix 2). The dried soil samples were sieved using a 2 mm sieve to remove

larger soil particles, and pulverised using a mechanical mortar and grinding ball (diameter 70 mm) from FRITSCH Vibratory Micro-Mill "pulverisette 0" (Figure 3.8(a)) (FRITSCH, 2001). The vibration amplitude was set at 1 mm for 2 minutes, until the soil sample was ground into fine powder with particle size less than 0.25 mm (Figure 3.8(b)) (Appendix 2). Due to their high tendency to absorb moisture, the pulverised samples were stored in screw-capped glass vials and kept in a sealed container with silica crystals until processed.



Figure 3.8: Soil sample preparation for elemental analysis; (a) FRITSCH Vibratory Micro-Mill "pulverisette 0" (FRITSCH, 2001), (b) pulverised soil sample.

3.4.3.3 Procedure

For analysis, samples must be filled into small tin capsules (6×2.9 mm) which are sealed by crimping, and placed in nickel sleeves. These sleeves are inserted into the 64-position autosampler carousel of the analyser.

Before each sample run, a pre-sample setup run was carried out with a set of conditioners (~2 mg pure acetanilide), blanks (empty tin capsules, acting as negative control), and standards (~2 mg pure acetanilide, same as conditioners, acting as positive control) to calibrate the analyser and ensure its precision and accuracy. For the sample runs, the carousel of the analyser was filled with nickel sleeves containing tin capsules with triplicates of 16 soil samples at a time, along with conditioner, blanks, and standards placed at regular intervals. Results for total carbon, total nitrogen, and total hydrogen were returned as percentages and were recorded from the computer attached to the analysing system.

3.5 Tree health characteristics

The above-ground visual tree health status was also recorded as part of other postgraduate research, which included measuring trunk diameter at breast height (DBH), presence or absence of basal lesions (basal bleed) (Ecroyd, 1982; Halkett & Sale, 1986; Orwin, 2007b), age of the basal bleeds (whether the gummosis was dry or not), and canopy health. The canopy health scale

uses the intensity of chlorosis, defoliation, and number of dead branches as the basis for a score between 1-5, at increments of 0.5. A score of 1 is for absence of chlorosis and defoliation, and no dead branches, and 5 is for a dead tree (Waipara et al., 2013). As the designated sites (asymptomatic and symptomatic) were not necessarily representative of the presence of *Phytophthora agathidicida*, these symptoms, which are characteristic of kauri dieback, they were used instead to determine the health status of the trees (healthy or unhealthy) with regards to the presence of dieback.

For the Waitākere region, kauri trees with presence of basal bleeds or with canopy score above 2.5 were considered “unhealthy”, as they displayed strong symptoms of kauri dieback. All other trees (without basal bleeds and with canopy score of 2.5 or lower) were considered “healthy”. The health of kauri trees was classified based on the work of Bellgard et al. (2013) and the technical report – 2021 Waitākere Ranges Kauri Population Health Monitoring Survey (Froud et al., 2022).

3.6 Statistical analysis

Measuring the physical soil characteristics required about 150 g of soil per sample. Due to the limited amount of soil available per sample, only one measurement was recorded for each of the physical soil characterisation experiments. Measuring the soil chemical characteristics only required about 25 g of soil, hence tests were done in triplicate. The mean value of the triplicate readings was calculated to represent the measurement for each sample.

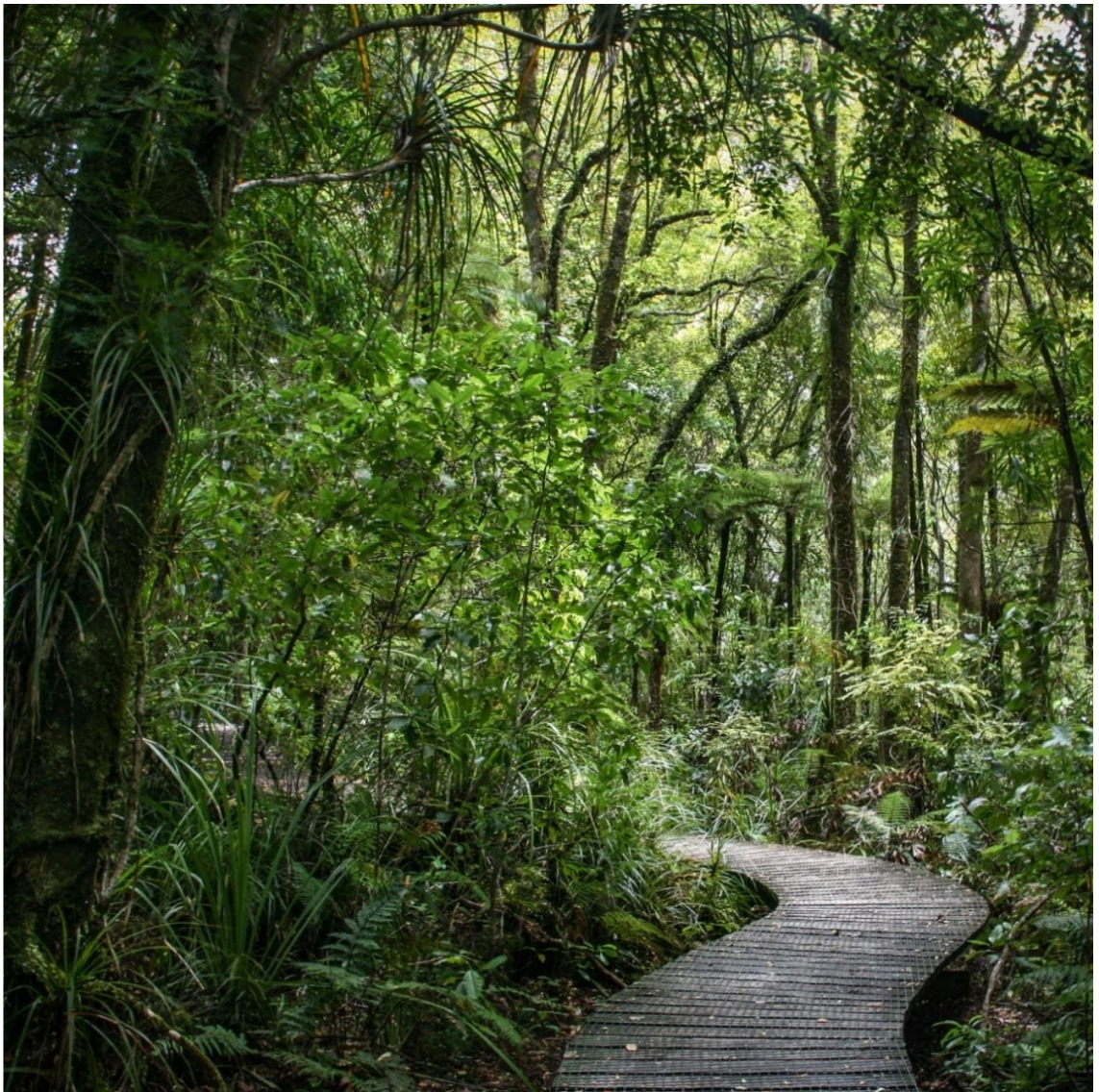
Data was grouped according to site, location, health status by location, and health status by region. Groups of data were analysed using Shapiro-Wilks test for normality, carried out with significance threshold of 0.05. If the p value was < 0.05 , the null hypothesis was rejected and data was assumed to not follow normal distribution.

Comparison between data groups was carried out using two-sample unpaired t-test (for data that was normally distributed) or two-sample unpaired Wilcoxon test (non-parametric test for data that was not normally distributed). A significance threshold of 0.05 was used. A p value < 0.05 indicated a significant difference between mean values of the two data groups.

The presence of correlation between two groups of continuous data was determined using the Kendall rank coefficient test with a significance threshold of 0.05. A p value < 0.05 indicated that the two groups of data were statistically dependent.

Statistical testing and data visualisation was carried out using R (version 4.2.3) and RStudio (version 2023.03.0).

Chapter 4: Results



Kaplick (2018)

In this study, soil samples were taken from two regions in Aotearoa New Zealand: Waitākere and Coromandel. The Waitākere region had three locations (Cascade, Huia, and Piha) with two sites in each location (asymptomatic and symptomatic). A total of 96 soil samples were collected from the Waitākere region, 16 soil samples from each of the sites. In the Coromandel region, Tairua and Whangapoua were the two locations studied. A total of 23 soil samples were considered for this study, 15 samples from Tairua and 8 pooled samples from Whangapoua. All samples were characterised based on the physical and chemical properties of the soil.

4.1 Tree health status

In the three locations of the Waitākere region, not all trees at symptomatic sites showed symptoms. Similarly, sites that were considered asymptomatic at the time when the plots were created now contained symptomatic trees. However, in the Coromandel region, all trees in the Tairua location showed no symptoms of kauri dieback and all trees in the Whangapoua location showed kauri dieback symptoms. Therefore, the soil samples from each location in the Coromandel region were representative of the disease condition of the trees.

Therefore, instead of separating by site, it was more prudent for the Waitākere soil samples to consider the health characteristics of each tree and separate according to the health status – healthy or unhealthy with regards to kauri dieback.

The physical and chemical properties of the soil were first investigated according to their originally designated asymptomatic and symptomatic sites. The location and sites from the Waitākere region follow these abbreviations: AC = Asymptomatic Cascade, SC = Symptomatic Cascade, AH = Asymptomatic Huia, SH = Symptomatic Huia, AP = Asymptomatic Piha, SP = Symptomatic Piha. Later, health status of kauri trees was used to compare the soil properties. In the graphs below, the trees have been grouped by health status and abbreviated as follows: HC = Healthy Cascade, UC = Unhealthy Cascade, HH = Healthy Huia, UH = Unhealthy Huia, HP = Healthy Piha, UP = Unhealthy Piha.

4.2 Waitākere region

4.2.1 Physical characteristics by site designation

The results for soil samples collected from the different locations and sites in the Waitākere region are shown in Table 4.1 below. In this study, the soil samples were observed to be yellow-brown to brown in colour, with granular structure. Across the Waitākere sites, the means of the recorded measurements for C_u ranged from 4.05 ± 1.43 to 6.28 ± 1.67 for particle size determination, bulk density ranged from $0.27 \pm 0.08 \text{ g/cm}^3$ to $0.42 \pm 0.11 \text{ g/cm}^3$, moisture factor ranged from $57.86 \pm 12.01\%$ to $101.32 \pm 31.22\%$, and water holding capacity ranged from $55.98 \pm 3.08\%$ to $64.53 \pm 3.41\%$. Notably, the asymptomatic Cascade site had the lowest bulk density of $0.27 \pm 0.08 \text{ g/cm}^3$ as well as the highest moisture factor of $101.32 \pm 31.22\%$.

When comparing asymptomatic and symptomatic sites of the Cascade location, significant differences were observed in bulk density ($p = 0.00254$, symptomatic higher) and water holding capacity ($p = 0.000591$, asymptomatic higher). On the other hand, between asymptomatic and symptomatic sites of the Huia location, significant difference was found only in bulk density, in the opposite direction to Cascade ($p = 0.0117$, asymptomatic higher). And between asymptomatic and symptomatic sites of the Piha location, significant difference was found only in C_u ($p = 0.00144$, asymptomatic higher). These results are displayed in Figure 4.1.

In this study, soil particle fractions were also measured during the PSD experiment. The vast majority of soil samples across the Waitākere region, irrespective of site designation, were predominantly sandy soil (above 90% sand and below 1% silt and clay). These results are displayed in Appendix 3.

Table 4.1: Summary of soil physical characteristics for designated sites from Waitākere locations.

Characteristic	Unit	Cascade			Huia			Piha		
		Asymptomatic n=16	Symptomatic n=16	<i>p</i> value	Asymptomatic n=16	Symptomatic n=16	<i>p</i> value	Asymptomatic n=16	Symptomatic n=16	<i>p</i> value
PSD - C _u	-	4.22 ± 0.35	4.05 ± 1.43	NS	6.28 ± 1.67	5.83 ± 3.16	NS	5.98 ± 2.60	5.39 ± 0.42	0.00144
Bulk density	g/cm ³	0.27 ± 0.08	0.35 ± 0.04	0.00254	0.41 ± 0.09	0.34 ± 0.06	0.0117	0.42 ± 0.11	0.39 ± 0.05	NS
Moisture factor	%	101.32 ± 31.22	86.64 ± 16.72	NS	94.23 ± 13.88	95.30 ± 17.70	NS	57.86 ± 12.01	63.02 ± 8.57	NS
Water holding capacity	%	63.05 ± 6.33	55.98 ± 3.08	0.000591	64.53 ± 3.41	62.66 ± 3.68	NS	56.83 ± 6.14	59.04 ± 3.60	NS

NS: not significant, *p* value > 0.05

The results for soil samples collected from the different locations in the Waitākere region are shown in Table 4.2 below. Across the Waitākere locations, the means of the recorded measurements for C_u ranged from 4.14 ± 1.12 to 6.06 ± 2.49 for particle size determination, bulk density ranged from $0.31 \pm 0.08 \text{ g/cm}^3$ to $0.41 \pm 0.08 \text{ g/cm}^3$, moisture factor ranged from $60.44 \pm 11.59\%$ to $94.76 \pm 15.65\%$, and water holding capacity ranged from $57.93 \pm 5.08\%$ to $63.59 \pm 3.62\%$. Notably, the Piha location a much lower moisture factor measurement than the other two locations.

Comparing the soil physical characteristics between the locations, the Cascade and Huia locations showed significant differences in C_u ($p = 0.000141$, Huia higher), bulk density ($p = 0.00533$, Huia higher), and water holding capacity ($p = 0.00195$, Huia higher). Significant differences were also observed in moisture factor ($p = 2.37 \times 10^{-14}$, Huia higher) and water holding capacity ($p = 3.662 \times 10^{-6}$, Huia higher) between the Huia and Piha locations, and between the Piha and Cascade locations, significant differences were observed for C_u ($p = 0.000648$, Piha higher), bulk density ($p = 6.42 \times 10^{-6}$, Piha higher), and moisture factor ($p = 2.32 \times 10^{-12}$, Cascade higher). These results are displayed in Figure 4.1.

Table 4.2: Comparison of soil physical characteristics for Waitākere locations. (NS: p value > 0.05).

Characteristic	Unit	Cascade n=32	Cascade vs. Huia p value	Huia n=32	Huia vs. Piha p value	Piha n=32	Piha vs. Cascade p value
PSD - C_u	-	4.14 ± 1.02	0.000141	6.06 ± 2.49	NS	5.19 ± 2.01	0.000648
Bulk density	g/cm^3	0.31 ± 0.08	0.00533	0.37 ± 0.08	NS	0.41 ± 0.08	6.42×10^{-6}
Moisture factor	%	93.98 ± 25.74	NS	94.76 ± 15.65	2.37×10^{-14}	60.44 ± 10.59	2.32×10^{-12}
Water holding capacity	%	59.51 ± 6.07	0.00195	63.59 ± 3.62	3.662×10^{-6}	57.93 ± 5.08	NS

NS: not significant, p value > 0.05

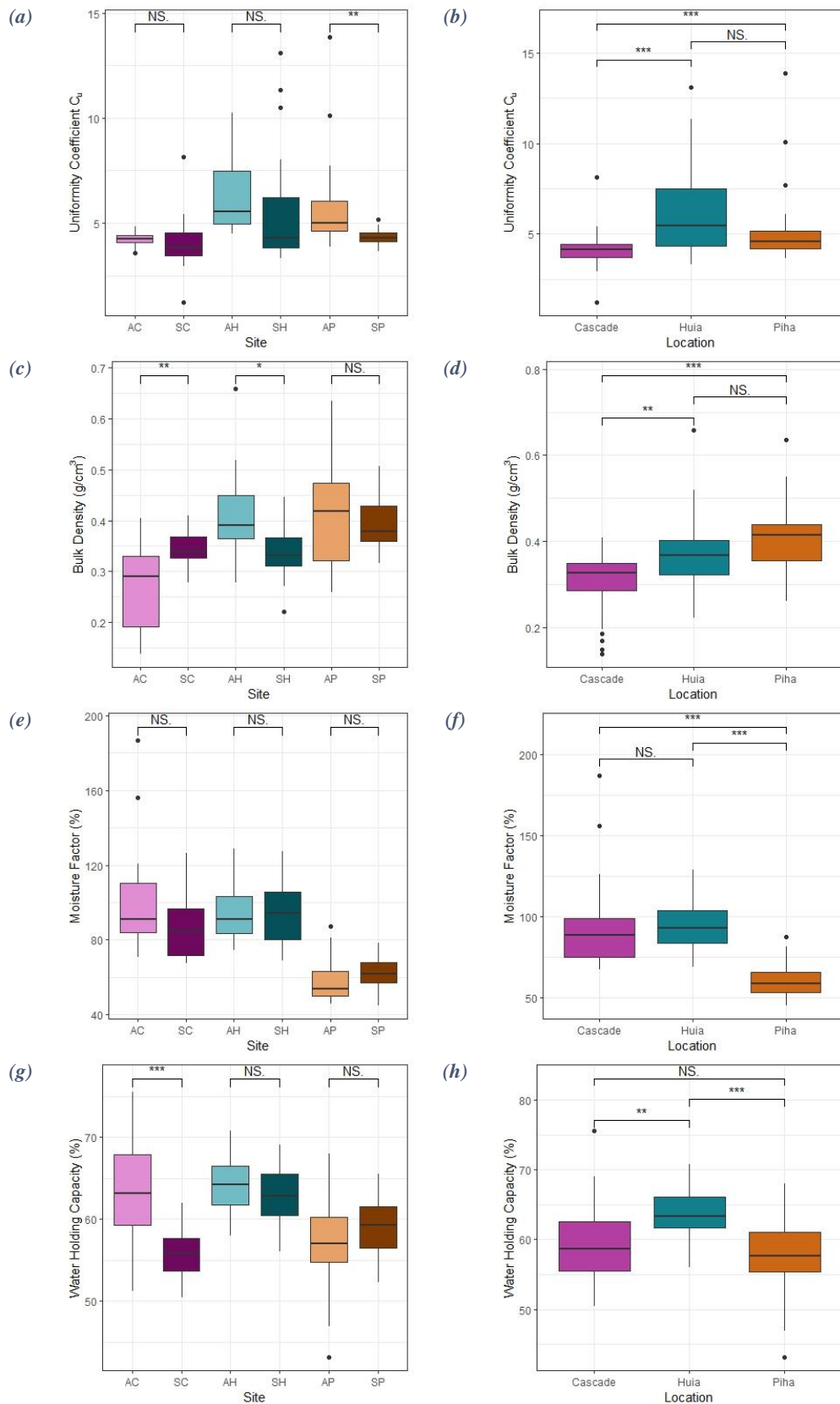


Figure 4.1: Soil physical characteristics for Waitākere region. (a) C_u by site, (b) C_u by location, (c) BD by site, (d) BD by location, (e) MF by site, (f) MF by location, (g) WHC by site, (h) WHC by location. (NS: p value > 0.05, *: p value < 0.05, **: p value < 0.01, *: p value < 0.001).**

4.2.2 Physical characteristics by tree health status

The results based on tree health status for soil samples collected from the different locations in the Waitākere region are shown in Table 4.3 below. Across the Waitākere locations, the means of the recorded measurements for C_u ranged from 3.87 ± 0.58 to 6.25 ± 2.69 for particle size determination, bulk density ranged from $0.29 \pm 0.08 \text{ g/cm}^3$ to $0.42 \pm 0.09 \text{ g/cm}^3$, moisture factor ranged from $56.10 \pm 9.16\%$ to $101.10 \pm 26.80\%$, and water holding capacity ranged from $56.23 \pm 6.11\%$ to $64.11 \pm 2.84\%$. Notably, unhealthy Cascade soil had the lowest bulk density of $(0.29 \pm 0.08) \text{ g/cm}^3$ as well as the highest moisture factor of $101.10 \pm 26.80\%$.

Comparing healthy and unhealthy trees of the Cascade location, significant differences were observed in C_u ($p = 0.00609$, unhealthy higher), moisture factor ($p = 0.0244$, unhealthy higher), and water holding capacity ($p = 0.0158$, unhealthy higher). Between healthy and unhealthy trees of the Piha location, significant difference was found only in C_u , in the opposite direction to Cascade ($p = 0.00144$, healthy higher). On the other hand, between healthy and unhealthy trees of the Huia location, no significant differences were found. These results are displayed in Figure 4.2.

As mentioned earlier, the vast majority of soil samples across the Waitākere region were predominantly sandy soil (above 90% sand and below 1% silt and clay). This holds true regardless of the health status of the soil. These results are displayed in Appendix 3.

Table 4.3: Summary of soil physical characteristics for healthy and unhealthy trees from Waitākere locations. (NS: p value > 0.05).

Characteristic	Unit	Cascade			Huia			Piha		
		Healthy n=15	Unhealthy n=17	p value	Healthy n=15	Unhealthy n=17	p value	Healthy n=16	Unhealthy n=16	p value
PSD - C_u	-	3.87 ± 0.58	4.38 ± 1.27	0.00609	6.25 ± 2.69	5.87 ± 2.37	NS	5.41 ± 1.54	4.96 ± 2.41	0.00144
Bulk density	g/cm ³	0.32 ± 0.06	0.29 ± 0.08	NS	0.39 ± 0.07	0.36 ± 0.10	NS	0.42 ± 0.09	0.39 ± 0.08	NS
Moisture factor	%	85.91 ± 21.69	101.10 ± 26.80	0.0244	93.73 ± 13.90	95.68 ± 17.43	NS	56.10 ± 9.16	64.78 ± 10.38	NS
Water holding capacity	%	56.85 ± 4.85	61.86 ± 6.19	0.0158	64.11 ± 2.84	63.14 ± 4.22	NS	56.23 ± 6.11	59.63 ± 3.14	NS

NS: not significant, p value > 0.05

The results based on tree health status for soil samples collected from the Waitākere region are shown in Table 4.4 below. Comparing the physical soil characteristics, irrespective of the locations, showed significant differences for bulk density ($p = 0.0481$, healthy higher), moisture factor ($p = 0.0481$, unhealthy higher), and water holding capacity ($p = 0.0224$, unhealthy higher) between healthy and unhealthy soil. These results are displayed in Figure 4.2.

Table 4.4: Comparison of soil physical characteristics for healthy and unhealthy trees from Waitākere region. (NS: p value > 0.05).

Characteristic	Unit	Healthy n=46	Unhealthy n=50	Healthy vs. Unhealthy p value
PSD - C _u	-	5.183 ± 2.031	5.072 ± 2.129	NS
Bulk density	g/cm ³	0.379 ± 0.084	0.347 ± 0.094	0.0481
Moisture factor	%	78.09 ± 22.85	87.63 ± 24.95	0.0481
Water holding capacity	%	59.00 ± 5.94	61.58 ± 4.84	0.0224

NS: not significant, p value > 0.05

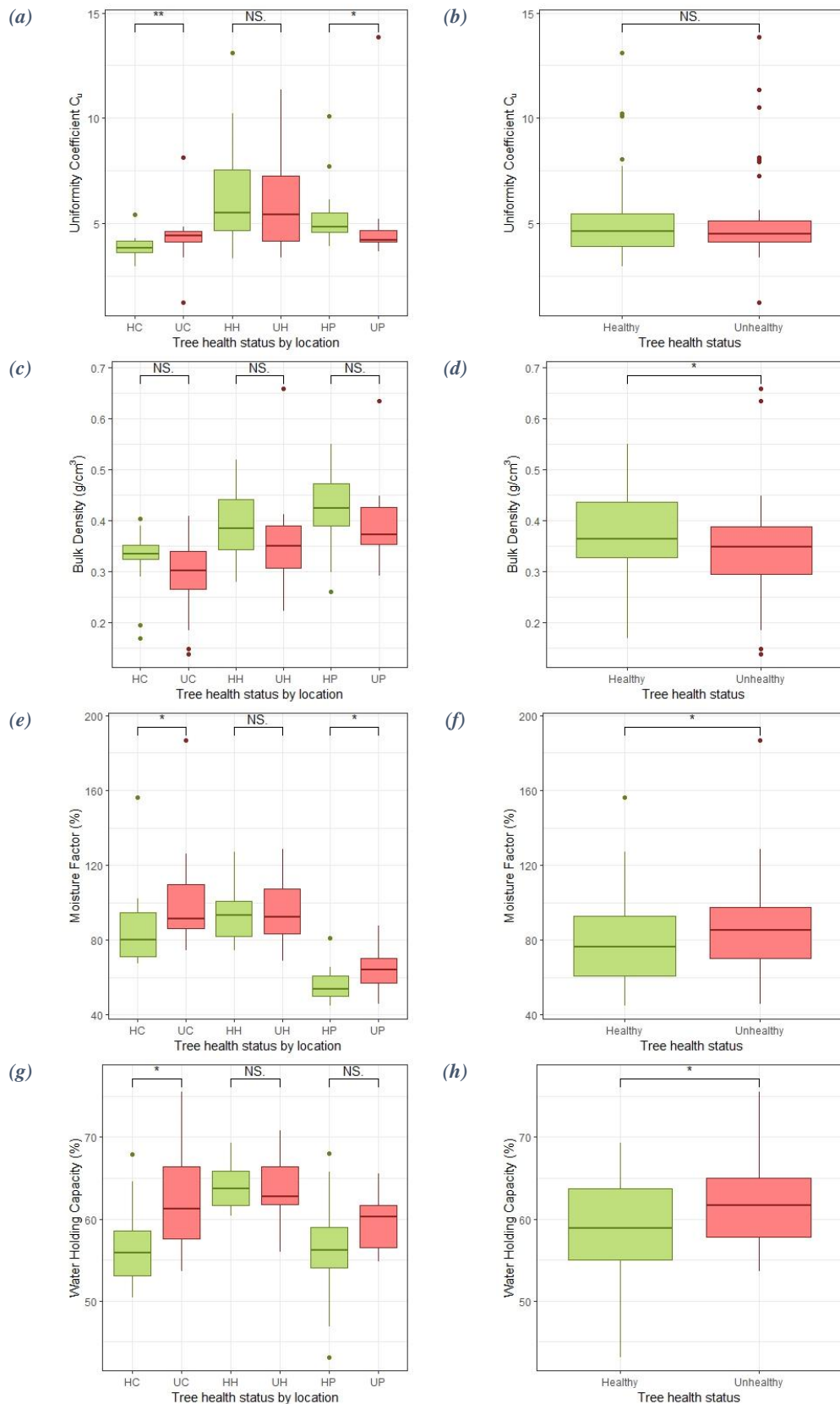


Figure 4.2: Soil physical characteristics by tree health status. (a) C_u for Waitākere locations, (b) C_u for Waitākere region, (c) BD for Waitākere locations, (d) BD for Waitākere region, (e) MF for Waitākere locations, (f) MF for Waitākere region, (g) WHC for Waitākere locations, (h) WHC for Waitākere region. (NS: p value > 0.05, *: p value < 0.05, **: p value < 0.01, *: p value < 0.001).**

4.2.3 Chemical characteristics by site designation

The results for soil samples collected from the different locations and sites in the Waitākere region are shown in Table 4.5 below. Across the Waitākere sites, the means of the recorded measurements for soil pH ranged from 4.89 ± 0.63 to 5.64 ± 0.64 , electrical conductivity ranged from $83.4 \pm 38.9 \mu\text{S}/\text{cm}$ to $156.4 \pm 8.9 \mu\text{S}/\text{cm}$, total carbon ranged from $10.32 \pm 2.61\%$ to $17.63 \pm 8.88\%$, total nitrogen ranged from $0.43 \pm 0.08\%$ to $0.71 \pm 0.19\%$, C:N ratio ranged from 17.76 ± 3.56 to 24.47 ± 3.26 , and total hydrogen ranged from $2.13 \pm 0.30\%$ to $2.96 \pm 0.70\%$. Notably, the symptomatic Cascade site had the highest electrical conductivity of $156.4 \pm 8.9 \mu\text{S}/\text{cm}$, while the asymptomatic Cascade site had the highest total carbon of $17.63 \pm 8.88\%$, highest total nitrogen of $0.71 \pm 0.19\%$, and highest total hydrogen of $2.96 \pm 0.70\%$.

Comparing the asymptomatic and symptomatic sites of the Cascade location, significant differences were observed in soil pH ($p = 0.000103$, symptomatic higher), electrical conductivity ($p = 3.003 \times 10^{-7}$, symptomatic higher), total carbon ($p = 0.0318$, asymptomatic higher), and total nitrogen ($p = 0.00221$, asymptomatic higher). Meanwhile, between asymptomatic and symptomatic sites of the Huia location, significant differences were found in soil pH in the opposite direction to Cascade ($p = 0.0104$, asymptomatic higher), C:N ratio ($p = 0.00109$, symptomatic higher), and total hydrogen ($p = 0.026$, symptomatic higher). On the other hand, between asymptomatic and symptomatic sites of the Piha location, significant differences were observed in total nitrogen in the opposite direction to Cascade ($p = 4.705 \times 10^{-5}$, symptomatic higher) and C:N ratio in the opposite direction to Huia ($p = 2.969 \times 10^{-5}$, asymptomatic higher). These results are displayed in Figure 4.3 and Figure 4.4.

Table 4.5: Summary of soil chemical characteristics for designated sites from Waitākere locations. (NS: p value > 0.05).

Characteristic	Unit	Cascade			Huia			Piha		
		Asymptomatic n=16	Symptomatic n=16	p value	Asymptomatic n=16	Symptomatic n=16	p value	Asymptomatic n=16	Symptomatic n=16	p value
Soil pH	mol/L	4.89 ± 0.63	5.72 ± 0.27	0.000103	5.64 ± 0.64	5.01 ± 0.37	0.0104	5.20 ± 0.34	5.31 ± 0.26	NS
Electrical conductivity	μS/cm	93.4 ± 30.3	156.4 ± 8.9	3.003×10^{-7}	83.7 ± 30.5	83.4 ± 38.9	NS	110.7 ± 33.6	110.8 ± 23.9	NS
Total carbon	%	17.63 ± 8.88	11.90 ± 2.88	0.0318	10.59 ± 2.28	13.57 ± 5.60	NS	10.39 ± 3.44	10.32 ± 2.61	NS
Total nitrogen	%	0.71 ± 0.19	0.53 ± 0.09	0.00221	0.52 ± 0.09	0.54 ± 0.15	NS	0.43 ± 0.08	0.59 ± 0.11	4.705×10^{-5}
C:N ratio	-	23.72 ± 5.15	22.44 ± 2.78	NS	20.58 ± 2.78	24.47 ± 3.26	0.00109	23.96 ± 3.35	17.76 ± 3.56	2.969×10^{-5}
Total hydrogen	%	2.96 ± 0.70	2.54 ± 0.29	NS	2.13 ± 0.30	2.48 ± 0.45	0.026	2.27 ± 0.31	2.18 ± 0.30	NS

NS: not significant, p value > 0.05

The results for soil samples collected from the different locations in the Waitākere region are shown in Table 4.6 below. Across the Waitākere locations, the means of the recorded measurements for soil pH ranged from 5.26 ± 0.31 to 5.32 ± 0.61 , electrical conductivity ranged from $83.6 \pm 34.4 \mu\text{S/cm}$ to $124.9 \pm 38.8 \mu\text{S/cm}$, total carbon ranged from $10.35 \pm 3.00\%$ to $14.77 \pm 7.12\%$, total nitrogen ranged from $0.51 \pm 0.12\%$ to $0.62 \pm 0.17\%$, C:N ratio ranged from 20.86 ± 4.64 to 23.08 ± 4.13 , and total hydrogen ranged from $2.23 \pm 0.31\%$ to $2.75 \pm 0.57\%$. Notably, the Cascade location had the highest electrical conductivity of $124.9 \pm 38.8 \mu\text{S/cm}$, highest total carbon of $14.77 \pm 7.12\%$, highest total nitrogen of $0.62 \pm 0.17\%$, and highest total hydrogen of $2.75 \pm 0.57\%$.

Comparing the soil chemical characteristics between the locations, the Cascade and Huia locations showed significant differences in electrical conductivity ($p = 6.856 \times 10^{-5}$, Cascade higher), total carbon ($p = 0.0472$, Cascade higher), total nitrogen ($p = 0.0178$, Cascade higher), and total hydrogen ($p = 0.000222$, Cascade higher). Between the Huia and Piha locations, significant differences were observed between electrical conductivity ($p = 3.054 \times 10^{-5}$, Piha higher) and total carbon ($p = 0.0426$, Huia higher). Between the Piha and Cascade locations, significant differences were observed between total carbon ($p = 0.000222$, Cascade higher), total nitrogen ($p = 0.00522$, Cascade higher), and total hydrogen ($p = 2.875 \times 10^{-6}$, Cascade higher). Across all locations, there were no significant differences observed for both soil pH and C:N ratio. These results are displayed in Figure 4.3 and Figure 4.4.

Table 4.6: Comparison of soil chemical characteristics for Waitākere locations. (NS: p value > 0.05).

Characteristic	Unit	Cascade n=32	Cascade vs. Huia p value	Huia n=32	Huia vs. Piha p value	Piha n=32	Piha vs. Cascade p value
Soil pH	mol/L	5.30 ± 0.64	NS	5.32 ± 0.61	NS	5.26 ± 0.31	NS
Electrical conductivity	$\mu\text{S/cm}$	124.9 ± 38.8	6.856×10^{-5}	83.6 ± 34.4	3.054×10^{-5}	110.7 ± 28.7	NS
Total carbon	%	14.77 ± 7.12	0.0472	12.08 ± 4.46	0.0426	10.35 ± 3.00	0.000222
Total nitrogen	%	0.62 ± 0.17	0.0178	0.53 ± 0.12	NS	0.51 ± 0.12	0.00522
C:N ratio	-	23.08 ± 4.13	NS	22.53 ± 3.57	NS	20.86 ± 4.64	NS
Total hydrogen	%	2.75 ± 0.57	0.000222	2.31 ± 0.42	NS	2.23 ± 0.31	2.875×10^{-6}

NS: not significant, p value > 0.05

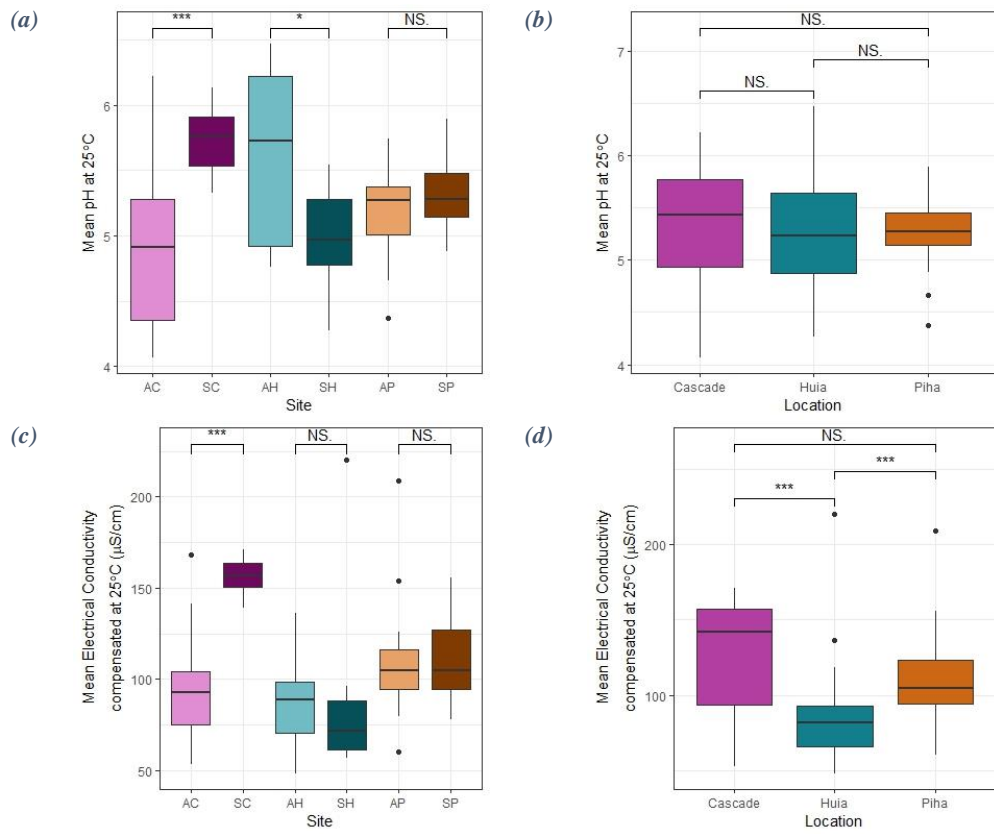


Figure 4.3: Soil chemical characteristics for Waitākere region. (a) mean pH by site, (b) mean pH by location, (c) mean EC by site, (d) mean EC by location. (NS: p value > 0.05, *: p value < 0.05, **: p value < 0.01, *: p value < 0.001).**

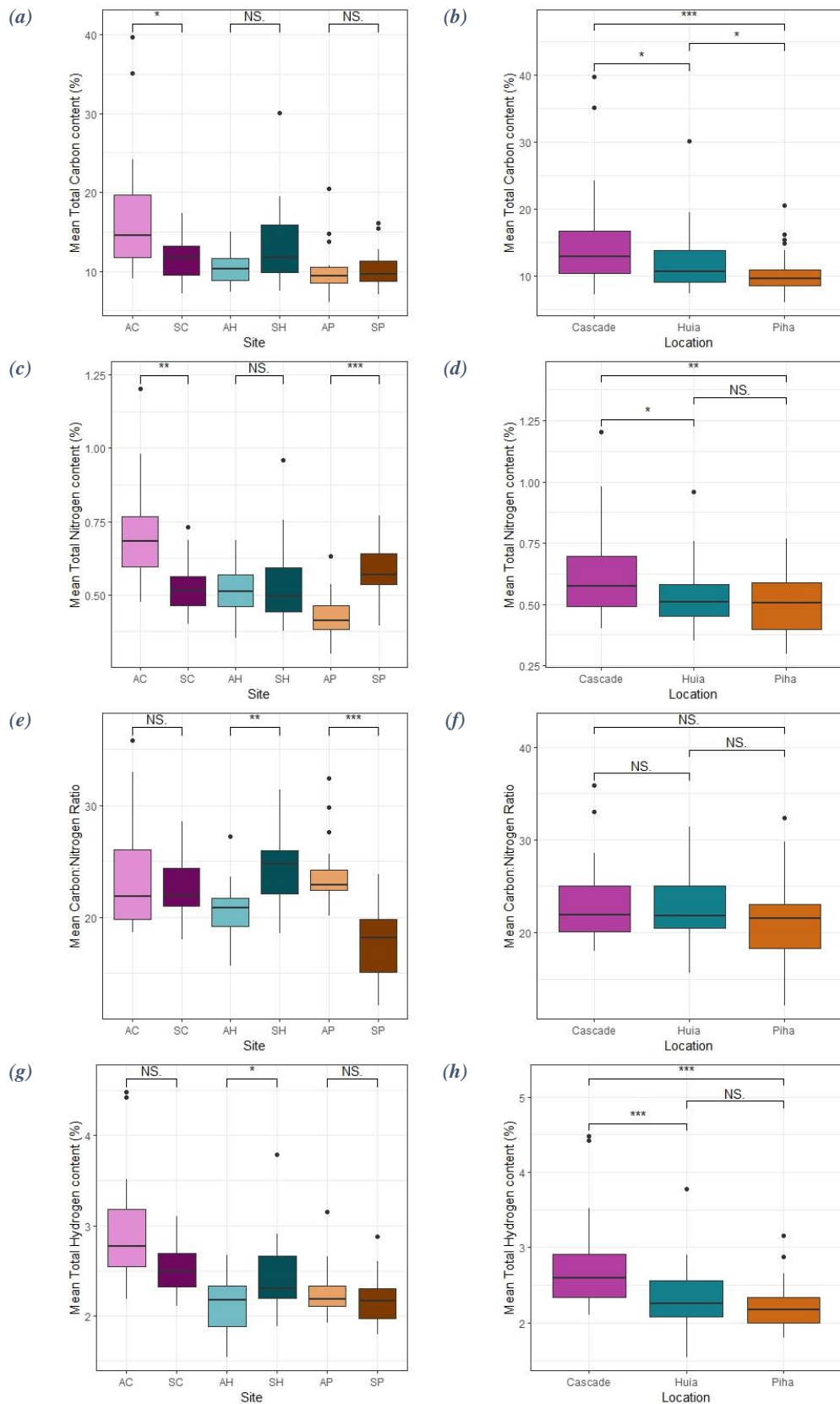


Figure 4.4: Soil chemical characteristics for Waitūkere region derived from elemental analysis. (a) mean TC content by site, (b) mean TC content by location, (c) mean TN content by site, (d) mean TN content by location, (e) mean C:N ratio by site, (f) mean C:N ratio by location, (g) mean TH content by site, (h) mean TH content by location.

(NS: p value > 0.05, *: p value < 0.05, **: p value < 0.01, ***: p value < 0.001).

4.2.4 Chemical characteristics by tree health status

The results based on tree health status for soil samples collected from the different locations in the Waitākere region are shown in Table 4.7 below. Across the Waitākere locations, the means of the recorded measurements for soil pH ranged from 5.09 ± 0.51 to 5.58 ± 0.61 , electrical conductivity ranged from $79.6 \pm 23.7 \mu\text{S}/\text{cm}$ to $128.3 \pm 41.9 \mu\text{S}/\text{cm}$, total carbon ranged from $9.51 \pm 2.25\%$ to $16.71 \pm 7.05\%$, total nitrogen ranged from $0.43 \pm 0.07\%$ to $0.68 \pm 0.18\%$, C:N ratio ranged from 19.41 ± 4.92 to 24.00 ± 3.54 , and total hydrogen ranged from $2.16 \pm 0.31\%$ to $2.93 \pm 0.52\%$. Notably, healthy Piha soil had the lowest total carbon of $9.51 \pm 2.25\%$ as well as the lowest total nitrogen of $0.43 \pm 0.07\%$.

Comparing healthy and unhealthy trees of the Cascade location, significant differences were observed in all results obtained from elemental analysis – total carbon ($p = 0.00411$, unhealthy higher), total nitrogen ($p = 0.00609$, unhealthy higher), C:N ratio ($p = 0.0331$, unhealthy higher), and total hydrogen ($p = 0.00204$, unhealthy higher). Meanwhile, between healthy and unhealthy trees of the Huia location, significant differences were found in pH ($p = 0.0199$, healthy higher), and out of the results from elemental analysis, only C:N ratio ($p = 0.0136$, unhealthy higher). On the other hand, no significant differences were observed in any chemical characteristics between healthy and unhealthy trees of the Piha location. These results are displayed in Figure 4.5 and Figure 4.6.

Table 4.7: Summary of soil chemical characteristics for healthy and unhealthy trees from Waitākere locations. (NS: p value > 0.05).

Characteristic	Unit	Cascade			Huia			Piha		
		Healthy n=15	Unhealthy n=17	p value	Healthy n=15	Unhealthy n=17	p value	Healthy n=16	Unhealthy n=16	p value
Soil pH	mol/L	5.48 ± 0.55	5.15 ± 0.68	NS	5.58 ± 0.61	5.09 ± 0.51	0.0199	5.23 ± 0.27	5.28 ± 0.34	NS
Electrical conductivity	μS/cm	128.3 ± 41.9	121.9 ± 36.9	NS	79.6 ± 23.7	89.4 ± 38.4	NS	103.8 ± 21.9	117.6 ± 33.5	NS
Total carbon	%	12.56 ± 6.76	16.71 ± 7.05	0.00411	10.59 ± 2.44	13.40 ± 5.43	NS	9.51 ± 2.25	11.19 ± 3.47	NS
Total nitrogen	%	0.55 ± 0.14	0.68 ± 0.18	0.00609	0.51 ± 0.09	0.55 ± 0.14	NS	0.43 ± 0.07	0.58 ± 0.12	NS
C:N ratio	-	22.04 ± 4.60	24.00 ± 3.54	0.0331	20.92 ± 2.97	23.94 ± 3.53	0.0136	22.33 ± 3.96	19.41 ± 4.92	NS
Total hydrogen	%	2.54 ± 0.57	2.93 ± 0.52	0.00204	2.16 ± 0.31	2.43 ± 0.47	NS	2.18 ± 0.24	2.28 ± 0.36	NS

NS: not significant, p value > 0.05

The results based on tree health status for soil samples collected from the Waitākere region are shown in Table 4.8 below. Comparing the chemical soil characteristics, irrespective of the locations, showed significant differences for soil pH ($p = 0.0162$, healthy higher), total carbon ($p = 0.000559$, unhealthy higher), total nitrogen ($p = 4.621 \times 10^{-5}$, unhealthy higher), and total hydrogen ($p = 0.00953$, unhealthy higher). These results are displayed in Figure 4.5 and Figure 4.6.

Table 4.8: Comparison of soil chemical characteristics for healthy and unhealthy trees from Waitākere region. (NS: p value > 0.05).

Characteristic	Unit	Healthy n=46	Unhealthy n=50	Healthy vs. Unhealthy p value
Soil pH	mol/L	5.43 ± 0.51	5.17 ± 0.53	0.0162
Electrical conductivity	µS/cm	103.9 ± 35.7	109.5 ± 38.5	NS
Total carbon	%	10.86 ± 4.40	13.82 ± 5.89	0.000559
Total nitrogen	%	0.49 ± 0.12	0.60 ± 0.16	4.621×10^{-5}
C:N ratio	-	21.78 ± 3.87	22.51 ± 4.50	NS
Total hydrogen	%	2.29 ± 0.42	2.55 ± 0.53	0.00953

NS: not significant, p value > 0.05

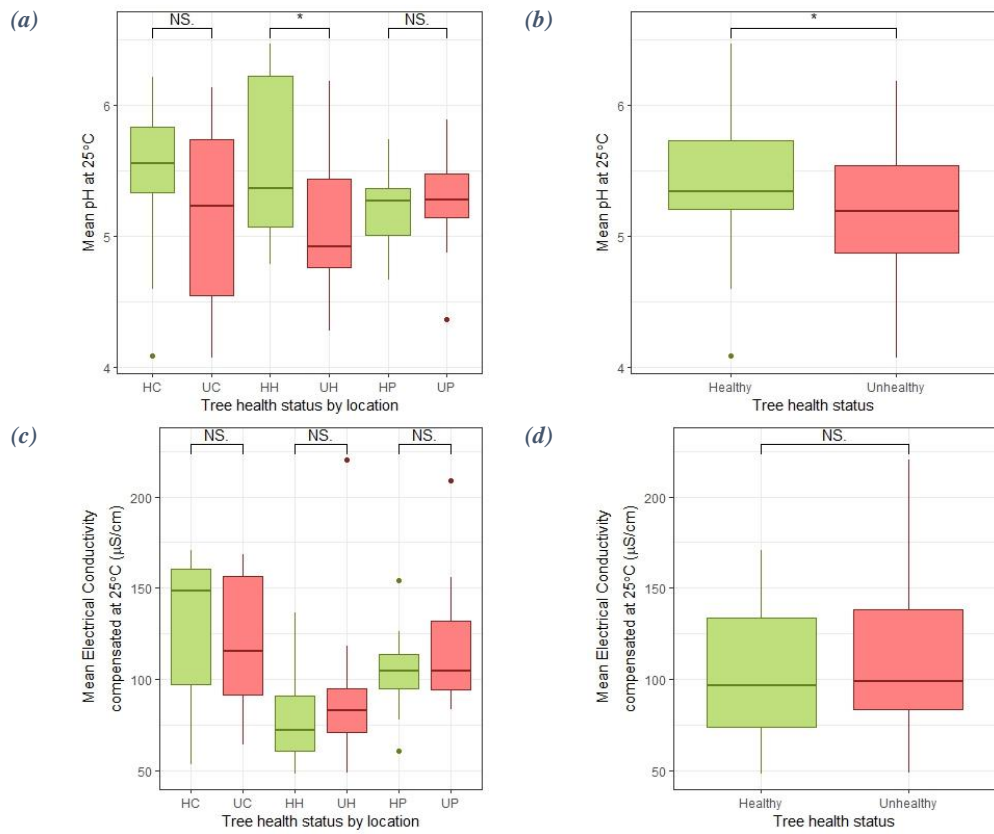


Figure 4.5: Soil chemical characteristics by tree health status. (a) Mean pH for Waitākere locations, (b) mean pH for Waitākere region, (c) mean EC for Waitākere locations, (d) mean EC for Waitākere region. (NS: p value > 0.05, *: p value < 0.05, **: p value < 0.01, *: p value < 0.001).**

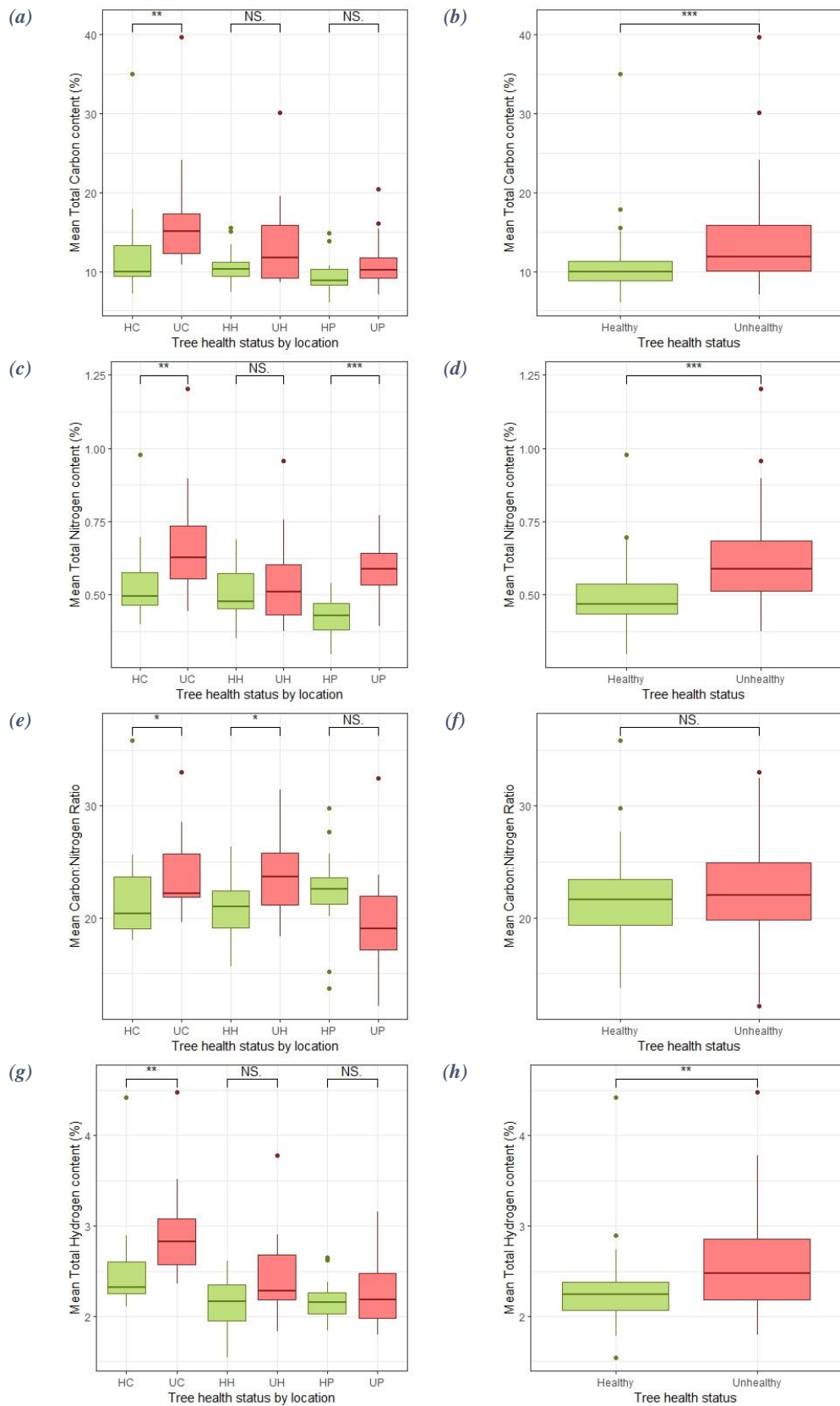


Figure 4.6: Soil chemical characteristics by tree health status derived from elemental analysis. (a) Mean TC content for Waitākere locations, (b) mean TC content for Waitākere region, (c) mean TN content for Waitākere locations, (d) mean TN content for Waitākere region, (e) mean C:N ratio for Waitākere locations, (f) mean C:N ratio for Waitākere region, (g) mean TH content for Waitākere locations, (h) mean TH content for Waitākere region.

(NS: p value > 0.05, *: p value < 0.05, **: p value < 0.01, ***: p value < 0.001).

4.3 Coromandel region

In the Coromandel region, the Tairua and Whangapoua locations were designated to be asymptomatic and symptomatic, respectively. In Whangapoua, all trees showed either presence of basal bleeds or canopy scores above 2.5, fulfilling the requirement to be classified as unhealthy. Moreover, in Tairua, all trees had no basal bleeds and had canopy scores of 2.5 or lower, and so were classified as healthy. Hence, unlike in the Waitākere region, the designation and health status of the locations of the Coromandel region were equivalent.

4.3.1 Physical characteristics

The results for soil samples collected from the Coromandel region are shown in Table 4.9 below. Comparing the physical soil characteristics of the healthy Tairua and unhealthy Whangapoua locations, significant differences were observed in C_u ($p = 0.000244$, healthy Tairua higher), moisture factor ($p = 0.00239$, unhealthy Whangapoua higher), and water holding capacity ($p = 0.0347$, unhealthy Whangapoua higher). These results are displayed in Figure 4.7.

In this study, soil particle fractions were also measured during the PSD experiment. The vast majority of soil samples across the Coromandel region, irrespective of designated locations or tree health status, were predominantly sandy soil (above 90% sand and below 1% silt and clay). These results are displayed in Appendix 3.

Table 4.9: Comparison of soil physical characteristics for Coromandel locations. (NS: p value > 0.05).

Characteristic	Unit	Tairua (Healthy) n=15	Whangapoua (Unhealthy) n=8	Tairua vs. Whangapoua p value
PSD - C_u	-	6.22 ± 1.02	4.31 ± 0.88	0.000244
Bulk density	g/cm ³	0.33 ± 0.07	0.34 ± 0.05	NS
Moisture factor	%	41.68 ± 7.31	65.14 ± 14.89	0.00239
Water holding capacity	%	64.78 ± 2.69	68.71 ± 4.12	0.0347

NS: not significant, p value > 0.05

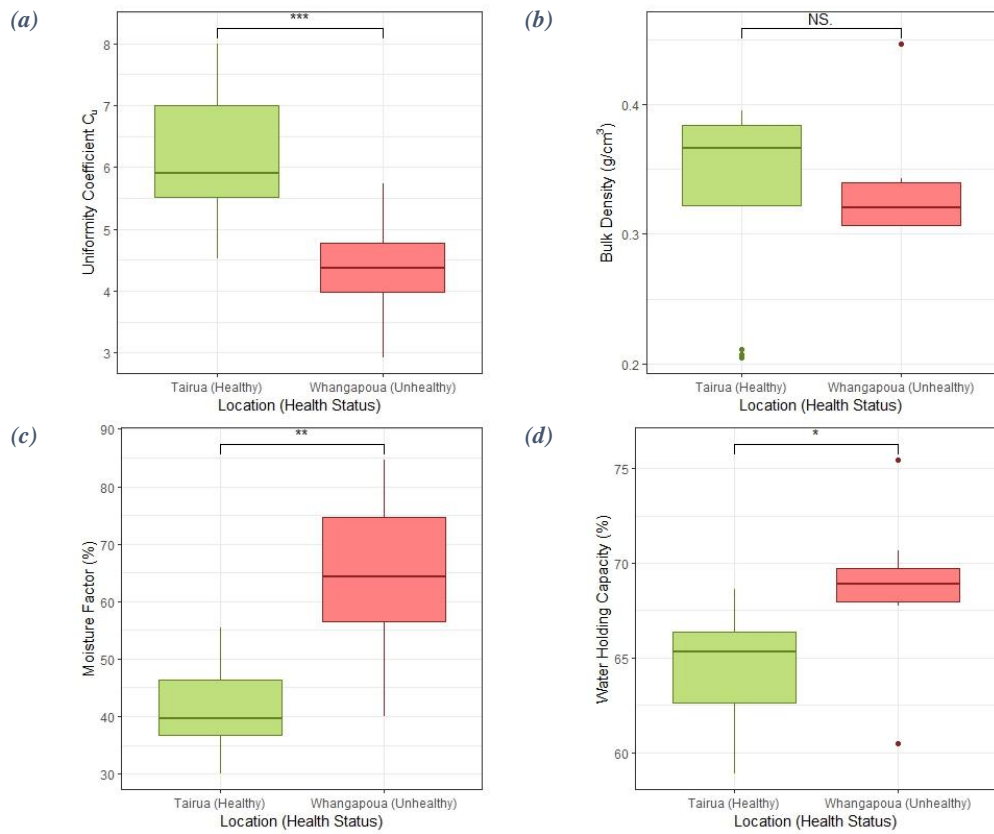


Figure 4.7: Soil physical characteristics for Coromandel region. (a) C_u by location, (b) BD by location, (c) MF by location, (d) WHC by location. (NS: p value > 0.05 , *: p value < 0.05 , **: p value < 0.01 , *: p value < 0.001).**

4.3.2 Chemical characteristics

The results for soil samples collected from the Coromandel region are shown in Table 4.10 below. Comparing the chemical soil characteristics of the healthy Tairua and unhealthy Whangapoua locations, significant differences were observed in electrical conductivity ($p = 0.0259$, unhealthy Whangapoua higher), total carbon ($p = 0.0235$, unhealthy Whangapoua higher), total nitrogen ($p = 0.0318$, unhealthy Whangapoua higher), and total hydrogen ($p = 0.0265$, unhealthy Whangapoua higher). These results are displayed in Figure 4.8.

Table 4.10: Comparison of soil chemical characteristics for Coromandel locations. (NS: p value > 0.05).

Characteristic	Unit	Tairua (Healthy) n=15	Whangapoua (Unhealthy) n=8	Tairua vs. Whangapoua p value
Soil pH	mol/L	4.69 ± 0.19	4.67 ± 0.39	NS
Electrical conductivity	µS/cm	90.1 ± 48.9	121.8 ± 25.5	0.0259
Total carbon	%	13.29 ± 3.81	19.52 ± 6.18	0.0235
Total nitrogen	%	0.49 ± 0.11	0.70 ± 0.21	0.0318
C:N ratio	-	26.83 ± 3.66	27.76 ± 2.16	NS
Total hydrogen	%	2.30 ± 0.42	2.89 ± 0.58	0.0265

NS: not significant, p value > 0.05

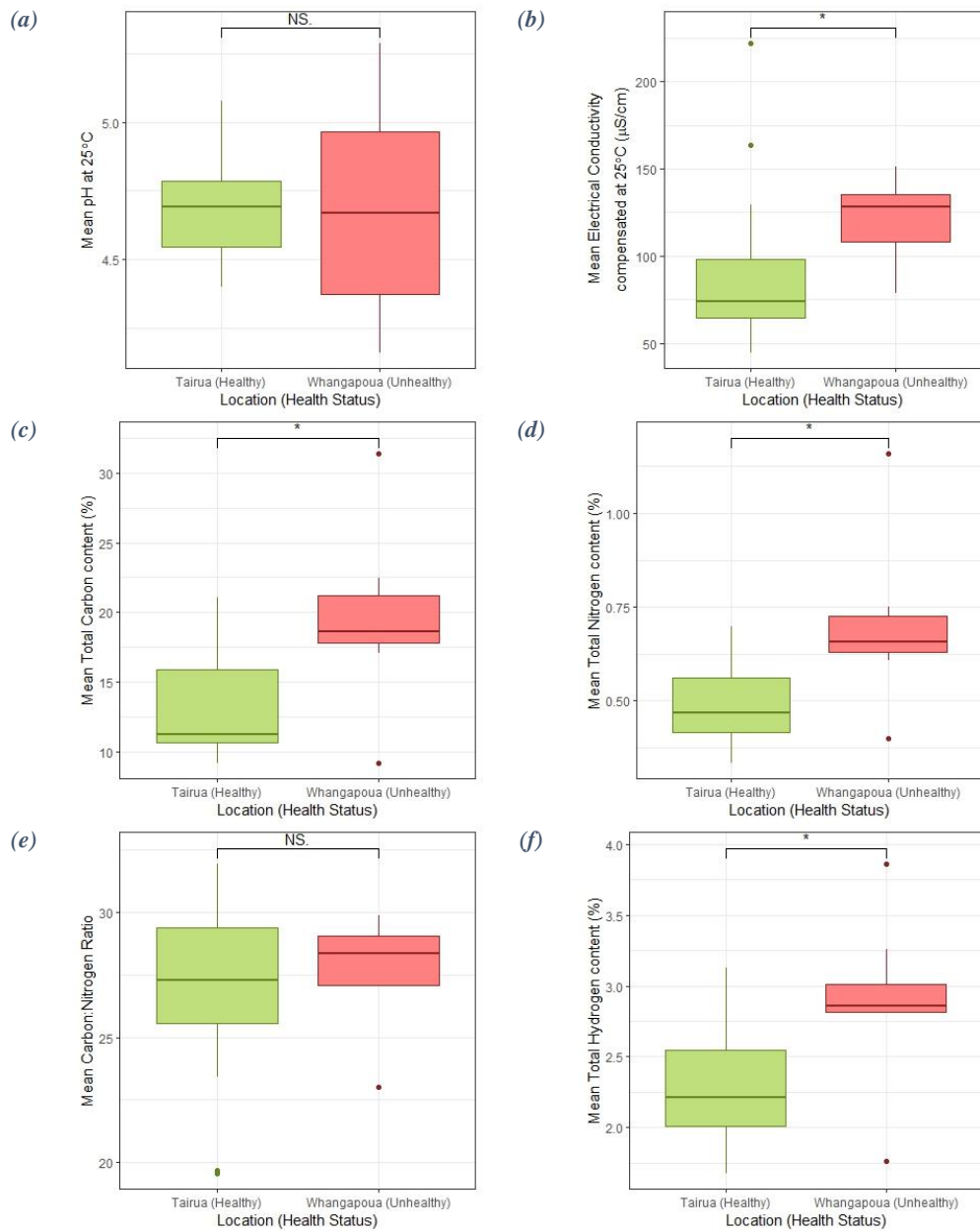


Figure 4.8: Soil physical characteristics for Coromandel region. (a) Mean pH by location, (b) mean EC by location, (c) mean TC content by location, (d) mean TN content by location, (e) mean C:N ratio by location, (f) mean TH content by location.

(NS: p value > 0.05, *: p value < 0.05, **: p value < 0.01, ***: p value < 0.001).

Chapter 5: Discussion



Priestly (2023)

5.1 Physical characteristics

Kauri forests can be found across different locations in the northern region of Aotearoa New Zealand with varied soil types ranging from well-defined soils derived from porphyritic textured, vesicular volcanic rocks, to poorly structured soils containing sandstones and mudstones (Jongkind et al., 2007; Silvester, 2000). Several soil classification documents and soil reports have described kauri to cause intense influence on soil formation and physical characteristics (Jongkind & Buurman, 2006). The soils developed under forests with trees such as kauri are often referred to as 'gumlands' (NZ Soil Bureau, 1968). They are described to have granular structure with a nutty, hard subsoil layer, and are yellow-grey or yellow-brown in colour. In this study, the soil samples were observed to be yellow-brown to brown in colour, with granular structure. Further, the description of soil characteristics usually reveals the soil under kauri stands to be podzolised with sandy, grey, and unattractive topsoil that lacks structure. This topsoil covers a grey siliceous subsoil pan made of humus and iron, which hinders drainage and is acidic and low in nutrients due to leaching (NZ Soil Bureau, 1968). Waikato Regional Council (2011) also found a hard, shallow soil pan beneath kauri vegetation in the Northland region, classified as Te Kopuru Sand. Jongkind et al. (2007) has described the soils in the Waitākere Ranges as originating from andesitic rocks. These andesites are made of vesicular volcanic rocks having medium to dark colour, and are mostly fine grained with characteristically porphyritic texture (i.e. containing bigger particles in a fine landmass) (Jongkind et al., 2007).

Kauri accumulates an extensive amount of organic material, which considerably reduces the pH of the soil and leads to podzolisation. These effects combine to cause variation in soil physical characteristics, which is more powerful closer to the kauri tree than near the dripline of the canopy (Jongkind & Buurman, 2006; Wyse et al., 2014). Furthermore, there is combined effect of natural weathering and transport of material due to overland flow. The significant amount of litter, the leachates under the tree canopy, and the prolonged life of kauri leading to continuous addition to the litter content, contribute to the impact that kauri trees have on the physical characteristics of the surrounding soil (Jongkind & Buurman, 2006).

5.1.1 Particle size distribution

In this study, within the Waitākere region, mean C_u of healthy (5.183) and unhealthy (5.072) soil were both above 4, with no significant difference found between them (Table 4.4). In geoen지니어ing terms, a poorly or uniformly graded soil has a low C_u (below 4), implying a high concentration of particles in a small range of particle size. Conversely, a well graded soil with high C_u (above 4) has a large, well-distributed range of particle size (Keaton, 2018; Zekkos, 2002). This indicates that the soil samples from the Waitākere region were predominantly well graded. Only healthy kauri soil from the Cascade location produced a mean C_u value less than 4, indicating it was the only group with poorly graded soil (Table 4.3). Overall, merely 21 (13 healthy, 8 unhealthy) out of 96 soil samples from the Waitākere region had C_u values under 4. In the Coromandel region, there was a significant difference ($p = 0.000244$) in mean C_u observed between healthy Tairua (6.22) and unhealthy Whangapoua (4.31) soil (Table 4.9). Despite this, soil samples from both locations were well graded on average. To date, no other comparable studies measure C_u , or focus on texture of soil from kauri forest, or any conifer forest.

In this study, the vast majority of soil samples across both Waitākere and Coromandel regions were predominantly sandy soil (above 90% sand and below 1% silt and clay) (Appendix 3). In contrast, Jongkind and Buurman (2006) measured the fraction of kauri soil greater than 0.2 mm (sand is classified as particles between 0.05-2 mm) at 10-50 cm depth, and found that this fraction was generally less than 10%. There are different classifications for sandy soil and the present study uses 0.075-4.75 mm as per USCS standards, which makes comparison difficult. There are several further factors that could cause this discrepancy between the results of Jongkind and Buurman (2006) and the present study, especially topographic conditions. If trees are located at the bottom of a slope, there can be accumulation of finer particles due to overland flow. Another factor could be the small sample size used by Jongkind and Buurman (2006) – only 19 kauri soil samples across 5 locations in the Waitākere Ranges were analysed. In comparison, this study analysed a much larger sample size – 96 soil samples across 3 locations in the Waitākere region.

Another potential reason for the higher proportion of sand found in the samples in this study could be the breakdown and leaching of fines, caused by the extensive amount of organic material from defoliation and canopy loss, which considerably reduces the pH and causes podzolisation of the soil under kauri (Jongkind & Buurman, 2006). This podzolisation effect was observed in another study carried out by Jongkind et al. (2007) with kauri soil from the Waitākere Ranges. A loss of fine clay particles was demonstrated, when compared to neighbouring broadleaf/treefern forest. This phenomenon is more powerful closer to the tree than near the dripline of the canopy (Jongkind & Buurman, 2006; Wyse et al., 2014). This suggests that kauri has a strong impact on texture of soil in its vicinity.

Hemkemeyer et al. (2018) determined that each soil fraction has different superficial properties and creates a microenvironment that is conducive to specific groups of bacteria. The surfaces of the soil particles play an important role in providing cell attachment and colony formation. Other necessities for microbial growth such as water requirements and carbon and nutrient availability are influenced by the mineralogical composition and deposition of both organic matter and sesquioxides on the soil particle surfaces (Hemkemeyer et al., 2018). Larger sand particles, like those found in this study, are preferred by bacterial species which have adapted to a wide substrate range and can disintegrate high-molecular-weight plant substrates, as well as species which have developed the capability to survive in limited nutrient conditions (Sessitsch et al., 2001). Generally, the sand fraction contains most of the particulate organic matter (POM), while finer particles (silt and clay) are largely combined with the soil organic matter (SOM) (Christensen, 2001). Chater et al. (2010) and Christensen (1992) observed that Streptomycetaceae, which are typically involved in the initial stages of decomposition, prefer the coarser sand fraction over finer fractions because of the presence of more POM (Chater et al., 2010; Christensen, 1992). Additionally, Sessitsch et al. (2001) found high occurrence of fungi, which is also associated with the initial disintegration of POM in the coarser fraction, which was confirmed through high xylanase activity. As *P. agathidicida* is morphologically similar to fungi, the high proportion of sand found in the samples of the present study may provide a suitable environment for its occurrence. By performing high throughput amplicon sequencing and GeoChip 5 S microarray analysis, (Byers, Condon, et al., 2020) confirmed that dieback symptomatic kauri soil showed significantly higher fungal diversity than asymptomatic kauri soil due to greater presence of organic matter, which supports this theory.

In the present study, the Coromandel region showed significantly higher C_u in unhealthy soil compared to healthy soil ($p = 0.000244$). The high C_u , as well as high percentage of sand fraction in unhealthy kauri soil may provide a conducive environment for growth and proliferation of microbes including *P. agathidicida*. As an oomycete, it has similar properties to fungi, which prefer the presence of POM in sandy soil as well as acidic conditions (Sessitsch et al., 2001). However, further studies are required in this direction.

5.1.2 Bulk density

In this study, a significant difference was observed ($p = 0.0481$) in mean BD between soils of healthy and unhealthy trees in the Waitākere region, where unhealthy soils (0.35 g/cm^3) had slightly lower mean BD than healthy soils (0.38 g/cm^3) (Table 4.4). Conversely, no significant difference was found between soils of healthy Tairua trees (0.33 g/cm^3) and unhealthy Whangapoua trees (0.34 g/cm^3) of the Coromandel region (Table 4.9). Usually, BD of sandy soil ranges between $1.38\text{-}1.99 \text{ g/cm}^3$ (Weil & Brady, 2017a), which is much higher than the results obtained in this study. Since these results show laboratory BD, they may not be an accurate reflection of field BD of kauri soil. However, results for laboratory BD from soil of Waitākere kauri forest obtained by Yang (2022) and Wyse and Burns (2013) showed similar range to that of the present study. In future research, field BD should be measured during sample collection using a widely accepted method, such as the core method, to achieve more accurate results.

BD, porosity, and organic matter of soil are all interlinked and closely related to the plant species (Sparling & Schipper, 2002). Kay and VandenBygaart (2002) suggest that porosity exists as a function of BD, and that the size and arrangement of the particles create varied pore space which significantly contributes towards the BD of the soil. Figure 5.1 demonstrates that a blend of dissimilarly sized particles (well-graded sand), typically displays higher BD (Weil & Brady, 2017a). Tanveera et al. (2016), Nath (2015) and Brown and Wherrett (2022) all confirmed a direct positive relationship between BD and sand content during their research. As the majority of samples in this study consisted of more than 90% sand, high soil BD was expected. However, this was not the case.

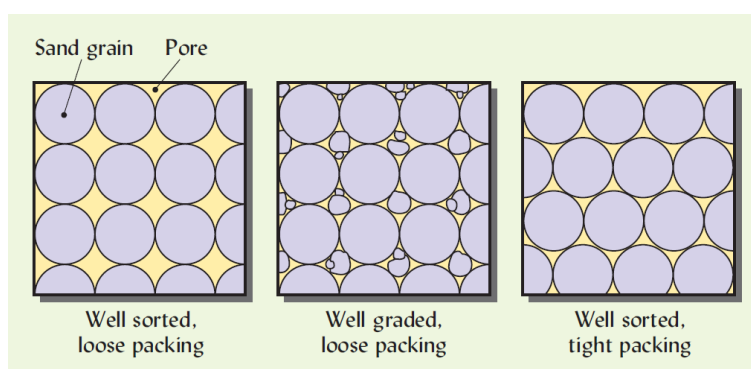


Figure 5.1: Effect of particle size and arrangement on BD of sandy soil (Weil & Brady, 2017a).

The low soil BD obtained might be explained by its relationship with soil organic matter. In the present study, BD was found to have strong negative correlation with organic matter (total carbon) for both healthy ($p = 0.000159$) as well as unhealthy ($p = 5.53 \times 10^{-9}$) kauri soil in the Waitākere region (Figure 5.2). A similar correlation between organic matter and BD of soils has also been demonstrated by several studies (Grüneberg et al., 2014; Leifeld et al., 2005; Perie & Ouimet, 2008; Sakin, 2012; Tanveera et al., 2016).

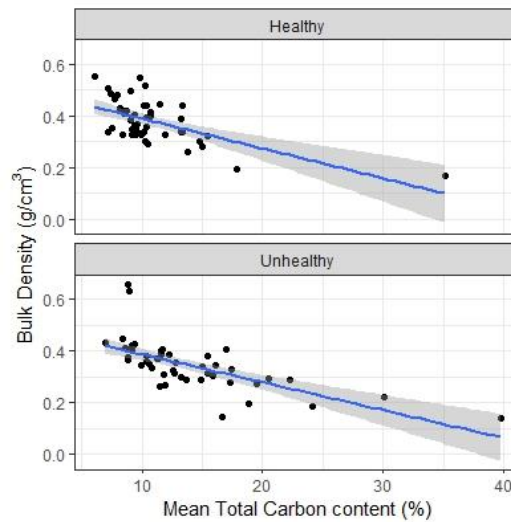


Figure 5.2: Relationship between BD and mean TC content (Healthy: $p = 0.000159$, Unhealthy: $p = 5.53 \times 10^{-9}$), using Kendall correlation (threshold $p < 0.05$).

Due to the large amount of litter in kauri forest, kauri soil naturally has high content of organic matter. Higher soil organic matter, and hence higher organic carbon, reinforces soil structure, thereby improving physical stability and lowering BD (Kay & VandenBygaart, 2002).

In the present study, BD was also found to have a strong negative correlation with moisture factor for both healthy ($p = 0.014$) and unhealthy ($p = 2.23 \times 10^{-5}$) kauri soil in the Waitākere region (Figure 5.3). A similar correlation was observed by Tanveera et al. (2016).

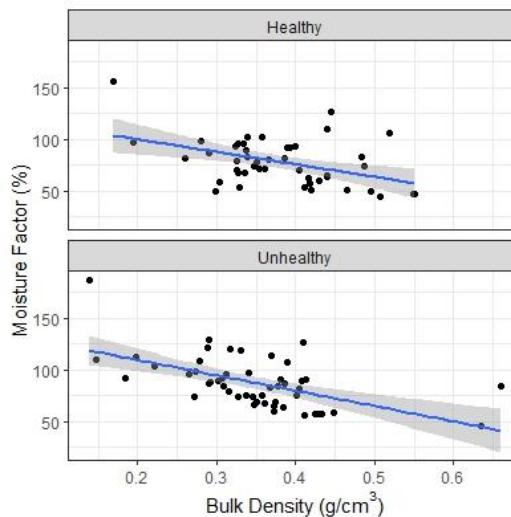


Figure 5.3: Relationship between BD and MF (Healthy: $p = 0.014$, Unhealthy: $p = 2.23 \times 10^{-5}$), using Kendall correlation (threshold $p < 0.05$).

Dec et al. (2008) demonstrated that BD has a direct impact on pore diameter and distribution, and their changes are in turn reflected in the hydraulic properties of the soil. As soil BD increases, there is reduction in pore space, which in turn reduces the hydraulic capacity of the soil. This relationship confirms the correlation between BD and moisture factor observed in this study. External factors such as climatic changes (e.g. rain and drought) can also affect the structural integrity of soil due to its ability to shrink and swell (Jin et al., 2013; Peth & Smucker,

2006). For this reason, BD varies with moisture factor in swelling soils (Blake & Hartge, 1986). As the samples of the present study were collected during the winter months, it is possible that increased precipitation and humidity may have contributed to higher moisture factor, which is linked to lower BD. However, climate data was not recorded during sample collection, which could be considered in the future.

Increased BD as a consequence of compaction brings about change in the microbial activity in soil (Jordan et al., 2003). Several studies demonstrated that microbial activities such as soil respiration and enzyme activity can considerably decrease at higher BD, due to decrease in air-filled pore spaces (Dick et al., 1988; Startsev et al., 1998; Wronski & Murphy, 1994). For example, Dick et al. (1988) revealed low soil phosphatase activity in compacted locations in the forest of Oregon. Furthermore, decrease in nitrogen uptake leading to decline in immobilised nitrogen in soil microbial biomass was observed by Jordan et al. (2003), due to probable anaerobic conditions in the reduced total pore volume. Reduced pore volume can also affect the mobility of microbes in the soil, including pathogens (Bengough, 2003). In the present study, unhealthy soil from the Waitākere region showed significantly lower BD than healthy soil. This implies higher pore volume in the soil, allowing microbial activity as well as greater mobility of pathogens, specifically zoospores of *P. agathidicida*, which may increase chances of proliferation and dieback infection.

From the results of this study, it is difficult to determine whether soil BD has an impact on presence of kauri dieback. Although a significant difference in mean BD was observed between healthy and unhealthy soils in the Waitākere region, no such difference was observed in the Coromandel region. Furthermore, the results were a measure of laboratory BD instead of field BD. As discussed, soil BD has the potential to have major influence on other soil physicochemical properties, as well as activity of microbes and other pathogens. Therefore, future investigation on the relationship between field BD and presence of kauri dieback could be worthwhile.

5.1.3 Moisture factor

In this study, a significant difference was observed ($p = 0.0481$) in mean MF between soils of healthy and unhealthy trees in the Waitākere region, where unhealthy soils (87.63%) had higher mean MF than healthy soils (78.09%) (Table 4.4). As the soil in the Coromandel region was collected before winter, it appeared to be drier. Nevertheless, a similar trend was observed, with an even more significant difference ($p = 0.00239$) found between soils of unhealthy Whangapoua trees (65.14%) and healthy Tairua trees (41.68%) (Table 4.9).

In the Cascade and Piha locations of the Waitākere Ranges, Yang (2022) measured gravimetric moisture factor of soil in the OH layer beneath kauri trees, and found all values to be within 62.1%-66.4%, with no significant differences observed between locations and designated sites (asymptomatic and symptomatic). These MF readings are considerably lower than those from the Waitākere region in the present study. However, time of year of sample collection has not been specified by Yang (2022), and difference in climate could be the cause of this discrepancy. This points towards the importance of gathering climate data during sample collection, which should be considered in the future.

The climate is a significant governing component in soil moisture variation, especially with regards to air temperature and precipitation (Feng & Liu, 2015). Dai et al. (2022) observed a significant positive relationship between soil moisture factor and precipitation, and a significant negative relationship between soil moisture factor and air temperature. In fact, several hydrogeological studies have acknowledged the combined effect of multiple climatic factors and their interactions on soil moisture dynamics (Gaur & Mohanty, 2013; Holsten et al., 2009; Wohl et al., 2012). Other studies further testified that the climate has a direct impact on soil hydraulic properties, and has an indirect correlation with chemical and biological soil attributes (Kutílek & Jendele, 2008; Lin, 2012; Lin et al., 2005).

For the last few decades, global environmental changes have caused rising air temperature and precipitation inconsistencies at annual and monthly levels, causing uncertainties in soil moisture dynamics (Dai et al., 2022; Feng & Liu, 2015). Soil moisture factor plays a vital role as a buffer for rising temperature and precipitation inconsistencies, thereby promoting continuity in the climate system (Seneviratne et al., 2010). Several studies have measured MF of kauri soil in Auckland during drought conditions, and recorded measurements are much lower than those obtained in this study. Macinnis-Ng and Schwendenmann (2015) used soil-water content reflectometers to measure MF below 30% at the soil-mineral layer interface, Wyse et al. (2013) measured kauri soil moisture content of 14.5%, and Verkaik and Braakhekke (2007) have even recorded gravimetric moisture factor levels down to 11%.

Recently, Aotearoa New Zealand has been experiencing unusual weather events which could be concerning to kauri health. While *A. australis* is resilient in drought conditions due to the conservative nature of its water usage (Macinnis-Ng et al., 2016; Wyse et al., 2013), periods of extreme rainfall can adversely affect kauri health. The resultant increase in soil water content can affect sporangial formation and hyphal growth and lead to increase in motility of *P. agathidicida* zoospores (Bellgard et al., 2013; Bradshaw et al., 2020). This can lead to higher chances of spread of kauri dieback from an infected kauri tree to surrounding healthy trees. The present study has shown that unhealthy kauri soil has significantly higher MF in both Waitākere and Coromandel regions. Hence, the hydromorphic edaphic conditions of kauri forest and the response of *P. agathidicida* with regards to such climatic shifts should be taken into consideration for further research studies. Furthermore, any future spatiotemporal research should include measurement of precipitation at each of the sites.

Climate factors such as air temperature and precipitation directly affect plant transpiration, which in turn has an impact on soil MF. Several studies have shown that water usage for transpiration is more correlated to tree diameter than tree species (Bucci et al., 2004; Dawson, 1996; Kaplick, 2018; Meinzer et al., 2005). Figure 5.4(a) below depicts that in the present study, as diameter at breast height (DBH) of the kauri trees increases, so too does the moisture factor of the soil. This significant positive correlation was present for both healthy ($p = 0.00521$) and unhealthy ($p = 0.000952$) kauri soil. This can be explained by the litter layer, which forms a barrier between the atmosphere and mineral soil, preventing evaporation of soil water and hence increasing MF (Liu et al., 2017; Zhu et al., 2021). Although evapotranspiration is a major contributing factor of soil moisture losses (del Campo et al., 2018; Wang et al., 2018; Zhang et al., 2011), evapotranspiration rates are typically low in temperate conifer forests such as kauri forests, leading to lower moisture loss from the soil (Perry & Jones, 2017).

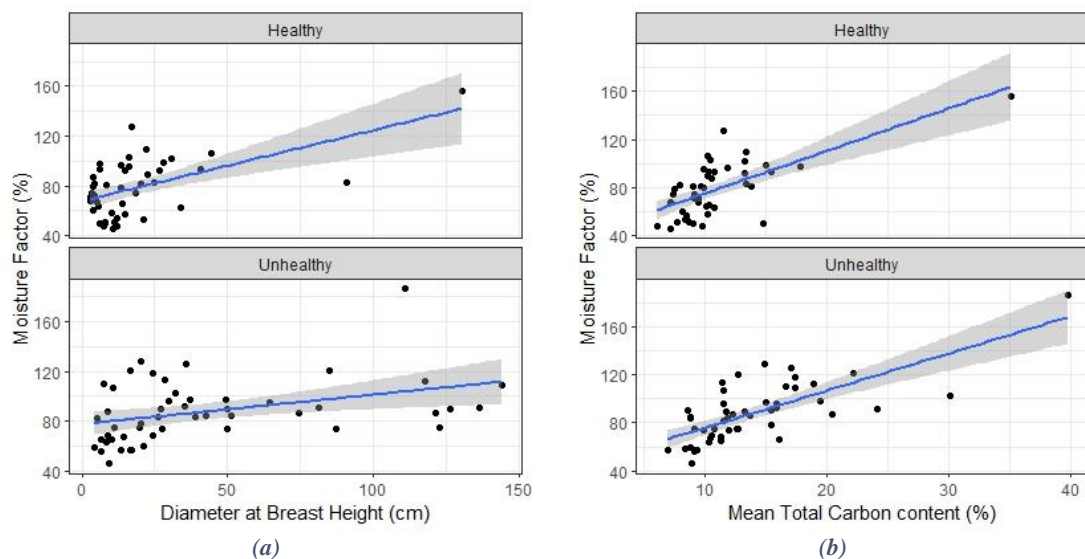


Figure 5.4: Relationship between (a) MF and DBH (Healthy: $p = 0.00521$, Unhealthy: $p = 0.000952$), (b) MF and mean TC content (Healthy: $p = 4.79 \times 10^{-6}$, Unhealthy: $p = 1.56 \times 10^{-7}$), using Kendall correlation (threshold $p < 0.05$).

This relationship between litter and soil MF is confirmed by Figure 5.4(b), which shows there is also a significant positive correlation between MF and mean TC content for both healthy ($p = 4.79 \times 10^{-6}$) and unhealthy ($p = 1.56 \times 10^{-7}$) kauri soil in this study. Rascón-Ramos et al. (2021) and Zhao et al. (2022) found similar results, where the moisture content of the soil increased with the litter content as well as the amount of SOC. Zhao et al. (2022) suggested that an increase in SOC caused by litter can improve soil pore-water connectivity and facilitate better storage and water holding capability, leading to higher soil water content. This is especially true in the case of kauri, as mature trees can gather up to 2 m of organic matter made of various leaves and woody plant materials such as twigs, branches and bark, making kauri litter a rich source of organic carbon (Silvester & Orchard, 1999; Verkaik, 2006).

5.1.4 Water holding capacity

In this study, a significant difference was observed ($p = 0.0224$) between mean WHC of healthy and unhealthy kauri soil in the Waitākere region, with healthy soil (59.00%) having a lower WHC on average in comparison to unhealthy soil (61.58%) (Table 4.4). In the Coromandel region, the soils had higher WHC in general, but again a significant difference was found ($p = 0.0347$) between mean WHC of healthy Tairua and unhealthy Whangapoua soil. The pooled samples from Tairua (64.78%) had a considerably lower mean WHC than those from Whangapoua (68.71%) (Table 4.9).

No previous studies have determined WHC of the sandy-textured soil from coniferous kauri forest. However, Irrigation New Zealand (1973) state that the typical WHC for sandy soil is 15%, which is much lower than the measurements obtained in this study. Blažka and Fischer (2014) measured WHC from sandy podzol soil (spodosol) from the top of a postglacial dune of the coniferous Kampinos forest in Poland, dominated by the conifer Scots pine (*Pinus sylvestris* L.). The WHC readings were very low, ranging between 0.48% - 3.94%. In a study carried out by Zhao et al. (2022) on the conifer Masson's pine (*Pinus massoniana*), the soil types sampled were primarily medium and heavy loam, which naturally have a much higher WHC than sandy soil (Irrigation New Zealand, 1973). However, the soil WHC was observed to be $43.92\% \pm 1.43\%$ (Zhao et al., 2022), which is still lower than the measurements obtained in this study.

The discrepancy with the studies compared above may be explained by the link between WHC and TC content. In this study, significant positive correlation was observed between WHC and TC content for both healthy ($p = 0.00298$) and unhealthy ($p = 7.09 \times 10^{-5}$) soil (Figure 5.5).

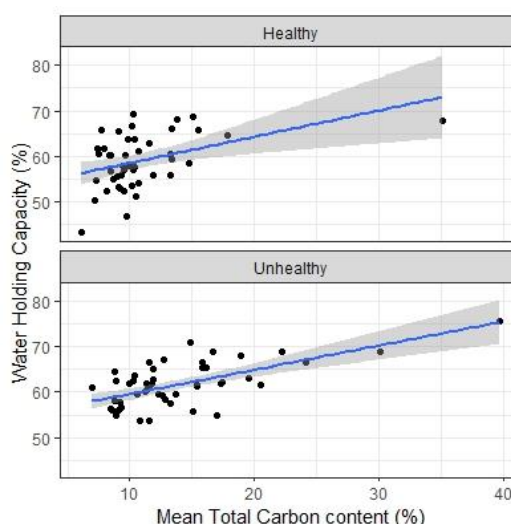


Figure 5.5: Relationship between WHC and mean TC content (Healthy: $p = 0.00298$, Unhealthy: $p = 7.09 \times 10^{-5}$), using Kendall correlation (threshold $p < 0.05$).

Like other conifers, *Agathis australis* accumulates a large amount of woody, recalcitrant litter consisting of more twigs, branches, and cones (over 55%) than leafy material (around 35%) (Silvester & Orchard, 1999). The litter collected under kauri canopy has a very slow

decomposition rate, with mean residency time of 9-78 years due to its high lignin and cellulose content (Girisha, 2001; Silvester & Orchard, 1999). Moreover, even though there is seasonal variation in type of litter accumulation, there is continuous addition of litter all year round (Macinnis-Ng & Schwendenmann, 2015). Therefore, the variation in decomposition rate results in the litter layer consisting of a combination of undecomposed, semi-decomposed, and completely decomposed organic matter (Girisha, 2001).

The semi-decomposition of litter results in formation of coarse fraction organic matter, called particulate organic matter or POM (usually ranging in size from 0.053-2 mm) (Cambardella & Elliott, 1992; USDA, 2011). Zhou et al. (2018) established that the water-retention capacity of semi-decomposed litter was considerably higher than that of undecomposed litter. POM is porous and is able to absorb and retain up to 20 times its own weight of rainwater, imparting a 'spongy effect' (Li et al., 2022; Rijkse & Guinto, 2010). Soil texture determines the location of water in the soil matrix and also controls the water absorbency of POM (Li et al., 2022). Li et al. (2022) demonstrated that the absorbency is more related to the texture of the soil than the moisture content of the soil, and stated that POM will absorb more water in sandy soil than in clayey soil.

As the kauri soil is sandy in nature, the presence of POM may help absorb more water resulting in greater water holding capacity of the kauri soil. This is clearly reflected in the results of the present study, where the WHC was found to be high, in spite of the poor water-retentive nature of the sandy soil. Soil POM may also explain the higher values of WHC found in this study compared to the studies conducted by Zhao et al. (2022) and Blažka and Fischer (2014), as litter deposition under kauri canopies (4.5-13.2 t/ha per year (Silvester & Orchard, 1999)) is much higher compared to other conifers (2.2-3.9 t/ha per year (Dušan et al., 2018)). Furthermore, kauri litter is also known to have very low decomposition rate (Silvester & Orchard, 1999; Wyse & Burns, 2013). Additionally, the correlation between POM and WHC exists for both healthy and unhealthy kauri soil, suggesting that the effect of POM on WHC exists regardless of the presence of dieback. However, as increased shedding of litter is a symptom of kauri dieback, infected kauri trees are more likely to have higher quantity of soil POM. This is corroborated by Schwendenmann and Michalzik (2019), who observed thinning of infected kauri canopies, implying more litter deposited in the soil. Therefore, POM may be the contributing factor for elevated WHC values of soil from unhealthy tree than healthy trees in this study.

A study carried out by Schwendenmann and Michalzik (2019) observed decrease in both canopy derived dissolved and particulate organic matter in the throughfall from dieback-infected kauri trees. This could imply that the thinning of the canopy due to infection has deposited more organic matter that contributes towards more POM in the soil (Beever et al., 2009; Bellgard et al., 2013). To date, no data is available quantifying POM in kauri soil and its relation to water retention. Further research regarding POM and its association with *P. agathidicida* is required.

5.2 Chemical characteristics

Soil is a very complicated chemical system where numerous varied chemical reactions occur in the soil concurrently at all times. These transformation processes regulate the solubility of chemical constituents, accessibility of nutrients for uptake by plants and microorganisms, and kinesis of key soil components (Osman, 2013b). The nature and type of the reactions depends on the soil heterogeneous environment which involves air, water, inorganic and organic solids, and microorganisms (Sparks, 2019). Even though the soil organic matter contributes to only 5% of the soil, it immensely impacts the soil chemistry by influencing the majority of soil reactions and processes. On the other hand, the inorganic components that comprise 90% of the soil majorly influence the equilibrium and kinetics of the chemical reactions (Sparks, 2019). In forests, the type and amount of organic matter being deposited, and its decomposition rate, dictates nutrient cycling and related biogeochemical processes within the ecosystem (Knoepp et al., 2005).

When the chemical properties of soils are influenced by plant litter, which is favourable for growth of the plants and enhances their own competitive performance, positive feedback is said to have been established between the plant and the soil (Binkley, 1995). The litter produced by mature kauri alters the soil conditions underneath the canopy by influencing the pH of the soil, reducing the nitrogen mineralisation process, increasing weathering of the underlying soil, and reducing moisture (Jongkind et al., 2007; Silvester, 2000). These poorly fertile soil conditions are conducive for kauri trees and seedlings, demonstrating positive feedback between kauri and the soil (van Breemen & Finzi, 1998). However, such soil conditions are not only unfavourable for the competitive angiosperm species, but also makes the soil selective to specific fungal and bacterial communities (Binkley, 1995; van Breemen & Finzi, 1998). Such alteration of soil conditions through chemical processes plays an important role in the dynamics of kauri forest ecosystems (Jongkind et al., 2007; Verkaik et al., 2007). With this soil transformation, kauri competes with the fast-growing angiosperms, creating niche partitioning with various coexisting species that are tolerant to low pH (Thompson et al., 2015). This gives rise to a kauri region with stress-tolerant plant communities, which is structurally and configurationally unique from the adjacent conifer-angiosperm forest community, portraying kauri as a foundation species (Jongkind et al., 2007; Wyse et al., 2014).

5.2.1 Soil pH

In this study, a significant difference ($p = 0.0162$) in soil pH was observed between the healthy and unhealthy trees of the Waitākere region, where the unhealthy tree soils (5.17) had lower mean pH than the healthy tree soils (5.43) (Table 4.8). However, in the Coromandel region, no significant difference was observed in soil pH between healthy Tairua soil (4.69) and unhealthy Whangapoua soil (4.67) (Table 4.10).

(Byers, Condrón, et al., 2020) found no significant difference in soil pH between asymptomatic (5.23 ± 0.09) and symptomatic (5.33 ± 0.08) kauri trees in the Waipoua forest. Lewis et al. (2019) also measured kauri soil pH in the Waipoua forest, and obtained similar results (5.92 ± 0.03). At five different locations of Waitākere forest, Jongkind et al. (2007) measured the pH from the soils of mature kauri trees, and obtained consistent and quite acidic pH of around 4, which is considerably lower than the present study as well as the studies carried out by (Byers, Condrón, et al., 2020) and Lewis et al. (2019).

Intense acidic conditions within the canopy dripline of *Agathis australis* can be explained by the accumulation of a huge amount of organic matter under the canopy (Jongkind et al., 2007; Wyse, 2012; Wyse & Burns, 2013). Mature kauri trees can amass up to 2 m of organic matter (Silvester & Orchard, 1999). As the kauri plant matures, there is an increase in lignin content, which is particularly high in woody tissues (Silvester & Orchard, 1999; Weil & Brady, 2017b). Lignin is a component of plant cell walls and is made of hundreds of intricate phenolic subunits forming phenylpropene-like structures with various connecting methoxyl ($-\text{OCH}_3$) groups (R or R'), as shown in Figure 5.6. Because of its structural complexity, lignin is relatively slow to decompose (Weil & Brady, 2017b). Additionally, the ability to break down lignin by microbial decomposing action is limited due to lack of enzymes in the decomposing microorganisms (Verkaik, 2006; Weil & Brady, 2017b). The woody material in litter contains a substantial amount of phenolic compounds and tannins, which are also slow to decompose (Silvester & Orchard, 1999; Wyse & Burns, 2013).

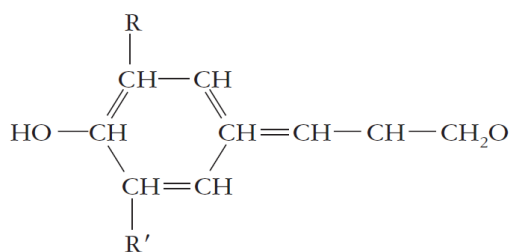


Figure 5.6: Phenolic ring subunit of lignin molecule, connected to other subunits through R and R' (Weil & Brady, 2017b).

The phenolic compounds in kauri litter leach into the deeper layers of the soil, making it more acidic (Silvester & Orchard, 1999). Additionally, these phenolic compounds (such as humic acid and fulvic acid), which are highly acidic and reactive, create an environment which is not

favourable for decomposing microorganisms and invertebrates such as earthworms, resulting in mor-humus formation or raw humus conditions, referred to as 'pukahukahu' in te reo Māori (Jongkind et al., 2007; Weil & Brady, 2017b; Wyse et al., 2014). Hence, increase in thickness of litter layer can increase acidity of the soil. Jongkind et al. (2007) connects thickness of the litter layer to DBH of the tree, and states that older and larger trees tend to have more acidic soil. This explains the intensely acidic results obtained by Jongkind et al. (2007), who sampled soil from mature kauri with DBH over 1.2 m, which implies a possible minimum age of 500 years. Each of the kauri had over 90 cm of litter deposited under the canopy, reducing toward the canopy edge.

However, in the present study, no significant correlation ($p > 0.05$) was found between mean pH and DBH for both unhealthy and healthy kauri. Additionally, in the Coromandel region, no significant difference was observed in soil pH between healthy Tairua soil (4.69) and unhealthy Whangapoua soil (4.67) (Table 4.10). This is in spite of the unhealthy Whangapoua kauri trees having a much larger median DBH (0.4 m) than healthy Tairua kauri (0.2 m), which should doubly lead to more litter fall and therefore lower soil pH in the Whangapoua location. The reason for this unexpected result could be the difference in topography between the locations, which can have a large impact on soil pH (Zhang et al., 2019). Many of the unhealthy kauri were located on sloping terrain. After precipitation, surface runoff can wash away litter, and infiltration can leach away tannins – hence, the topography can significantly affect spatial soil pH. Secondly, Zhang et al. (2019) state that the nature of the parent materials from which soil is formed can have a large influence on soil pH. As the Tairua and Whangapoua locations are at a considerable distance from each other, it is possible that there is variation in parent material, which negates the effect of acidic tannins in the litter on the soil pH in the Whangapoua location.

Jongkind et al. (2007) also states that increasing thickness of the litter layer is directly linked to an increase in soil carbon content. In the present study, a significant negative correlation ($p = 2.58 \times 10^{-5}$) between pH and mean TC content was observed in unhealthy soil (Figure 5.7).

This confirms that higher carbon content results in more acidic soil for dieback-infected kauri. As litter is a rich source of organic carbon, phenolic compounds, and acidic tannins, this connection aligns with the idea that high carbon and therefore low pH are caused not by increasing age or DBH, but by increased litter fall due to defoliation and canopy loss as symptoms of kauri dieback.

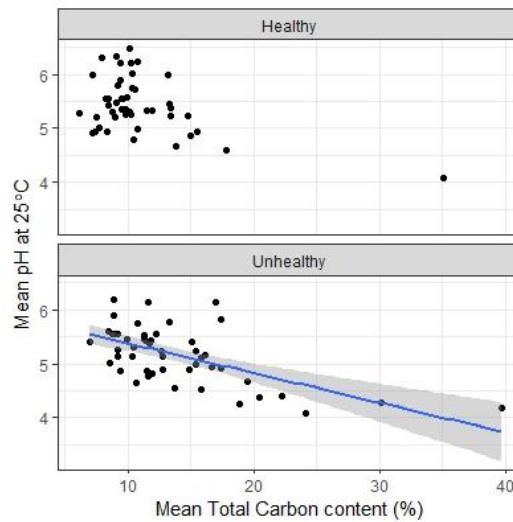


Figure 5.7: Relationship between mean pH and mean TC content (Healthy: $p = NS$, Unhealthy: $p = 2.58 \times 10^{-5}$), using Kendall correlation (threshold $p < 0.05$).

On the other hand, Lewis et al. (2019) have found that soil carbon content and pH do not affect sporulation of *P. agathidicida*. In fact, *Phytophthora* species are very tolerant to pH, surviving in ranges varying from 3.8-9.0, and normally prefer a higher pH for growth (Andrison, 1994; Kong et al., 2009; Schmitthenner & Canaday, 1983). In laboratory settings, *P. agathidicida* is cultivated on media such as V8 agar, potato dextrose agar, and sabouraud agar, which have pH between 5.6-6 (Delcán & Brasier, 2001; Dick & Kimberly, 2013; Xavier et al., 2010). This confirms that highly acidic conditions are not preferred for optimal growth of *P. agathidicida*. This implies that high soil carbon content and low pH in kauri soil may simply indicate the presence of the pathogen, rather than facilitating its growth.

5.2.2 Electrical conductivity

The results from this study demonstrate that there was no significant difference in mean EC between healthy (103.9 $\mu\text{S}/\text{cm}$ = 0.1039 dS/m) and unhealthy (109.5 $\mu\text{S}/\text{cm}$ = 0.1095 dS/m) trees across all locations of the Waitākere region (Table 4.8). Contrarily, a significant difference ($p = 0.0259$) in mean EC was observed between the healthy Tairua (90.1 $\mu\text{S}/\text{cm}$ = 0.0901 dS/m) and unhealthy Whangapoua (121.8 $\mu\text{S}/\text{cm}$ = 0.1218 dS/m) locations of the Coromandel region (Table 4.10). In spite of these results, EC values for both regions are very low and fall into the non-saline category for healthy and unhealthy trees alike, according to Table 5.1.

Table 5.1: Classes of salinity and corresponding EC in dS/m (1 dS/m = 1000 $\mu\text{S}/\text{cm}$) (USDA NRCS, 2011).

EC (dS/m)	Salinity Class
0 < 2	Non-saline
2 < 4	Very slightly saline
4 < 8	Slightly saline
8 < 16	Moderately saline
≥ 16	Strongly saline

Other studies measuring EC from the soils of temperate conifer forests have found similar values to those obtained in present study. Electrical conductivity ranging from 0.07 - 0.17 dS/m was noted by Rathod et al. (2020) from the soils of Himalayan mixed deodar-conifer forest. Wani et al. (2014) obtained average EC value of 0.218 dS/m for soils of temperate coniferous forests in southern region of Kashmir Himalaya. In another study, Jehangir et al. (2012) reported EC values of 0.139 dS/m in coniferous forests of Tangmarg in the far north of India. Different temperature and precipitation conditions may impact the weathering of the minerals and thereby the release of ions, affecting the EC of the soil (Kaushal et al., 2018). With annual temperature between -2°C and 35°C , and annual precipitation between 400-2300 mm, the climatic conditions of these forests are similar to that of the temperate conifer kauri forests in New Zealand. Hence, with similar temperature and moisture regimes, the EC readings obtained in this study are in line with those obtained by Rathod et al. (2020), Wani et al. (2014), and Jehangir et al. (2012), in particular their low values which fall into the non-saline category (Table 5.1).

Soil EC can also be affected by physical properties of the soil such as soil texture, porosity, water holding capacity, and drainage conditions (Alam et al., 2020; South Dakota Soil Health Coalition, 2023). In particular, the clay content of the soil, which contains SOM, has a large influence on EC. SOM holds all the nutrient elements required for plant growth (South Dakota Soil Health Coalition, 2023). Typically, kauri soil has high sand content and low clay content. In fact, in this study, the soil samples from the Waitākere region were found to contain above 90% sand and below 1% fines (silt and clay) on average. This indicates very poor SOM content, which is reflected in the low, non-saline EC measurements.

Lewis et al. (2019) measured the EC of kauri soils as well as kauri litter from the Waipoua Forest in the North Island of New Zealand. The low EC measurement of the upper layer of the soil (96.3 $\mu\text{S}/\text{cm}$) was similar to the results of the present study. Furthermore, Lewis et al. (2019) also found that the EC of the litter layer (194.1 $\mu\text{S}/\text{cm}$) fell into the non-saline category. Such low EC of litter demonstrates the capability of kauri to recycle nutrient elements and adapt to nutrient-deficient soil. Kauri has developed a mechanism to retract nutrient elements such as P, Mg, and N from leaves before they fall (Fitter & Hay, 2001). Upon defoliation, certain elements like K and Na are instantly leached from both dead and living leaves, and are removed from the litter (Fitter & Hay, 2001). On the other hand, Ca is trapped and restrained in the sclerophyllous leaf tissues, and released at a slower pace (Fitter & Hay, 2001). Hence, slow decomposition of litter and rapid leaching results in low EC of both kauri litter and soil (Enright & Ogden, 1987)

Typically, soil pH has a strong effect on the solubility of anions and cations, and has a direct bearing on the EC of the soil. In the present study, no correlation was found between pH and EC of kauri soil. The podzolisation effect, caused by low pH in kauri soils, leads to a decrease in EC with increasing soil depth (Bailey et al., 2019). This results from the leaching of nutrients from surface soils, and subsequent increase in their concentration in the lower soil layers (Rathod et al., 2020). Hence, the low EC found in the present study can be explained by the soil samples being collected from the surface layers (10 cm depth) of the soil. Lewis et al. (2019) also noticed similar reductions in EC with depth.

In the present study, extremely low values cause difficulty in relating EC to kauri dieback, in spite of the significant difference ($p = 0.0259$) between healthy and unhealthy Coromandel soil. Most microorganisms except *Actinomyces* and fungi are sensitive to high salinity, which can affect processes such as respiration and nitrification (Smith & Doran, 1996). When tested, Lewis et al. (2019) found no correlation between EC and the sporulation of *P. agathidicida* spores. More research is required in this area to build upon these initial findings. Moreover, the study conducted by Lewis et al. (2019) is linked to the sporulation of *P. agathidicida*, however, more work related to growth and proliferation of *P. agathidicida* is required to investigate the potential connection between soil EC and kauri dieback.

5.2.3 Total carbon

The results in this study displayed that there was a significant difference ($p = 0.000559$) in mean total carbon (TC) content between healthy (10.86%) and unhealthy (13.82%) kauri soil across all locations of the Waitākere region (Table 4.8). Similarly, a significant difference ($p = 0.0235$) in mean TC content was observed between the healthy Tairua (13.29%) and unhealthy Whangapoua (19.52%) locations of the Coromandel region (Table 4.10). In both cases, unhealthy kauri soil contained higher mean TC content than healthy kauri soil. Similar results were obtained for symptomatic and asymptomatic kauri trees in Waipoua forest by (Byers, Condrón, et al., 2020). The TC content of symptomatic kauri soil (18.53%) was higher than that of asymptomatic kauri soil (14.90%).

Carbon accumulates in deep layers of organic litter as dead biomass (Halkett & Sale, 1986; Silvester & Orchard, 1999). Up to 225 tonnes/hectare of carbon biomass have been recorded in kauri stands in North Auckland (Silvester & Orchard, 1999; Wyse, 2012). The average residence span of the litter ranges between 9-78 years owing to slow decomposition rate (Silvester & Orchard, 1999). Reduced decomposability of kauri litter and prolonged life of kauri trees combine together to create progressively thicker litter layers, resulting in prominent pedological impact to the territory under the canopy by influencing both plant and soil functions (Jongkind et al., 2007; Weil & Brady, 2017b). The concentration of carbon is much higher in kauri organic soil than other New Zealand soils (Blakemore et al., 1987). In fact, in dieback-infected forest, there is increased loss of carbon from trees via defoliation as well as reduced carbon uptake from soil, which results in the soil transitioning from a net carbon sink to a source of carbon for the ecosystem (Avila et al., 2016; Byers, Condrón, et al., 2020). This confirms the findings of (Byers, Condrón, et al., 2020) as well as the present study, which both show higher TC content in unhealthy soil.

In the present study, a significant positive correlation ($p = 0.00928$) between DBH and mean TC content was observed for unhealthy trees in the Waitākere region (Figure 5.8). This implies that larger trees produce more litter as a result of increased defoliation, which is a symptom of dieback. This leads to more organic matter and hence higher carbon content in infected soil. This is along the same line as the findings of Verkaik (2006), who demonstrated a positive correlation between the thickness of the litter layer and DBH of kauri trees selected from the Waitākere region, and Jongkind et al. (2007), who determined that the deterioration of litter is directly proportional to the thickness of the litter layer, resulting in high TC content in soil surface. However, these studies do not investigate the relationship between kauri litter and kauri dieback, which is evident in the present study.

Earlier, Figure 5.7 demonstrated a significant negative correlation ($p = 2.58 \times 10^{-5}$) between pH and mean TC content for unhealthy trees only, implying that higher carbon content

results in more acidic soil for dieback-infected kauri. This is supported by the findings of Finzi et al. (1998), who observed production of higher amounts of organic acid from the recalcitrant litter of conifer species, turning the soil acidic. In addition, Jongkind et al. (2007) recorded a decrease in soil pH with increase in litter content, and hence soil carbon content, under kauri trees. Once again, these findings corroborate the results of this study.

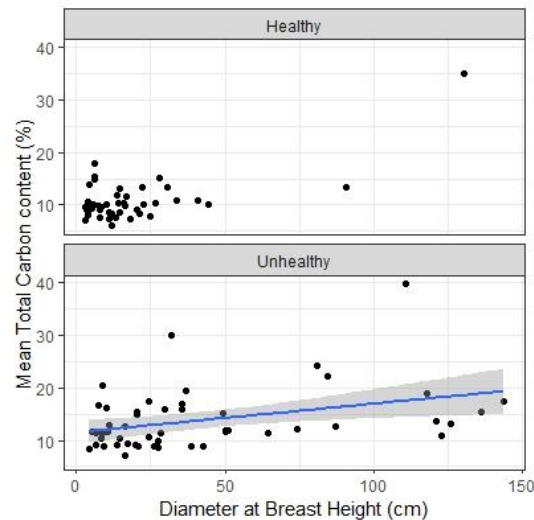


Figure 5.8: Relationship between mean TC content and DBH (Healthy: $p = NS$, Unhealthy: $p = 0.00928$), using Kendall correlation (threshold $p < 0.05$).

Increased soil TC content for unhealthy trees, observed in this study, may be a result of secondary infection following kauri dieback, which is associated with a larger presence of saprophytic fungal community, leading to more litter degradation as well as disintegration of necrotic kauri tissue. Moreover, low soil pH caused by high carbon content favours the growth of saprophytic fungi (Jung et al., 2018; Wu et al., 2019). (Byers, Condrón, et al., 2020) inferred this shift in fungal community by observing an increase in carbon-degrading and carbon-cycling genes in symptomatic kauri soils in the Waipoua forest. (Byers, Condrón, et al., 2020) also observed noticeable and significant differences in the diversity, structure, and functional properties of microbial communities between asymptomatic and symptomatic kauri soils. While there was an increased number of saprophytic fungi in symptomatic soil, the prevalence of disease-suppressive microbial taxa such as *Penicillium*, *Trichoderma*, *Enterobacteriaceae*, and *Pseudomonas* was significantly higher in asymptomatic soil.

For the same locations in Waipoua forest, Byers, Waipara, et al. (2020) conducted another experiment comparing the soil TC content of two conifer species, kauri (14.10%) and pine (10.84%), which were observed to be significantly different ($p < 0.001$). Their research also shows significant differences in the diversity and composition of soil microbial communities related with fragmented kauri forests and neighbouring pine plantations. Saprophytic fungi were detected to be more abundant in soils with high nutrient content in form of plant debris, such as kauri soils, while diverse ectomycorrhizal fungal species were detected in pine soils in their study.

Furthermore, the research also displayed modification in microbial communities surrounding remnant kauri forest, which involves the lack of microbial taxa associated with disease suppression. These changes can cause the kauri to be susceptible to pathogens (Byers, Waipara, et al., 2020). Thus, it can be derived that carbon content of the soil is associated with the health of kauri, aligning with the findings of this study which found higher TC content in unhealthy kauri soil. Similar studies are required to detect the difference in diversity and composition of soil bacterial and fungal communities between healthy and dieback-infected kauri in the Waitākere and Coromandel regions. Moreover, research should also be carried out to test the effectiveness of any disease-suppressing species, isolated from healthy kauri, as potential biological defence agents against *P. agathidicida*.

Lewis et al. (2019) performed an investigation to determine the growth response of *P. agathidicida*, and observed no significant influence of TC content on sporulation of both asexual (sporangia) and sexual (oospores) spores, which suggested that carbon was not restricting the growth of *P. agathidicida*. This implies that high soil TC content and low pH may indicate the presence of the pathogen, as suggested by this study, rather than facilitating its growth. Further research is required to investigate whether soil carbon supports the growth and proliferation of mycelia from the zoospores of *P. agathidicida* present in kauri soil.

5.2.4 Total nitrogen

In this study, a significant difference was observed ($p = 4.621 \times 10^{-5}$) in mean TN content between healthy (0.49%) and unhealthy (0.60%) trees across all locations of the Waitākere region (Table 4.8). Likewise, there was a significant difference ($p = 0.0318$) in mean TN content between the healthy Tairua (0.49%) and unhealthy Whangapoua (0.70%) locations of the Coromandel region (Table 4.10). In a kauri-dominated ecosystem, the organic and mineral soil layers underneath mature kauri trees have high total nitrogen content compared to other New Zealand soils (Blakemore et al., 1987; Silvester, 1978). Despite this, kauri forests are believed to experience nitrogen deficiency, restricting the growth of kauri trees (Ecroyd, 1982; Enright & Ogden, 1987; Schwendenmann & Michalzik, 2019; Silvester, 1978; Silvester, 2000). In kauri forest, limitation of nitrogen supply to kauri can be explained by a very small proportion of nitrogen being fixed symbiotically from the decaying leaves to be available for the plants. The remainder is accounted for by the accumulation of immobilised nitrogen in the litter (Silvester, 1978; Silvester, 2000). In this study, unhealthy kauri soil contained higher mean TN content than healthy kauri soil in both Waitākere and Coromandel regions. Other studies have also found increase in soil nitrogen content as an aftereffect of dieback (Edburg et al., 2012; Xiong et al., 2011). The most likely cause for this is increased defoliation and build-up of litter, which is one of the major symptoms of kauri dieback.

As already established, accumulated litter causes increased acidity of kauri soil. The present study also shows a significant negative correlation ($p = 0.00762$) between mean pH and mean TN content for only unhealthy soil in the Waitākere region (Figure 5.9).

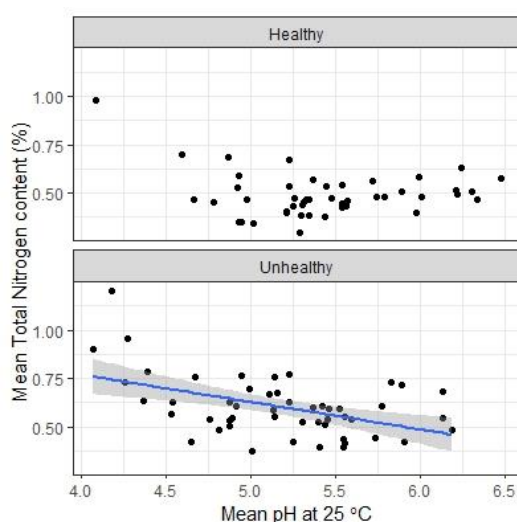


Figure 5.9: Relationship between mean TN content and mean pH (Healthy: $p = NS$, Unhealthy: $p = 0.00762$), using Kendall correlation (threshold $p < 0.05$).

The nature of the litter provides the major rationale behind the accumulation of organic matter, decrease in soil pH, and the huge amount of stored nitrogen. Highly acidic sclerophyllous kauri leaves contribute to 35% of the litter composition and have exceptionally thick cuticles that

are difficult to decompose (Enright & Ogden, 1987; Silvester & Orchard, 1999; Verkaik et al., 2007). Additionally, kauri leaves have high tannin content. Tannins are a type of polyphenols that comprise of several phenolic hydroxyl substituents, and have very high molecular weight (Verkaik et al., 2006). Tannins have the ability to sequester proteins by complexation through hydrogen bonding and hydrophobic effects, as shown in Figure 5.10. This results in immobilisation of nitrogen by preventing disintegration of the plant proteins and subsequent release of nitrogen for plant uptake (Verkaik, 2006; Verkaik et al., 2006).

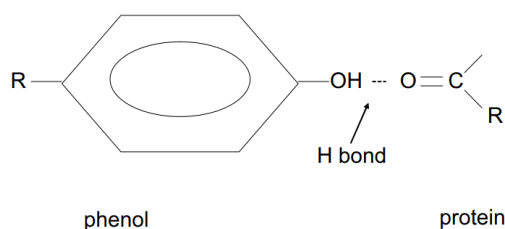


Figure 5.10: Hydrogen bonding of the hydroxyl group of a phenolic compound with the carbonyl group of a protein (Verkaik, 2006).

Additionally, other polyphenols present in plant cells and in the intercellular spaces prevent microbial decomposition by imparting toxicity to microbes, or by interfering with microbial enzymes (Verkaik et al., 2006). Further, the leaching of the acidic polyphenols creates an environment which is not favourable for decomposing microorganisms and invertebrates such as earthworms, resulting in partially decomposed mor-humus formation (Jongkind et al., 2007; Rayment et al., 2011b; Wyse, 2012). The resultant low molecular weight compounds in the mor-humus act as a source of carbon for opportunist microbes, causing additional immobilisation of nitrogen (Verkaik et al., 2006). Thus, the quantity and quality of litter leads to several phenomena which add to slow decomposability, prevention of nitrogen mineralisation, and the immobilisation of nitrogen, eventually causing nitrogen deficiency and reduced plant productivity in kauri stands (Enright & Ogden, 1987; Silvester, 2000; Verkaik et al., 2006).

Contrary to the results of the present study, Byers, Waipara, et al. (2020) observed no significant difference in mean TN content between symptomatic and asymptomatic kauri soil. On the other hand, significant differences were obtained in the composition and abundance of nitrogen cycling genes between asymptomatic and symptomatic kauri soil. This means that there can be a possible impact of tannins and phenolic compounds on microbial community related to nitrogen cycling, which is reflected by the variation in composition and abundance of nitrogen cycling genes. No specific trends associated to microbial gene function and presence of dieback were established by Byers, Waipara, et al. (2020). Hence, further research is required in this area.

This study demonstrates the impact of kauri litter and pH on TN content of the soil. Wyse et al. (2014) not only measured TN content, but also found that $\text{NH}_4\text{-N}$ was significantly more abundant directly under the canopy of kauri, while $\text{NO}_3\text{-N}$ was significantly more abundant outside the dripline. Soil pH is known to be a major factor affecting nitrification processes in the

nitrogen cycle (Zebarth et al., 2015), and thus could influence the presence of the different forms of mineralised nitrogen in kauri soil. Under unhealthy trees, further decrease in pH can drastically reduce nitrification rate and cause scarcity of plant-available nitrogen ($\text{NO}_3\text{-N}$) in the soil (Zebarth et al., 2015). This could result in starvation and eventual death of the tree. Further studies are required to understand the relationship between soil pH, specific forms of nitrogen, and dieback disease.

In an investigation to determine the growth response of *P. agathidicida*, TN content was observed to have 0.5% contribution towards variation of spore count of *P. agathidicida*. This suggested that nitrogen had minimal impact on sporangia and oospore production, and was not affecting the growth of *P. agathidicida* (Lewis et al., 2019). Instead, increased soil nitrogen content is a consequence of dieback, resulting from increased defoliation and litter build-up, which is one of the primary symptoms of dieback disease. Hence, higher TN content in unhealthy soil can be seen as an indicator of presence of dieback, rather than a cause for its occurrence.

5.2.5 Carbon:Nitrogen ratio

In this study, despite significantly higher TC and TN content in unhealthy soils, the results revealed that there was no significant difference in mean C:N ratio between healthy (21.78) and unhealthy (22.51) kauri soil across all locations of the Waitākere region (Table 4.8). Likewise, no significant difference was observed between the soil from the healthy Tairua (26.83) and unhealthy Whangapoua (27.76) locations of the Coromandel region (Table 4.10). This indicates that TC and TN content increase in similar proportion with the onset of dieback, resulting in no substantial change to C:N ratio. The lack of connection between C:N ratio and dieback disease can be confirmed by the findings of Lewis et al. (2019), who carried out an investigation to quantify the growth response of *P. agathidicida*. Soil C:N ratio had only a 6.6% contribution towards variation of spore count of *P. agathidicida*, implying that C:N ratio had minimal impact on sporangia and oospore production, and had negligible effect on the growth of *P. agathidicida*.

Lewis et al. (2019) measured the C:N ratio of different depths of kauri soil from Waipoua forest. In A- and B-horizons (upper soil layers), C:N ratios of 25.1 and 24.5 respectively were obtained, which are very similar to those found in this study. Additionally, Lewis et al. (2019) found that the C:N ratio of the litter layer (85.2) was more than three times that of the A- and B-horizons, confirming that litter contains much more carbon than nitrogen, in comparison to soil. In an analysis of varying depths of soil under two predominant kauri covers, Silvester (2000) also illustrated a decrease in C:N ratio with increase in depth, from litter layer to lower soil profiles. The decrease in C:N ratio (from 82 at litter layer to 39 at humus layer) was a result of corresponding increase in TN content due to microbial immobilisation under the layers of the soil. Moreover, Wyse (2012) also observed a significant decrease ($p < 0.001$) in C:N ratio between the organic and mineral layers of kauri soil. Wyse et al. (2014) found that the C:N ratio plummeted drastically between the litter layer directly under the tree to the litter layer 10 m away at the dripline of the canopy, indicating that continuous addition of litter is responsible for high C:N ratio.

Kauri forests are characterised by prolonged retention of leaves resulting in disproportion in the annual shedding of leaf biomass (leaves make up 35% of total litter mass) and woody material such as bark, branches, and reproductive cones (Silvester & Orchard, 1999). The nitrogen content of kauri leaves is very low as nitrogen is retracted before defoliation, while the bark and branches are high in complex carbon-rich molecules such as cellulose and lignin. These decomposable materials have high initial C:N ratio (Silvester, 2000), and do not provide heterotrophs with easily consumable carbon for increase in their biomass and nitrogen immobilisation (Silvester, 2000; Verkaik et al., 2006). Furthermore, not only bark and branches, but kauri foliage also contains tannins and other polyphenols, which lower the pH of the soil on leaching and deter microbial growth (Verkaik, 2006). All of these characteristics of kauri litter together discourage the growth of heterotrophic r-strategist microorganisms in the initial stage of

addition of litter, and eventually diminish the mineralisation process and causing deficiency of mineral nitrogen (in form of NH_4^+ or NO_3^-) accessible to plants (Weil & Brady, 2017b). Instead, these bacteria rely on the nitrogen supply from the soil solution, further depleting the resource of soluble nitrogen from the soil, causing nitrogen deficiency surrounding the kauri (Verkaik et al., 2006; Weil & Brady, 2017b). Secondly, insufficient nitrogen in kauri litter as well as the underlying soils does not fulfil the amount of prerequisite nitrogen to favour preliminary r-strategist microbial growth.

However, some species of saprophytic microorganisms such as fungi and Actinomycetes, known as 'K-strategists', take over as they can survive on slow decomposition of the very resistant and stable soil organic matter (Weil & Brady, 2017b). These organisms have specific enzymes that can break down materials such as cellulose and lignin, which are typically resistant to degradation (Brust, 2019; Weil & Brady, 2017b). This results in delay in litter decomposition, and accumulation of litter mass with higher C:N ratio (Enright & Ogden, 1987; Silvester, 2000; Verkaik et al., 2006). This explains the occurrence of high C:N ratio in healthy kauri soil. With unhealthy trees, the addition of litter mass as a symptom of dieback does not alter the conditions for the heterotrophic decomposers, which explains no variation in C:N ratio.

In this study, even though both mean TC and TN content were significantly higher in unhealthy soils than healthy soils, the ratio remained unaffected C:N ratio was high in both healthy and unhealthy soils, with no significant difference found between them. This implied that in both the cases, the soil nitrogen is immobilised and is not available for plant uptake. Therefore, C:N ratio of the kauri soil is not an indicator of health status of kauri with regards to dieback.

5.2.6 Total hydrogen

The results in this study depicted that there was a significant difference ($p = 0.00953$) in mean TH content between healthy (2.29%) and unhealthy (2.55%) kauri soil across all three locations of the Waitākere region (Table 4.8). A significant difference ($p = 0.0265$) in mean TH content was also observed between the healthy Tairua (2.30%) and unhealthy Whangapoua (2.89%) locations of the Coromandel region (Table 4.10). Mean TH content shows similar pattern to TC and TN content in this study, where unhealthy kauri soil contained higher mean TH content than healthy kauri soil.

This similarity is confirmed by the results of study, which showed significant positive correlation between mean TH and mean TC content for both healthy ($p = 1.47 \times 10^{-14}$) and unhealthy ($p = 7.92 \times 10^{-16}$) kauri soil in the Waitākere region (Figure 5.11).

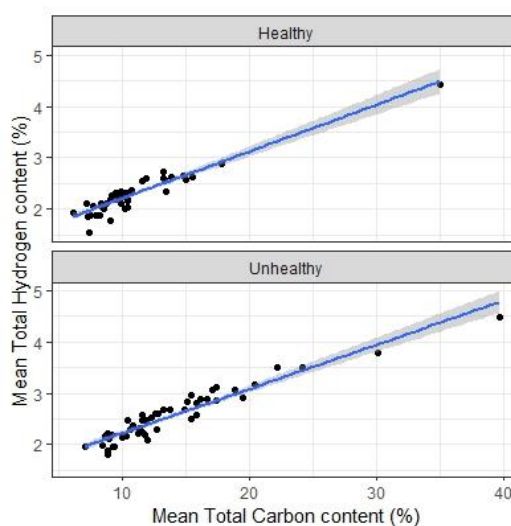


Figure 5.11: Relationship between mean TH content and mean TC content (Healthy: $p = 1.47 \times 10^{-14}$, Unhealthy: $p = 7.92 \times 10^{-16}$), using Kendall correlation (threshold $p < 0.05$).

The connection between between TH and TC content of kauri soil can be explained by their role in ecosystems as energy sources (Piché-Choquette & Constant, 2019). In soil ecosystems, the growth of microbes is governed primarily by the supply of carbon. However, with its ubiquity, low activation energy, high penetration ability, and easy permeability across microbial cells, H_2 provides an alternative to carbon as a source of energy (Morita, 1999). Moreover, there is an unceasing production of H_2 , both abiotically by the earth's crust and biotically by several microbial activities such as fermentation, N_2 fixation, and photoproduction (Morita, 1999; Piché-Choquette & Constant, 2019).

H_2 -oxidising microbes (HOM), categorised as K-strategists, disintegrate a wide variety of recalcitrant polymeric organic matter such as cellulose, hemicellulose, lignin, humic substances, and polycyclic aromatic compounds in the soil (Martinez et al., 2013). This initial turnover leads to the generation of simpler organic forms which are utilised by the wider heterotrophic (non-HOM) microbes, referred to as r-strategists earlier (Piché-Choquette &

Constant, 2019). As shown in Figure 5.12, this leads to other carbon cycling processes performed by HOM such as decomposition, humification, and hydrolysis.

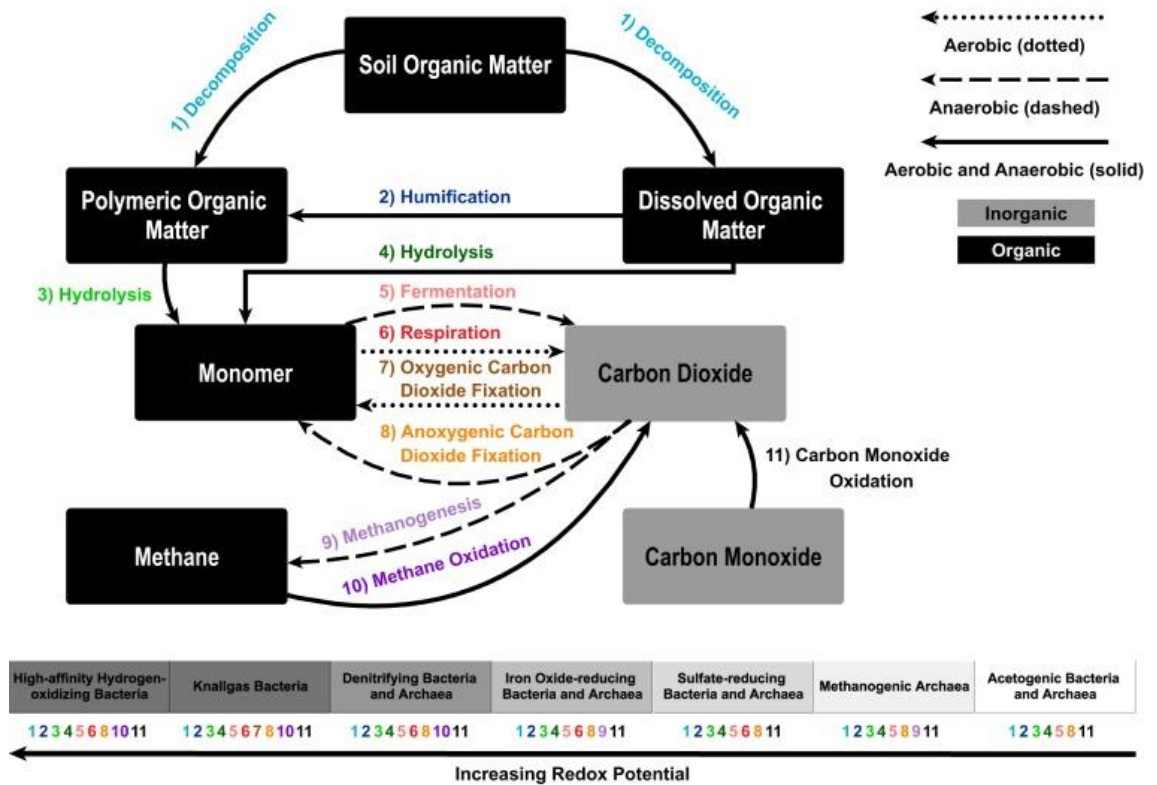


Figure 5.12: Key contributions of HOM towards carbon cycle via oxidation of H_2 , showing the microbial functional groups in order of redox potential and processes in which they involved (Piché-Choquette & Constant, 2019)

HOM are able to switch from dormant to metabolically active depending on the supply of carbon and H_2 (Morita, 1999). In kauri soil, continuous litter fall provides a source of complex organic matter. In this study, significantly higher TH content in unhealthy soil can be explained by excessive litter fall from dieback-infected kauri. Due to the involvement of HOM in the carbon cycle, increased carbon content in unhealthy soil means that HOM are not required to switch to H_2 as an alternative energy source, which leads to increased H_2 content in the dieback-infected environment. There is a lack of studies investigating the hydrogen content of kauri soils to directly compare results with. Therefore, further research is required in this area.

5.3 Limitations of the study

Determination of the soil physical properties had some limitations brought about by inadequate quantity of most soil samples. However, these were addressed in the design of the experiments and adaptations of some methods were applied across all samples.

5.3.1 Particle size determination

Several studies recommend performing sieve analysis for particle size determination with at least 250 g of soil for an accurate representation of each particle fraction in the soil (Geotechnical Engineering Bureau, 2015; Hossain et al., 2021a). In this study, around 50 g of soil was used due to the limitation of amount of soil available for each sample. For such experiments, soil requirements should be taken into consideration, and adequate soil volume should be sampled in future.

5.3.2 Bulk density

The kauri soil samples, which were collected as part of a previous project, were taken at 10 cm depth from four cardinal points around each tree and pooled together. Next, the samples were stacked in sample bags in the freezer. The pooling, stacking, and freezing of samples caused disturbance to the natural soil structure, therefore the samples were not a true representation of the soil volume in its natural state. Consequently, the method for reconstituted bulk density was adopted and applied consistently across all samples to minimise impact to the results. However, recommended core or clod methods can be used for sample collection from the field to obtain accurate measurements for bulk density.

5.3.3 Moisture factor

The soil was collected from the various sampling locations at different times of the year, which can have seasonal impact due to variation in climatic factors such as precipitation, humidity, and temperature (Ferre & Warrick, 2023; Holsten et al., 2009). It was unfortunate that climate data was not available to be included in the analyses for this study. These differing climatic factors may have had an impact on the moisture factor of the soil samples. Hence spatiotemporal studies are recommended, where the same locations are sampled during different seasons of the year and analysed alongside the climate data from those seasons.

5.3.4 Water holding capacity

The method for determining WHC of the soil samples involved the use of glass wool to allow drainage of excess water after saturation. While the glass wool used in this method is permeable, it also soaked water during the saturation step. The standard equation for calculation WHC requires the mass of saturated soil but does not consider the mass of water retained by the glass wool. While both saturated soil and glass wool are in the funnels, it is impossible to ascertain the mass of the saturated soil by itself. Furthermore, although the amount of soil used was constant

(25 g), it was not feasible to insert a consistent mass of glass wool in each funnel. This was due to the nature of the glass wool, slightly varying diameters of funnel stems, and sheer number of total samples. In order to compensate for this, a modified method was developed to find a relationship between mass of glass wool and its water retention (Appendix 1). The results of this novel method were then used to accurately obtain the WHC of the soil exclusively.

5.3.5 Overall limitations of the study

The comparisons in this study were made between healthy and unhealthy kauri, which were differentiated based on the visibility of dieback symptoms. However, as there is limited knowledge about the incubation period of kauri dieback, it is possible that there were infected trees that were yet to present any symptoms, due to the time lag between infection and disease expression (Bradshaw et al., 2020). Conversely, it is also possible that the visible symptoms were a result of climatic conditions, or infection by other pests or pathogens instead of *P. agathidicida* (Schwendenmann & Michalzik, 2021).

Additionally, the samples were collected during different seasons, which can have impact on soil physicochemical and biological processes, influencing physical properties such as soil structure, aggregate stability, soil moisture factor, and soil aeration. Furthermore, this can also affect pH, cationic exchange capacity, and availability of other plant nutrients, thereby affecting chemical properties of the soil. The variation in seasons also has a direct bearing on biological processes such as microbial activity (organic decomposition and nutrient cycling) and water and nutrient uptake by plants, which can influence the quantities of nutrient elements in the soil (Chen et al., 2021; Luo et al., 2020).

The initial step of sample collection can be used to provide a large amount of useful data, which can also reduce the need for time and equipment/consumables in the laboratory. Attributes such as pH, EC, moisture factor, and temperature of soil can be measured using field probes, and test-specific sample collection methods (such as core or clod methods for bulk density) should be taken into consideration. Additionally, meteorological climate data such as precipitation, humidity, and air temperature, as well as site-specific data such as topography (land contour and elevation) should be collected concurrently. Furthermore, a spatiotemporal study of kauri soil can provide a better understanding of its physicochemical properties and their variation throughout the year.

Chapter 6: Conclusion



Te Ara Whanui (2022)

This study aimed to perform physicochemical characterisation of soil from kauri forest in Waitākere Ranges Regional Park in Auckland, and Tairua and Whangapoua in Coromandel, in order to investigate the link between soil abiotic factors and kauri tree health. The physical and chemical characteristics of soil from kauri forest that is asymptomatic (healthy) and symptomatic (unhealthy) of dieback disease were investigated. The difference in these soil characteristics between asymptomatic (healthy) and symptomatic (unhealthy) kauri forest were also compared.

In the Waitākere region, the initial designation of asymptomatic and symptomatic sites based on the monitoring project in the three locations did not provide a factual picture, as dieback disease symptoms were observed among the asymptomatic plots. At the same time, not all trees within the symptomatic sites displayed evident symptoms of the disease. Therefore, tree health status was assigned based on observable disease expression data collected as part of another study. This tree health status, which indicated the presence of dieback symptoms, was used to provide more accurate correlation between physicochemical characteristics and symptoms of kauri dieback.

By using current accepted methods of soil analysis, physical characteristics (particle size, bulk density, and moisture factor) and chemical characteristics (pH, electrical conductivity, total carbon, total nitrogen, C:N ratio, and total hydrogen) of kauri soil were measured. Additionally, a modified method was developed to determine the water holding capacity of the soil.

In both the Waitākere (Auckland) and Coromandel regions, unhealthy kauri soil showed significantly higher moisture factor and water holding capacity. This may suggest that wetter soil provides more favourable conditions for growth and proliferation of *Phytophthora agathidicida* (Nesbitt et al., 1979). Additionally, wet soil conditions are more likely to cause damage to fine roots, and hence increase the vulnerability of kauri to infection (Marks et al., 1972; Weste & Taylor, 1971). Hence, high moisture factor and water holding capacity are soil physical characteristics that may contribute to the vulnerability of the kauri tree to dieback disease. Moreover, canopy loss is a major symptom of dieback, which results in large quantities of litter accumulation under kauri canopies. The litter can trap moisture in the soil, so high moisture factor and water holding capacity can potentially be both the cause as well as effect of dieback, creating a vicious cycle.

In both Waitākere (Auckland) and Coromandel regions, unhealthy kauri soil also exhibited significantly higher total carbon, total nitrogen, and total hydrogen in comparison to healthy kauri soil. As litter is a rich source of carbon, increased litter fall from dieback-infected kauri leads to more organic matter in soil and therefore higher total carbon content (Silvester & Orchard, 1999). In this study, a significant positive correlation was observed between total carbon content and diameter at breast height for unhealthy kauri only, implying that unhealthy trees shed

larger quantities of litter as they get older and with progression of the disease. No such correlation was found for healthy kauri, indicating that the correlation may be linked to the presence of dieback disease among the stands. Moreover, a significant negative correlation was observed between pH and total carbon for unhealthy kauri only. This is likely caused by the recalcitrant litter under unhealthy kauri, which produces high amounts of organic acid, turning the soil acidic and lowering pH (Finzi et al., 1998).

Kauri litter also contains large amount of sclerophyllous leaves, which have high tannin content. Tannins have the ability to sequester proteins via complexation, resulting in immobilisation of nitrogen and therefore higher total nitrogen content in the soil under unhealthy kauri (Verkaik, 2006; Verkaik et al., 2006). In this study, a significant negative correlation was observed between total nitrogen content and pH for unhealthy trees only. Due to increased defoliation in unhealthy kauri, increased quantity of litter leads to higher amount of acidic tannins that leach into the soil, hence lowering soil pH. Both kauri and saprophytes are well adapted to survive in acidic conditions (Byers, Condrón, et al., 2020; Wyse, 2012). Additionally, *Phytophthora* species are tolerant to pH ranges varying from 3.8-9.0 and normally prefer a higher pH for growth (Andrivon, 1994; Kong et al., 2009; Schmitthenner & Canaday, 1983).

Increased carbon content in the soil as a result of defoliation also leads to increased total hydrogen content due to the involvement of H₂-oxidising microbes in the carbon cycle (Piché-Choquette & Constant, 2019).

Higher quantities of total carbon, total nitrogen, and total hydrogen in unhealthy kauri soil are caused as a result of increased defoliation and thinning of canopies, which are symptoms of dieback. Hence, measurement of these soil chemical characteristics may help to confirm the presence of the disease. Furthermore, this data could be used to map the spread of dieback in kauri forest.

This study determined the health status of each tree on the basis of presence or absence of symptoms using disease expression data collected as part of another study, instead of the designation of the sampling sites. Hence, this study contributes towards presenting more accurate insight into the link between soil physicochemical characteristics and kauri dieback symptoms in the Waitākere and Coromandel regions. Thus, these findings can provide a foundation for ongoing research being carried out as part of the NRT project and Waikato Council projects.

Future research is required to identify the link between the abiotic (physical and chemical soil characteristics) and the biotic (kauri and soil microbiota) components of the ecosystem and associated biogeochemical cycles. This can provide further understanding of the role of the physical and chemical soil attributes on kauri susceptibility to the pathogen, as well as how these factors can influence the adaptability of the *Phytophthora* species and other pathogens. Research

in this area can provide information about the role that physicochemical factors play on disease expression and severity. Moreover, such investigations can provide better perception of the connectivity between the three components of the disease triangle – host vulnerability, pathogenicity, and the contributing physicochemical properties for disease expression. This knowledge can help to find innovative approaches to mitigate further spread of the disease and possibly design interventions to reduce additional kauri tree fatality caused by dieback.

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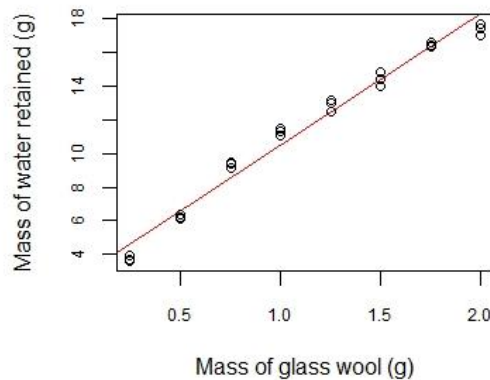
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Appendix 1 Development of water holding capacity method

This was done by carrying out the same WHC procedure without soil, but with triplicates of varying masses of glass wool (0.25 g, 0.5 g, 0.75 g, 1.0 g, 1.25 g, 1.5 g, 1.75 g, 2.0 g). After soaking each funnel for at least 16 hrs with 50 mL of water and draining for a minimum of 3 hrs, the funnels with glass wool were weighed, dried in the oven for 16 hrs at 105°C, and weighed again after cooling. The difference in mass before and after drying gave the water loss, which was equivalent to the water retained by each saturated sample of glass wool.

The mass of water retained was plotted against the mass of glass wool, and linear regression was performed to find the relationship between the two variables. The equation obtained is shown below, and an R^2 of 0.9784 indicates a strong fit.

$$mass_{water\ retained\ by\ glass\ wool} = 7.7799mass_{glass\ wool} + 2.7018 \quad R^2 = 0.9784$$



Water holding capacity of soil

The formula for calculating WHC of soil is as shown below:

$$\begin{aligned} WHC &= \frac{mass_{saturated\ soil} - mass_{dried\ soil}}{mass_{saturated\ soil}} \times 100\% \\ &= \frac{mass_{water\ lost\ from\ soil}}{mass_{saturated\ soil}} \times 100\% \end{aligned}$$

The WHC of soil was measure by getting the weight measurements before drying (saturated soil and saturated glass wool, i.e. $mass_{sat.soil+sat.glass\ wool}$), and after drying (dried soil and dried glass wool, i.e. $mass_{dried\ soil+dried\ glass\ wool}$) and following the formula:

$$\begin{aligned} WHC &= \frac{mass_{saturated\ soil} - mass_{dried\ soil}}{mass_{saturated\ soil}} \times 100\% \\ &= \frac{mass_{water\ lost\ from\ soil}}{mass_{saturated\ soil}} \times 100\% \end{aligned}$$

The difference in these two values gave the mass of the water lost from both the soil and glass wool. However, the regression equation can be used to calculate water retained during saturation (and lost during drying) by the respective amounts of glass wool in each funnel, which can be subtracted to find the water lost from the soil alone.

$$\begin{aligned} WHC &= \frac{mass_{saturated\ soil} - mass_{dried\ soil}}{mass_{saturated\ soil}} \times 100\% \\ &= \frac{mass_{water\ lost\ from\ soil}}{mass_{saturated\ soil}} \times 100\% \end{aligned}$$

The regression equation was used to calculate the mass of water retained during saturation by the respective amounts of glass wool in each funnel. Since this is equal to the mass of water lost by the glass wool during drying, this value was subtracted to find the water lost from the soil alone.

$$\begin{aligned} WHC &= \frac{mass_{water\ lost\ from\ soil}}{mass_{saturated\ soil}} \times 100\% \\ &= \frac{mass_{total\ water\ loss} - mass_{water\ lost\ from\ glass\ wool}}{mass_{saturated\ soil}} \times 100\% \\ &= \frac{mass_{total\ water\ loss} - (7.7799mass_{glass\ wool} + 2.7018)}{mass_{saturated\ soil}} \times 100\% \end{aligned}$$

The final equation was used to calculate WHC for the kauri soil samples.

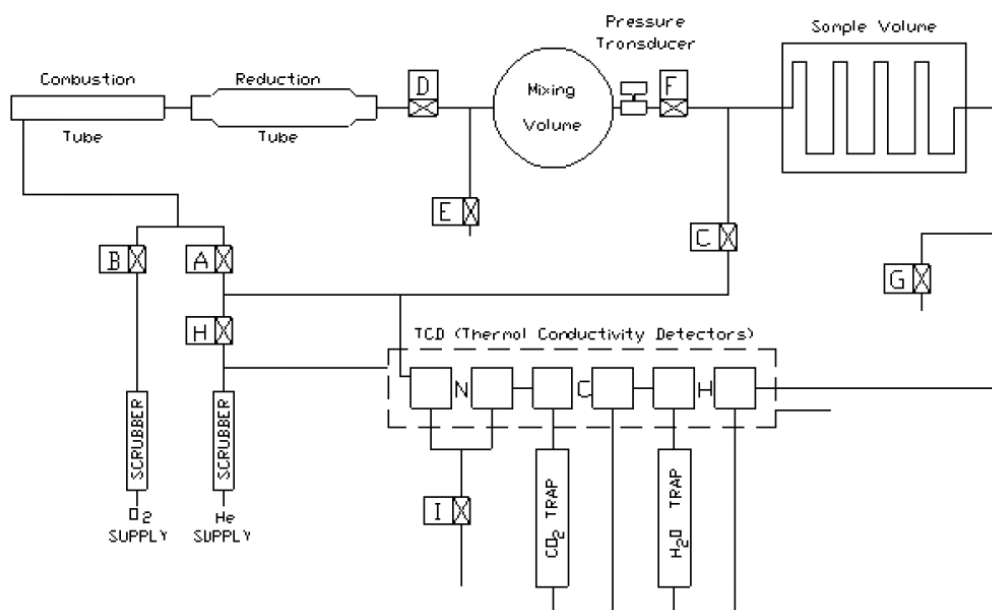
Appendix 2 Standardisation of elemental analyser method

Elemental analyser operation

The Exeter CE-440 Elemental Analyser (Figure A2.1) simultaneously determines content of both organic and inorganic forms of carbon, hydrogen, and nitrogen in the sample (Exeter Analytical Limited, 2003). The samples, once loaded in the carousel, go through a combustion train which comprises of four main sectors: combustion, reduction, homogenisation, and detection (Jimenez & Ladha, 1993). The analytical system requires Helium (He) at 18 psig as a carrier gas to purge the instrument. Helium possesses the dual property of being inert and having a high coefficient of thermal conductivity (Exeter Analytical Limited, 2003).



Figure A2.1: Exeter CE-440 Elemental analyser (Exeter Analytical Limited, 2003).



Schematic flow diagram of Exeter CE-440 Elemental Analyser sample processing (Exeter Analytical Limited, 2003).

In a static system, the weighed samples are combusted in presence of pure oxygen and a series of catalysts in the combustion zone (Exeter Analytical Limited, 2003; Jimenez & Ladha, 1993). A complete oxidation process occurs at oxygen pressure \sim 20-25 psig and at 980°C, resulting in the formation of carbon dioxide (CO₂), water (H₂O) and a mixture of both nitrogen (N₂) and nitrous oxide (NO₂). The unwanted byproducts are eliminated at this stage (Hemming,

2016). Secondly, in the reduction tube, at 700°C, nitrous oxide is reduced to molecular nitrogen and residual oxygen is eliminated in the presence of the fine copper (Cu) wire catalyst (Exeter Analytical Limited, 2003; Hemming, 2016; Jimenez & Ladha, 1993). Thirdly, the mixture of gases (CO₂, H₂O and N₂) is rapidly homogenised into a mixing chamber at constant temperature and pressure (Hemming, 2016). Finally, a precise volume of gas mixture is released into the thermal conductivity detector once a set pressure of 1500 mmHg (about 29 psig) is reached (Hemming, 2016). The differential signal read before and after each trap detects and indicates the concentration of hydrogen, carbon, and nitrogen, in that particular order (Exeter Analytical Limited, 2003). The cycle ends with the release of sample gases out of the system and takes only 5 minutes per sample to process. With the appearance of the calculated results on the connected computer screen, ultimately, the system is ready for the next sample to be analysed (Exeter Analytical Limited, 2003).

Scale operation

Due to the sensitivity of elemental analyser, the weighing of the sample required precision. A microbalance Sartorius CP Model CPA2P was used to weigh finely-ground samples. Each sample was filled in a tared tin capsule (6 × 2.9 mm). The microbalance specifications showed standard deviation at the 2 mg range was $\leq \pm 0.003$ mg, with error of ± 0.005 mg at 2.1 g (Sartorius DMS Inc., 2008). The balance was calibrated with inbuilt auto-calibrating system before every use.

Optimisation and method development

Even though the analyser is accurate, efficient, and rapid, the results achieved by this system are impacted by factors such as the type of the soil sample (with respect to its moisture content), quantity of the sample analysed, C and N content, and the particle size of the samples (Dhaliwal et al., 2011). Thus, optimisation of CHN analyser was necessary. For standardisation of this experiment, three factors were taken into consideration:

- A. oven temperature when drying samples,
- B. mass of the samples to be analysed, and
- C. size of the soil particles.

A pre-sample run was performed each time before evaluating the samples through the analyser. The pre-sample run was carried out with conditioner (~2 mg pure acetanilide), blanks (empty tin capsules), and standard (~2 mg acetanilide) to ensure the functionality of the analyser before sample determination.

Optimisation of temperature

The purpose behind standardisation of the drying temperature was the varying level of moisture content of the samples. For temperature optimisation, different drying temperatures

(60°C, 80°C, 100°C) were applied to the set of 16 samples selected from all locations with varying moisture factor.

Once the samples were dried at each specific temperature, the rest of the procedure of sample preparation was followed as mentioned above. A set mass of ~2 mg of each ground soil sample was weighed and filled in the tin capsules and placed in nickel sleeves in three replicates, for elemental analysis of C, H, and N.

To find the effect of drying temperature on nitrogen content of soil samples, van Erp et al. (2001) dried soil at temperatures from 40-105°C, and found that N content available for detection increased by 2-3 times for every 30-35°C raise in drying temperature. Hence, a drying temperature of 60°C was deemed to be unsuitable. The results from the elemental analyser were used to compare total N content between samples dried at 80°C and 100°C. A two-sided, paired Wilcoxon test determined that there was no significant difference in mean N content ($p = 0.1705$).

Additionally, the water loss (difference in soil weight before and after drying) was compared to assess the effectiveness of drying temperature. A two-sided, paired t-test proved that there was once more no significant difference in mean water loss between samples dried at 80°C and 100°C ($p = 0.2071$). Hence, as both drying temperatures yielded equivalent results, 80°C was selected for economical purpose.

Optimisation of mass

Once the drying temperature was optimised at 80°C, further optimisation of amount of the same sample set in replicates of three were analysed with different weights of soil samples (2 mg, 5 mg, 10 mg, and 20 mg) in separate runs of the elemental analyser. A larger sample weight produces a stronger voltage response in the elemental analyser for the detection of each element, particularly nitrogen. A larger voltage response also means less error and hence a more accurate result (Exeter Analytical Limited, 2003).

From the results, the percentages of C and N in the 10 mg samples were significantly higher than that of 2 mg and 5 mg. Also, nitrogen was not detected in some samples with lesser mass (2 mg and 5 mg) as kauri soil usually is very low in nitrogen content (Schwendenmann & Michalzik, 2019; Steward & Beveridge, 2010). Although the 20 mg samples produced large readings for C and N content, packaging the 20 mg samples in the tin capsules proved to be too difficult due to limitation of the size of the capsule. As a result, the sample mass of 20 mg was eliminated. The optimum mass was determined to be 10 mg.

Optimisation of particle size

The optimisation of particle size was based on the experiment of Dhaliwal et al. (2011) which used soils of three different textures. Each soil texture was separated into fractions of

different particle size (<0.25 mm, <0.5 mm, <1.0 mm, <2.0 mm) by sieving through various mesh sizes prior to elemental analysis. This differentiation of soil particles separated the organic matter (source of carbon and nitrogen) into a finer fraction (<0.25 mm), which showed higher C and N content than other fractions (Dhaliwal et al., 2011). Although it can be useful to separate the soil into fractions, this experiment does not reveal the overall total carbon and total nitrogen content in each soil sample.

Instead of fractioning the kauri soil, all soil <2 mm was pulverised to the particle size <0.25 mm. The grinding of the soil produces finer homogenised particles with better representation of the carbon and nitrogen content of the sample. Additionally, the finer particles produced have a higher surface area, resulting in increased exposure to oxidation in the elemental analyser. Larger particles are less likely to be completely oxidised, leaving some C and N undetected. Furthermore, finer particles ease the process of packing of soil samples into the tin capsules. Therefore, pulverising the soil to <0.25 mm was taken into consideration.

Finally, the variables were optimised as:

- D. drying temperature of 80°C,
- E. sample mass of 10 mg, and
- F. particle size of < 0.25 mm.

Appendix 3 Raw data of soil physical characteristics

Particle size distribution - Asymptomatic Cascade site

Tree code	Gravel	Sand	Fines	D ₆₀	D ₁₀	C _u
	(%)	(%)	(%)	(mm)	(mm)	
UC-A43	0.646	98.451	0.903	1.659	0.365	4.545
UC-A68	1.696	97.727	0.577	1.641	0.370	4.436
UC-A86	0.396	98.022	1.582	1.308	0.297	4.412
UC-A94	1.060	98.583	0.357	1.394	0.300	4.650
UC-B70	0.559	98.937	0.504	1.549	0.361	4.293
UC-B128	5.510	94.124	0.366	1.930	0.524	3.681
UC-B134	2.406	97.030	0.564	1.536	0.377	4.077
UC-C1	0.301	99.143	0.556	1.254	0.285	4.394
UC-C62	0.147	99.002	0.851	1.259	0.260	4.834
UC-C134	1.588	97.907	0.505	1.391	0.315	4.411
UC-C137	0.000	99.377	0.623	0.948	0.224	4.226
UC-C180	0.882	98.809	0.309	1.540	0.430	3.578
UC-D2	3.431	96.351	0.218	1.489	0.363	4.096
UC-D29	2.476	97.302	0.222	1.536	0.376	4.091
UC-D45	0.198	99.356	0.446	1.135	0.274	4.146
UC-D81	0.882	98.609	0.509	1.043	0.281	3.711

Particle size distribution – Symptomatic Cascade site

Tree code	Gravel	Sand	Fines	D ₆₀	D ₁₀	C _u
	(%)	(%)	(%)	(mm)	(mm)	
IC-A26	28.031	70.514	1.455	3.901	0.480	8.129
IC-A107	7.250	92.210	0.540	2.147	0.563	3.814
IC-A143	4.212	94.703	1.085	2.331	0.431	5.413
IC-A172	1.933	96.882	1.185	1.830	0.398	4.598
IC-B84	0.557	98.854	0.589	1.293	0.310	4.166
IC-B126	1.878	97.002	1.120	0.477	0.382	1.247
IC-B191	0.863	98.413	0.724	1.407	0.387	3.634
IC-B314	0.000	99.268	0.732	0.982	0.257	3.820
IC-C2	0.119	99.253	0.628	1.429	0.426	3.355
IC-C39	0.000	99.310	0.690	0.926	0.265	3.496
IC-C93	0.741	98.052	1.207	1.659	0.397	4.176
IC-C141	0.063	99.451	0.486	0.776	0.265	2.928
IC-D1	0.288	98.440	1.272	1.312	0.281	4.677
IC-D63	0.679	98.187	1.134	1.493	0.332	4.501
IC-D126	0.375	99.244	0.381	1.335	0.421	3.174
IC-D154	0.000	99.089	0.911	1.175	0.306	3.838

Particle size distribution – Asymptomatic Huia site

Tree code	Gravel	Sand	Fines	D ₆₀	D ₁₀	C _u
	(%)	(%)	(%)	(mm)	(mm)	
UH-A1	6.371	92.645	0.984	1.768	0.392	4.514
UH-A2	0.746	98.042	1.212	1.446	0.319	4.527
UH-A3	0.985	97.518	1.497	1.242	0.260	4.771
UH-A4	7.355	90.020	2.625	2.427	0.318	7.640
UH-B3	6.177	89.710	4.113	1.443	0.258	5.593
UH-B9	2.208	94.570	3.222	1.798	0.390	4.612
UH-B15	21.944	76.529	1.527	3.629	0.501	7.236
UH-B22	36.627	61.350	2.023	4.481	0.438	10.233
UH-C1	13.095	85.990	0.915	2.536	0.506	5.013
UH-C4	7.373	90.747	1.880	1.730	0.320	5.403
UH-C11	14.497	84.313	1.190	2.641	0.482	5.485
UH-C17	50.179	48.648	1.173	5.832	0.702	8.306
UH-D3	8.235	90.961	0.804	2.953	0.534	5.527
UH-D12	14.412	84.132	1.456	2.446	0.386	6.341
UH-D17	1.693	95.710	2.597	1.660	0.223	7.443
UH-D25	16.331	82.448	1.221	2.963	0.375	7.910

Particle size distribution – Symptomatic Huia site

Tree code	Gravel	Sand	Fines	D ₆₀	D ₁₀	C _u
	(%)	(%)	(%)	(mm)	(mm)	
IH-A6	0.845	98.647	0.508	1.368	0.405	3.374
IH-A39	2.398	97.185	0.417	1.748	0.525	3.330
IH-A90	47.126	50.766	2.108	5.725	0.437	13.108
IH-A123	10.072	88.616	1.312	2.280	0.406	5.611
IH-B41	1.345	98.041	0.614	1.327	0.319	4.155
IH-B53	0.632	98.707	0.661	1.527	0.420	3.632
IH-B86	8.325	89.519	2.156	2.452	0.305	8.032
IH-B96	5.955	90.336	3.709	2.123	0.202	10.515
IH-C19	0.329	98.347	1.324	1.781	0.452	3.940
IH-C75	0.000	98.971	1.029	1.637	0.326	5.024
IH-C114	0.000	98.469	1.531	1.170	0.300	3.897
IH-C131	0.325	98.136	1.539	1.052	0.238	4.419
IH-D26	38.058	60.036	1.906	4.555	0.401	11.347
IH-D89	0.000	99.212	0.788	1.225	0.220	5.576
IH-D107	0.334	99.019	0.647	1.120	0.277	4.038
IH-D142	0.195	99.069	0.736	1.547	0.463	3.341

Particle size distribution – Asymptomatic Piha site

Tree code	Gravel	Sand	Fines	D ₆₀	D ₁₀	C _u
	(%)	(%)	(%)	(mm)	(mm)	
UP-A4	4.422	94.065	1.513	1.167	0.193	6.053
UP-A117	0.215	98.776	1.009	1.044	0.214	4.874
UP-A186	2.598	96.130	1.272	1.204	0.197	6.116
UP-A282	0.574	98.546	0.880	0.890	0.213	4.181
UP-B22	0.000	98.829	1.171	0.869	0.192	4.515
UP-B138	0.299	97.858	1.843	0.669	0.172	3.883
UP-B171	27.780	71.838	0.382	2.803	0.202	13.866
UP-B284	17.439	82.313	0.248	1.686	0.167	10.103
UP-C10	0.544	98.537	0.919	1.129	0.240	4.701
UP-C79	0.238	98.685	1.077	1.044	0.224	4.664
UP-C158	0.410	98.415	1.175	0.953	0.208	4.587
UP-C239	23.456	75.670	0.874	1.950	0.253	7.719
UP-D37	0.527	98.418	1.055	1.313	0.249	5.280
UP-D124	0.011	98.926	1.063	1.272	0.247	5.143
UP-D228	0.000	98.887	1.113	1.122	0.234	4.788
UP-D1044	7.335	91.886	0.779	1.241	0.235	5.277

Particle size distribution – Symptomatic Piha site

Tree code	Gravel	Sand	Fines	D ₆₀	D ₁₀	C _u
	(%)	(%)	(%)	(mm)	(mm)	
IP-A26	1.016	98.216	0.768	0.899	0.221	4.065
IP-A71	0.000	99.282	0.718	0.962	0.242	3.981
IP-A129	0.000	98.977	1.023	0.882	0.195	4.513
IP-A211	1.262	98.247	0.491	1.280	0.307	4.176
IP-B10	4.068	95.278	0.654	1.197	0.262	4.562
IP-B72	0.000	99.012	0.988	0.924	0.220	4.193
IP-B123	0.325	98.798	0.877	0.969	0.236	4.110
IP-B185	0.250	99.060	0.690	1.016	0.278	3.660
IP-C5	0.306	99.188	0.506	1.242	0.304	4.084
IP-C117	1.975	97.538	0.487	1.355	0.309	4.393
IP-C147	0.000	98.863	1.137	1.151	0.222	5.188
IP-C231	0.569	98.618	0.813	1.059	0.235	4.505
IP-D49	0.527	98.173	1.300	0.984	0.219	4.490
IP-D103	1.202	97.900	0.898	1.287	0.250	5.158
IP-D173	0.196	99.269	0.535	1.276	0.260	4.906
IP-D203	0.000	99.195	0.805	0.934	0.222	4.210

Particle size distribution – Asymptomatic Tairua site

Tree code	Gravel	Sand	Fines	D ₆₀	D ₁₀	C _u
	(%)	(%)	(%)	(mm)	(mm)	
WRC AUT tree 2	0.000	98.685	1.315	0.861	0.163	5.287
AUT tree 3	0.000	88.554	11.446	0.491	0.066	7.494
AUT tree 4	0.254	96.443	3.303	0.989	0.166	5.961
AUT tree 5	0.000	93.965	6.035	0.479	0.106	4.514
AUT tree 6	1.414	95.257	3.329	0.833	0.152	5.476
AUT tree 7	0.951	97.528	1.521	1.286	0.220	5.854
AUT tree 8	0.237	96.083	3.680	0.900	0.159	5.664
AUT tree 9	0.323	97.318	2.359	0.959	0.177	5.421
AUT tree 10	0.657	97.760	1.583	1.889	0.236	8.000
AUT tree 11	0.785	97.337	1.878	1.428	0.203	7.026
AUT tree 12	0.000	91.565	8.435	0.536	0.087	6.152
AUT tree 13	0.000	98.746	1.254	1.591	0.210	7.559
AUT tree 14	2.439	95.920	1.641	1.196	0.172	6.938
AUT tree 15	2.439	97.356	0.205	1.154	0.199	5.794

Particle size distribution – Symptomatic Whangapoua site

Tree code	Gravel	Sand	Fines	D ₆₀	D ₁₀	C _u
	(%)	(%)	(%)	(mm)	(mm)	
G1	0.000	98.569	1.431	0.500	0.171	2.928
G2	0.000	99.482	0.518	0.916	0.191	4.789
G3	0.000	99.641	0.359	0.994	0.229	4.338
G4	0.000	98.885	1.115	0.894	0.187	4.776
G5	0.316	98.016	1.668	0.982	0.172	5.728
G6	3.125	96.325	0.550	1.171	0.267	4.391
G7	0.294	99.029	0.677	0.938	0.223	4.212
G8	13.892	85.602	0.506	1.194	0.360	3.315

Bulk density and moisture factor – Asymptomatic Cascade site

Tree code	Crucible weight (g)	Wet soil + crucible weight (g)	Dry soil + crucible weight (g)	Dry soil weight (g)	Water loss (g)	Moisture factor (%)	Bulk density (g/cm ³)
UC-A43	66.395	157.149	113.965	47.570	43.184	90.780	0.381
UC-A68	69.126	133.838	102.242	33.116	31.596	95.410	0.265
UC-A86	67.947	147.865	104.111	36.164	43.754	120.988	0.289
UC-A94	65.941	115.713	83.287	17.346	32.426	186.936	0.139
UC-B70	67.432	121.613	88.584	21.152	33.029	156.151	0.169
UC-B128	72.062	139.965	108.336	36.274	31.629	87.195	0.290
UC-B134	67.703	154.057	118.250	50.547	35.807	70.839	0.404
UC-C1	66.677	138.040	107.585	40.908	30.455	74.448	0.327
UC-C62	66.480	134.074	102.750	36.270	31.324	86.363	0.290
UC-C134	65.938	118.490	90.694	24.756	27.796	112.280	0.198
UC-C137	69.242	113.435	92.337	23.095	21.098	91.353	0.185
UC-C180	66.595	142.240	110.013	43.418	32.227	74.225	0.347
UC-D2	70.501	141.510	109.084	38.583	32.426	84.042	0.309
UC-D29	65.927	104.626	84.371	18.444	20.255	109.819	0.148
UC-D45	68.844	146.383	111.225	42.381	35.158	82.957	0.339
UC-D81	65.228	113.300	89.576	24.348	23.724	97.437	0.195

Bulk density and moisture factor – Symptomatic Cascade site

Tree code	Crucible weight (g)	Wet soil + crucible weight (g)	Dry soil + crucible weight (g)	Dry soil weight (g)	Water loss (g)	Moisture factor (%)	Bulk density (g/cm ³)
IC-A26	67.520	183.250	118.681	51.161	64.569	126.207	0.409
IC-A107	68.974	154.740	111.436	42.462	43.304	101.983	0.340
IC-A143	66.090	146.452	106.994	40.904	39.458	96.465	0.327
IC-A172	65.338	149.345	107.920	42.582	41.425	97.283	0.341
IC-B84	62.889	138.831	107.236	44.347	31.595	71.245	0.355
IC-B126	69.444	161.441	119.986	50.542	41.455	82.021	0.404
IC-B191	69.248	142.377	109.900	40.652	32.477	79.890	0.325
IC-B314	70.415	138.747	111.258	40.843	27.489	67.304	0.327
IC-C2	69.063	140.475	106.701	37.638	33.774	89.734	0.301
IC-C39	63.484	132.838	104.085	40.601	28.753	70.818	0.325
IC-C93	64.567	158.170	113.194	48.627	44.976	92.492	0.389
IC-C141	69.112	139.351	111.038	41.926	28.313	67.531	0.335
IC-D1	69.185	141.805	103.938	34.753	37.867	108.960	0.278
IC-D63	69.276	159.641	117.563	48.287	42.078	87.141	0.386
IC-D126	68.526	146.180	113.640	45.114	32.540	72.128	0.361
IC-D154	66.352	140.165	108.532	42.180	31.633	74.995	0.337

Bulk density and moisture factor – Asymptomatic Huia site

Tree code	Crucible weight (g)	Wet soil + crucible weight (g)	Dry soil + crucible weight (g)	Dry soil weight (g)	Water loss (g)	Moisture factor (%)	Bulk density (g/cm ³)
UH-A1	66.799	146.618	108.935	42.136	37.683	89.432	0.337
UH-A2	72.167	159.144	119.280	47.113	39.864	84.614	0.377
UH-A3	63.755	160.236	113.683	49.928	46.553	93.240	0.399
UH-A4	68.622	178.782	128.975	60.353	49.807	82.526	0.483
UH-B3	71.240	140.631	106.165	34.925	34.466	98.686	0.279
UH-B9	67.268	163.866	118.218	50.950	45.648	89.594	0.408
UH-B15	68.189	219.509	150.619	82.430	68.890	83.574	0.659
UH-B22	67.723	201.281	132.569	64.846	68.712	105.962	0.519
UH-C1	70.268	164.644	119.272	49.004	45.372	92.588	0.392
UH-C4	65.065	149.466	111.054	45.989	38.412	83.524	0.368
UH-C11	69.373	156.676	117.522	48.149	39.154	81.318	0.385
UH-C17	67.008	182.142	121.898	54.890	60.244	109.754	0.439
UH-D3	67.239	150.345	103.583	36.344	46.762	128.665	0.291
UH-D12	66.961	173.051	127.808	60.847	45.243	74.355	0.487
UH-D17	69.271	159.760	113.948	44.677	45.812	102.540	0.357
UH-D25	66.247	167.026	114.878	48.631	52.148	107.232	0.389

Bulk density and moisture factor – Symptomatic Huia site

Tree code	Crucible weight (g)	Wet soil + crucible weight (g)	Dry soil + crucible weight (g)	Dry soil weight (g)	Water loss (g)	Moisture factor (%)	Bulk density (g/cm ³)
IH-A6	66.691	154.331	116.859	50.168	37.472	74.693	0.401
IH-A39	72.461	155.329	118.209	45.748	37.120	81.140	0.366
IH-A90	68.103	194.649	123.791	55.688	70.858	127.241	0.446
IH-A123	68.171	166.360	119.752	51.581	46.608	90.359	0.413
IH-B41	60.020	133.964	103.784	43.764	30.180	68.961	0.350
IH-B53	67.670	143.990	106.610	38.940	37.380	95.994	0.312
IH-B86	68.418	158.631	109.716	41.298	48.915	118.444	0.330
IH-B96	71.447	158.890	111.069	39.622	47.821	120.693	0.317
IH-C19	64.659	146.171	106.332	41.673	39.839	95.599	0.333
IH-C75	67.675	145.632	108.046	40.371	37.586	93.101	0.323
IH-C114	67.189	134.786	101.361	34.172	33.425	97.814	0.273
IH-C131	67.913	141.736	106.276	38.363	35.460	92.433	0.307
IH-D26	68.105	166.468	114.250	46.145	52.218	113.161	0.369
IH-D89	67.829	124.155	95.562	27.733	28.593	103.101	0.222
IH-D107	68.954	127.838	102.864	33.910	24.974	73.648	0.271
IH-D142	69.137	147.389	112.993	43.856	34.396	78.429	0.351

Bulk density and moisture factor – Asymptomatic Piha site

Tree code	Crucible weight (g)	Wet soil + crucible weight (g)	Dry soil + crucible weight (g)	Dry soil weight (g)	Water loss (g)	Moisture factor (%)	Bulk density (g/cm ³)
UP-A4	65.942	158.437	127.779	61.837	30.658	49.579	0.495
UP-A117	68.977	153.582	120.957	51.980	32.625	62.765	0.416
UP-A186	66.089	126.058	104.000	37.911	22.058	58.184	0.303
UP-A282	69.273	137.711	105.775	36.502	31.936	87.491	0.292
UP-B22	69.184	156.843	127.394	58.210	29.449	50.591	0.466
UP-B138	68.524	127.438	101.028	32.504	26.410	81.252	0.260
UP-B171	67.519	183.283	146.923	79.404	36.360	45.791	0.635
UP-B284	69.443	125.636	106.823	37.380	18.813	50.329	0.299
UP-C10	63.481	145.517	115.777	52.296	29.740	56.869	0.418
UP-C79	62.889	164.472	131.688	68.799	32.784	47.652	0.550
UP-C158	69.062	132.113	110.082	41.020	22.031	53.708	0.328
UP-C239	69.245	170.435	137.915	68.670	32.520	47.357	0.549
UP-D37	69.123	147.985	120.487	51.364	27.498	53.536	0.411
UP-D124	67.944	158.803	122.875	54.931	35.928	65.406	0.439
UP-D228	66.350	156.378	121.237	54.887	35.141	64.024	0.439
UP-D1044	70.414	149.793	122.913	52.499	26.880	51.201	0.420

Bulk density and moisture factor – Symptomatic Piha site

Tree code	Crucible weight (g)	Wet soil + crucible weight (g)	Dry soil + crucible weight (g)	Dry soil weight (g)	Water loss (g)	Moisture factor (%)	Bulk density (g/cm ³)
IP-A26	71.273	146.728	116.306	45.033	30.422	67.555	0.360
IP-A71	67.449	152.220	121.486	54.037	30.734	56.876	0.432
IP-A129	69.620	141.469	112.957	43.337	28.512	65.791	0.347
IP-A211	69.033	147.125	113.663	44.630	33.462	74.976	0.357
IP-B10	69.787	150.025	121.282	51.495	28.743	55.817	0.412
IP-B72	69.648	146.496	116.240	46.592	30.256	64.938	0.373
IP-B123	67.486	146.408	114.212	46.726	32.196	68.904	0.374
IP-B185	67.435	142.605	110.582	43.147	32.023	74.218	0.345
IP-C5	71.862	160.790	127.895	56.033	32.895	58.706	0.448
IP-C117	66.825	152.914	120.603	53.778	32.311	60.082	0.430
IP-C147	68.480	138.946	107.950	39.470	30.996	78.531	0.316
IP-C231	66.618	144.981	114.562	47.944	30.419	63.447	0.384
IP-D49	66.396	158.203	129.675	63.279	28.528	45.083	0.506
IP-D103	67.547	151.709	121.160	53.613	30.549	56.981	0.429
IP-D173	68.116	142.540	114.735	46.619	27.805	59.643	0.373
IP-D203	67.556	150.722	120.589	53.033	30.133	56.820	0.424

Bulk density and moisture factor – Asymptomatic Tairua site

Tree code	Crucible weight (g)	Wet soil + crucible weight (g)	Dry soil + crucible weight (g)	Dry soil weight (g)	Water loss (g)	Moisture factor (%)	Bulk density (g/cm ³)
WRC AUT tree 2	66.688	117.464	103.441	36.753	14.023	38.155	0.368
AUT tree 3	70.269	123.483	106.655	36.386	16.828	46.249	0.364
AUT tree 4	69.241	119.225	107.663	38.422	11.562	30.092	0.384
AUT tree 5	60.020	90.832	80.507	20.487	10.325	50.398	0.205
AUT tree 6	71.445	101.703	92.140	20.695	9.563	46.209	0.207
AUT tree 7	67.724	120.850	106.350	38.626	14.500	37.539	0.386
AUT tree 8	67.678	112.968	99.894	32.216	13.074	40.582	0.322
AUT tree 9	68.102	121.823	107.470	39.368	14.353	36.459	0.394
AUT tree 10	67.189	95.667	88.250	21.061	7.417	35.217	0.211
AUT tree 11	67.266	110.963	100.092	32.826	10.871	33.117	0.328
AUT tree 12	67.234	118.244	103.970	36.736	14.274	38.856	0.367
AUT tree 14	65.935	119.404	102.489	36.554	16.915	46.274	0.366
AUT tree 15	70.500	131.881	110.015	39.515	21.866	55.336	0.395

Bulk density and moisture factor – Symptomatic Whangapoua site

Tree code	Crucible weight (g)	Wet soil + crucible weight (g)	Dry soil + crucible weight (g)	Dry soil weight (g)	Water loss (g)	Moisture factor (%)	Bulk density (g/cm ³)
G2	66.686	120.437	100.995	34.309	19.442	56.667	0.343
G3	70.265	122.712	100.831	30.566	21.881	71.586	0.306
G4	69.239	131.819	113.915	44.676	17.904	40.075	0.447
G5	66.796	115.145	97.788	30.992	17.357	56.005	0.310
G6	71.443	126.003	104.555	33.112	21.448	64.774	0.331
G7	67.723	117.801	98.315	30.592	19.486	63.696	0.306

Water holding capacity – Asymptomatic Cascade site

Tree code	Funnel weight (g)	Glass wool weight (g)	Saturated soil + GW weight (g)	Dry soil weight (g)	Total water loss (g)	Water retained by GW (g)	Soil water loss (g)	Saturated soil weight (g)	WHC (%)
UC-A43	52.608	1.108	45.751	13.179	32.572	11.322	21.250	34.429	61.72
UC-A68	51.527	0.985	42.612	12.490	30.122	10.365	19.757	32.247	61.27
UC-A86	62.438	0.953	43.820	10.516	33.304	10.116	23.188	33.704	68.80
UC-A94	58.567	1.789	52.590	8.793	43.797	16.620	27.177	35.970	75.55
UC-B70	58.085	1.235	41.851	9.491	32.360	12.310	20.050	29.541	67.87
UC-B128	52.466	1.217	38.992	13.106	25.886	12.170	13.716	26.822	51.14
UC-B134	57.754	0.781	43.012	14.454	28.558	8.778	19.780	34.234	57.78
UC-C1	52.862	0.739	42.946	14.051	28.895	8.451	20.444	34.495	59.27
UC-C62	55.173	0.772	41.806	13.363	28.443	8.708	19.735	33.098	59.63
UC-C134	58.085	0.872	47.010	12.018	34.992	9.486	25.506	37.524	67.97
UC-C137	58.382	1.035	48.300	12.603	35.697	10.754	24.943	37.546	66.43
UC-C180	58.961	0.908	40.436	14.332	26.104	9.766	16.338	30.670	53.27
UC-D2	55.477	0.991	49.439	13.616	35.823	10.412	25.411	39.027	65.11
UC-D29	52.450	1.077	49.243	11.815	37.428	11.081	26.347	38.162	69.04
UC-D45	52.460	0.835	42.717	13.648	29.069	9.198	19.871	33.519	59.28
UC-D81	127.865	1.141	47.271	12.630	34.641	11.579	23.062	35.692	64.61

Water holding capacity – Symptomatic Cascade site

Tree code	Funnel weight (g)	Glass wool weight (g)	Saturated soil + GW weight (g)	Dry soil weight (g)	Total water loss (g)	Water retained by GW (g)	Soil water loss (g)	Saturated soil weight (g)	WHC (%)
IC-A26	56.442	1.063	35.345	10.989	24.356	10.972	13.384	24.373	54.91
IC-A107	52.018	0.694	38.241	11.869	26.372	8.101	18.271	30.140	60.62
IC-A143	57.586	0.874	38.744	12.919	25.825	9.501	16.324	29.243	55.82
IC-A172	57.581	0.874	37.300	12.311	24.989	9.501	15.488	27.799	55.71
IC-B84	54.247	1.071	47.659	15.747	31.912	11.034	20.878	36.625	57.00
IC-B126	53.883	1.132	40.050	13.239	26.811	11.509	15.302	28.541	53.61
IC-B191	57.181	0.865	42.206	13.784	28.422	9.431	18.991	32.775	57.94
IC-B314	51.985	1.565	46.075	14.869	31.206	14.877	16.329	31.198	52.34
IC-C2	57.899	1.371	44.537	13.230	31.307	13.368	17.939	31.169	57.55
IC-C39	58.031	1.087	42.275	14.660	27.615	11.159	16.456	31.116	52.89
IC-C93	57.655	1.188	39.045	11.958	27.087	11.944	15.143	27.101	55.88
IC-C141	53.983	1.049	42.059	15.469	26.590	10.863	15.727	31.196	50.41
IC-D1	58.615	0.927	41.605	12.060	29.545	9.914	19.631	31.691	61.95
IC-D63	51.395	1.059	43.487	13.199	30.288	10.941	19.347	32.546	59.45
IC-D126	52.330	0.857	42.188	14.479	27.709	9.369	18.340	32.819	55.88
IC-D154	57.739	0.951	41.290	14.452	26.838	10.100	16.738	31.190	53.66

Water holding capacity – Asymptomatic Huia site

Tree code	Funnel weight (g)	Glass wool weight (g)	Saturated soil + GW weight (g)	Dry soil weight (g)	Total water loss (g)	Water retained by GW (g)	Soil water loss (g)	Saturated soil weight (g)	WHC (%)
UH-A1	58.565	1.882	53.666	12.104	41.562	17.344	24.218	36.322	66.68
UH-A2	58.082	1.661	54.849	13.927	40.922	15.624	25.298	39.225	64.49
UH-A3	55.477	1.839	49.971	12.775	37.196	17.009	20.187	32.962	61.24
UH-A4	52.459	1.870	52.749	13.576	39.173	17.250	21.923	35.499	61.76
UH-B3	58.084	1.490	54.387	12.498	41.889	14.294	27.595	40.093	68.83
UH-B9	58.380	1.327	47.927	13.350	34.577	13.026	21.551	34.901	61.75
UH-B15	52.450	1.642	51.255	13.406	37.849	15.476	22.373	35.779	62.53
UH-B22	52.607	1.475	53.396	12.044	41.352	14.177	27.175	39.219	69.29
UH-C1	52.864	1.354	46.960	12.247	34.713	13.236	21.477	33.724	63.68
UH-C4	51.523	1.342	45.391	13.547	31.844	13.142	18.702	32.249	57.99
UH-C11	57.753	1.766	56.212	13.726	42.486	16.441	26.045	39.771	65.49
UH-C17	52.468	1.485	49.842	12.115	37.727	14.255	23.472	35.587	65.96
UH-D3	58.961	1.860	55.708	11.239	44.469	17.172	27.297	38.536	70.83
UH-D12	55.171	1.702	53.525	14.392	39.133	15.943	23.190	37.582	61.70
UH-D17	62.437	1.175	44.795	11.902	32.893	11.843	21.050	32.952	63.88
UH-D25	127.867	1.220	47.316	11.785	35.531	12.193	23.338	35.123	66.45

Water holding capacity – Symptomatic Huia site

Tree code	Funnel weight (g)	Glass wool weight (g)	Saturated soil + GW weight (g)	Dry soil weight (g)	Total water loss (g)	Water retained by GW (g)	Soil water loss (g)	Saturated soil weight (g)	WHC (%)
IH-A6	56.506	1.694	49.307	14.697	34.610	15.881	18.729	33.426	56.03
IH-A39	52.032	1.339	48.849	14.157	34.692	13.119	21.573	35.730	60.38
IH-A90	57.625	1.229	45.243	12.266	32.977	12.263	20.714	32.980	62.81
IH-A123	57.606	1.682	46.665	13.557	33.108	15.788	17.320	30.877	56.09
IH-B41	54.247	1.190	54.513	17.253	37.260	11.960	25.300	42.553	59.46
IH-B53	53.827	1.461	51.890	13.073	38.817	14.068	24.749	37.822	65.44
IH-B86	57.170	1.250	41.707	11.108	30.599	12.427	18.172	29.280	62.06
IH-B96	51.983	1.562	49.485	11.382	38.103	14.854	23.249	34.631	67.13
IH-C19	57.892	1.152	40.711	10.561	30.150	11.664	18.486	29.047	63.64
IH-C75	58.028	1.276	51.758	13.379	38.379	12.629	25.750	39.129	65.81
IH-C114	57.656	1.797	51.569	12.926	38.643	16.682	21.961	34.887	62.95
IH-C131	53.979	1.539	54.240	13.227	41.013	14.675	26.338	39.565	66.57
IH-D26	58.612	1.552	47.513	12.495	35.018	14.776	20.242	32.737	61.83
IH-D89	51.388	1.181	52.805	12.681	40.124	11.890	28.234	40.915	69.01
IH-D107	52.327	1.355	54.495	15.344	39.151	13.244	25.907	41.251	62.80
IH-D142	57.738	1.271	49.775	14.700	35.075	12.590	22.485	37.185	60.47

Water holding capacity – Asymptomatic Piha site

Tree code	Funnel weight (g)	Glass wool weight (g)	Saturated soil + GW weight (g)	Dry soil weight (g)	Total water loss (g)	Water retained by GW (g)	Soil water loss (g)	Saturated soil weight (g)	WHC (%)
UP-A4	58.552	0.828	46.441	16.580	29.861	9.144	20.717	37.297	55.55
UP-A117	58.077	1.409	47.098	15.309	31.789	13.664	18.125	33.434	54.21
UP-A186	55.471	0.918	46.648	15.793	30.855	9.844	21.011	36.804	57.09
UP-A282	52.454	1.486	49.453	13.523	35.930	14.263	21.667	35.190	61.57
UP-B22	58.081	1.211	52.268	13.743	38.525	12.123	26.402	40.145	65.77
UP-B138	58.378	1.151	55.842	14.143	41.699	11.656	30.043	44.186	67.99
UP-B171	52.450	1.216	49.559	16.878	32.681	12.162	20.519	37.397	54.87
UP-B284	52.606	0.736	47.263	16.089	31.174	8.428	22.746	38.835	58.57
UP-C10	52.860	0.864	46.363	15.931	30.432	9.424	21.008	36.939	56.87
UP-C79	51.520	1.241	42.228	16.976	25.252	12.357	12.895	29.871	43.17
UP-C158	57.754	1.037	51.879	16.351	35.528	10.770	24.758	41.109	60.23
UP-C239	52.464	1.152	49.169	19.921	29.248	11.664	17.584	37.505	46.88
UP-D37	58.958	1.036	51.273	16.059	35.214	10.762	24.452	40.511	60.36
UP-D124	55.169	0.914	45.262	15.059	30.203	9.813	20.390	35.449	57.52
UP-D228	62.434	1.270	46.026	15.509	30.517	12.582	17.935	33.444	53.63
UP-D1044	127.858	1.016	47.370	16.570	30.800	10.606	20.194	36.764	54.93

Water holding capacity – Symptomatic Piha site

Tree code	Funnel weight (g)	Glass wool weight (g)	Saturated soil + GW weight (g)	Dry soil weight (g)	Total water loss (g)	Water retained by GW (g)	Soil water loss (g)	Saturated soil weight (g)	WHC (%)
IP-A26	57.735	1.323	54.001	14.926	39.075	12.995	26.080	41.006	63.60
IP-A71	52.034	1.049	51.115	15.689	35.426	10.863	24.563	40.252	61.02
IP-A129	57.623	1.085	53.162	14.488	38.674	11.143	27.531	42.019	65.52
IP-A211	57.607	1.296	46.941	14.249	32.692	12.785	19.907	34.156	58.28
IP-B10	58.614	1.263	49.097	15.921	33.176	12.528	20.648	36.569	56.46
IP-B72	53.829	1.183	49.553	14.911	34.642	11.905	22.737	37.648	60.39
IP-B123	58.029	1.096	48.434	14.783	33.651	11.229	22.422	37.205	60.27
IP-B185	51.983	1.117	49.317	14.478	34.839	11.392	23.447	37.925	61.82
IP-C5	57.896	1.197	47.712	15.570	32.142	12.014	20.128	35.698	56.38
IP-C117	52.326	1.285	44.813	15.342	29.471	12.699	16.772	32.114	52.23
IP-C147	54.245	0.966	48.226	14.656	33.570	10.217	23.353	38.009	61.44
IP-C231	53.980	1.175	52.302	15.153	37.149	11.843	25.306	40.459	62.55
IP-D49	56.506	1.084	48.948	17.131	31.817	11.135	20.682	37.813	54.70
IP-D103	51.391	0.985	46.730	15.777	30.953	10.365	20.588	36.365	56.61
IP-D173	57.178	1.204	47.842	15.871	31.971	12.069	19.902	35.773	55.63
IP-D203	57.651	1.093	49.231	16.078	33.153	11.205	21.948	38.026	57.72

Water holding capacity – Asymptomatic Tairua site

Tree code	Funnel weight (g)	Glass wool weight (g)	Saturated soil + GW weight (g)	Dry soil weight (g)	Total water loss (g)	Water retained by GW (g)	Soil water loss (g)	Saturated soil weight (g)	WHC (%)
WRC AUT tree 1	57.625	0.648	45.420	14.245	31.175	7.743	23.432	37.677	68.64
WRC AUT tree 2	51.522	0.790	54.040	18.344	35.696	8.848	26.848	45.192	66.05
AUT tree 3	52.461	0.562	45.615	17.244	28.371	7.074	21.297	38.541	62.20
AUT tree 4	58.089	0.788	47.288	19.427	27.861	8.832	19.029	38.456	58.92
AUT tree 5	58.966	0.851	52.566	16.815	35.751	9.322	26.429	43.244	68.01
AUT tree 6	52.869	0.790	52.923	17.065	35.858	8.848	27.010	44.075	67.76
AUT tree 7	57.901	0.896	49.154	18.362	30.792	9.673	21.119	39.481	62.64
AUT tree 8	58.571	0.830	53.342	17.992	35.350	9.159	26.191	44.183	66.27
AUT tree 9	52.331	0.886	53.683	18.601	35.082	9.595	25.487	44.088	65.35
AUT tree 10	56.500	0.904	52.890	18.593	34.297	9.735	24.562	43.155	64.85
AUT tree 11	54.246	1.036	52.971	18.771	34.200	10.762	23.438	42.209	64.56
AUT tree 12	52.453	0.927	47.779	18.255	29.524	9.914	19.610	37.865	61.79
AUT tree 13	51.982	0.780	44.786	16.757	28.029	8.770	19.259	36.016	62.58
AUT tree 14	55.474	1.026	50.060	17.192	32.868	10.684	22.184	39.376	65.66
AUT tree 15	57.758	0.919	48.410	16.249	32.161	9.852	22.309	38.558	66.43

Water holding capacity – Symptomatic Whangapoua site

Tree code	Funnel weight (g)	Glass wool weight (g)	Saturated soil + GW weight (g)	Dry soil weight (g)	Total water loss (g)	Water retained by GW (g)	Soil water loss (g)	Saturated soil weight (g)	WHC (%)
G1	57.756	0.970	57.492	14.111	13.141	10.248	2.893	47.244	75.46
G2	52.451	0.910	50.822	16.248	34.574	9.782	24.792	41.040	68.03
G3	51.523	0.815	48.432	14.813	33.619	9.042	24.577	39.390	69.41
G4	58.963	0.910	45.825	18.095	17.185	9.782	7.403	36.043	60.51
G5	52.462	0.838	50.422	16.271	34.151	9.221	24.930	41.201	67.73
G6	52.864	0.825	50.281	15.518	34.763	9.120	25.643	41.161	69.14
G7	58.086	0.763	50.278	15.747	14.984	8.638	6.346	41.640	68.68
G8	58.568	0.759	45.365	13.303	32.062	8.607	23.455	36.758	70.68

Appendix 4 Raw data of soil chemical characteristics

Soil pH – Asymptomatic Cascade site

Tree code	Soil weight (g)	pH reading 1	Soil weight (g)	pH reading 2	Soil weight (g)	pH reading 3	Mean pH	± SD
UC-A43	4.000	5.00	4.002	4.97	4.001	5.01	4.99	0.02
UC-A68	4.007	4.70	4.000	4.87	4.001	5.05	4.87	0.18
UC-A86	4.003	4.34	4.002	4.46	4.000	4.37	4.39	0.06
UC-A94	4.006	4.25	4.003	4.15	4.000	4.15	4.18	0.06
UC-B70	4.005	4.11	4.000	4.06	4.005	4.09	4.09	0.03
UC-B128	4.002	5.63	4.000	5.68	4.000	5.84	5.72	0.11
UC-B134	4.005	6.18	4.006	6.23	4.002	6.25	6.22	0.04
UC-C1	4.004	5.40	4.003	5.11	4.001	5.18	5.23	0.15
UC-C62	4.002	4.66	4.003	4.54	4.000	4.43	4.54	0.12
UC-C134	4.004	4.26	4.006	4.28	4.005	4.23	4.26	0.03
UC-C137	4.000	4.00	4.001	4.13	4.002	4.09	4.07	0.07
UC-C180	4.002	5.42	4.006	5.58	4.000	5.44	5.48	0.09
UC-D2	4.001	5.37	4.005	5.45	4.003	5.45	5.42	0.05
UC-D29	4.001	4.93	4.002	4.98	4.001	4.93	4.95	0.03
UC-D45	4.000	5.21	4.001	5.23	4.004	5.24	5.23	0.02
UC-D81	4.002	4.63	4.004	4.58	4.003	4.57	4.59	0.03

Soil pH – Symptomatic Cascade site

Tree code	Soil weight (g)	pH reading 1	Soil weight (g)	pH reading 2	Soil weight (g)	pH reading 3	Mean pH	± SD
IC-A26	4.001	6.10	4.003	6.20	4.002	6.10	6.13	0.06
IC-A107	4.004	5.51	4.004	5.84	4.003	4.99	5.45	0.43
IC-A143	4.008	5.07	3.999	5.83	4.007	5.09	5.33	0.43
IC-A172	4.005	5.59	4.000	5.43	4.002	5.17	5.40	0.21
IC-B84	4.009	4.73	4.001	5.69	4.008	5.61	5.34	0.53
IC-B126	3.999	6.01	4.006	6.18	4.009	6.20	6.13	0.10
IC-B191	4.006	5.70	4.005	5.32	4.008	5.69	5.57	0.22
IC-B314	4.002	5.46	4.001	5.51	4.001	5.71	5.56	0.13
IC-C2	4.002	5.75	4.001	5.84	4.001	5.73	5.77	0.06
IC-C39	4.008	5.71	4.006	5.87	4.002	5.78	5.79	0.08
IC-C93	4.000	5.94	4.007	5.99	4.003	6.05	5.99	0.06
IC-C141	4.009	5.97	4.008	5.95	4.005	6.01	5.98	0.03
IC-D1	4.006	5.86	4.005	5.80	4.004	5.82	5.83	0.03
IC-D63	4.006	5.56	4.001	5.45	4.000	5.66	5.56	0.11
IC-D126	4.007	5.93	4.000	5.83	4.002	5.90	5.89	0.05
IC-D154	4.001	5.87	4.002	5.71	4.000	5.63	5.74	0.12

Soil pH – Asymptomatic Huia site

Tree code	Soil weight (g)	pH reading 1	Soil weight (g)	pH reading 2	Soil weight (g)	pH reading 3	Mean pH	± SD
UH-A1	4.005	6.27	4.001	6.43	4.001	6.72	6.47	0.23
UH-A2	4.002	5.54	4.002	5.56	4.003	5.56	5.55	0.01
UH-A3	4.001	6.15	4.003	6.29	4.004	6.29	6.24	0.08
UH-A4	4.003	6.27	4.003	6.32	4.004	6.31	6.30	0.03
UH-B3	4.005	4.93	4.004	4.81	4.002	4.86	4.87	0.06
UH-B9	4.001	5.35	4.004	5.29	4.000	5.47	5.37	0.09
UH-B15	4.004	6.07	4.003	6.17	4.003	6.31	6.18	0.12
UH-B22	4.003	6.23	4.001	6.22	4.000	6.17	6.21	0.03
UH-C1	4.003	5.99	4.001	5.97	4.000	6.06	6.01	0.05
UH-C4	4.002	5.94	4.001	5.93	4.002	5.84	5.90	0.06
UH-C11	4.006	6.32	4.000	6.39	4.006	6.30	6.34	0.05
UH-C17	4.003	5.41	4.000	5.39	4.005	5.30	5.37	0.06
UH-D3	4.003	4.86	4.002	4.93	4.002	4.88	4.89	0.04
UH-D12	4.003	4.85	4.003	4.96	4.002	4.99	4.93	0.07
UH-D17	4.004	4.85	4.003	4.76	4.005	4.74	4.78	0.06
UH-D25	4.005	4.80	4.000	4.89	4.003	4.59	4.76	0.15

Soil pH – Symptomatic Huia site

Tree code	Soil weight (g)	pH reading 1	Soil weight (g)	pH reading 2	Soil weight (g)	pH reading 3	Mean pH	± SD
IH-A6	4.000	5.65	4.003	5.47	4.001	5.51	5.54	0.09
IH-A39	4.007	5.58	4.004	5.45	4.005	5.58	5.54	0.08
IH-A90	4.003	5.30	4.005	5.38	4.004	5.27	5.32	0.06
IH-A123	4.005	4.97	4.006	5.03	4.002	5.03	5.01	0.03
IH-B41	4.003	4.53	4.000	4.68	4.001	4.75	4.65	0.11
IH-B53	4.003	4.57	4.004	4.51	4.007	4.51	4.53	0.03
IH-B86	4.001	4.85	4.004	4.91	4.006	4.99	4.92	0.07
IH-B96	4.005	4.87	4.003	4.85	4.005	4.92	4.88	0.04
IH-C19	4.001	5.32	4.003	5.24	4.002	5.21	5.26	0.06
IH-C75	4.004	4.82	4.002	5.02	4.000	4.95	4.93	0.10
IH-C114	4.002	4.68	4.005	4.66	4.000	4.68	4.67	0.01
IH-C131	4.003	5.21	4.007	5.01	4.002	5.12	5.11	0.10
IH-D26	4.004	5.38	4.001	5.54	4.004	5.40	5.44	0.09
IH-D89	4.002	4.34	4.005	4.22	4.002	4.26	4.27	0.06
IH-D107	4.000	4.80	4.004	4.81	4.001	4.83	4.81	0.02
IH-D142	4.004	5.20	4.002	5.19	4.001	5.24	5.21	0.03

Soil pH – Asymptomatic Piha site

Tree code	Soil weight (g)	pH reading 1	Soil weight (g)	pH reading 2	Soil weight (g)	pH reading 3	Mean pH	± SD
UP-A4	4.005	5.11	4.001	5.23	4.005	5.29	5.21	0.09
UP-A117	4.005	4.95	4.001	4.94	4.005	5.04	4.98	0.06
UP-A186	4.005	5.21	4.001	5.24	4.005	5.31	5.25	0.05
UP-A282	4.005	4.38	4.001	4.31	4.005	4.41	4.37	0.05
UP-B22	4.005	5.02	4.001	4.97	4.005	5.07	5.02	0.05
UP-B138	4.005	4.59	4.001	4.73	4.005	4.67	4.66	0.07
UP-B171	4.005	5.45	4.001	5.49	4.005	5.69	5.54	0.13
UP-B284	4.005	5.19	4.001	5.27	4.005	5.21	5.22	0.04
UP-C10	4.005	5.52	4.001	5.54	4.005	5.55	5.54	0.02
UP-C79	4.005	5.31	4.001	5.26	4.005	5.29	5.29	0.03
UP-C158	4.005	4.98	4.001	4.94	4.005	4.91	4.94	0.04
UP-C239	4.005	5.32	4.001	5.37	4.005	5.35	5.35	0.03
UP-D37	4.005	5.40	4.001	5.45	4.005	5.46	5.44	0.03
UP-D124	4.005	5.69	4.001	5.76	4.005	5.77	5.74	0.04
UP-D228	4.005	5.35	4.001	5.31	4.005	5.25	5.30	0.05
UP-D1044	4.005	5.22	4.001	5.37	4.005	5.30	5.30	0.08

Soil pH – Symptomatic Piha site

Tree code	Soil weight (g)	pH reading 1	Soil weight (g)	pH reading 2	Soil weight (g)	pH reading 3	Mean pH	± SD
IP-A26	4.001	5.25	4.001	5.33	4.003	5.33	5.30	0.05
IP-A71	4.005	5.33	4.003	5.47	4.001	5.43	5.41	0.07
IP-A129	4.001	5.19	4.001	5.12	4.001	5.15	5.15	0.04
IP-A211	4.001	5.15	4.005	5.06	4.005	5.22	5.14	0.08
IP-B10	4.001	5.29	4.003	5.19	4.004	5.28	5.25	0.06
IP-B72	4.001	5.55	4.006	5.51	4.005	5.51	5.52	0.02
IP-B123	4.002	5.51	4.003	5.39	4.004	5.48	5.46	0.06
IP-B185	4.005	5.49	4.001	5.46	4.003	5.41	5.45	0.04
IP-C5	4.001	5.43	4.001	5.67	4.002	5.69	5.60	0.14
IP-C117	4.004	5.53	4.006	5.55	4.000	5.54	5.54	0.01
IP-C147	4.004	5.22	4.001	5.22	4.006	5.25	5.23	0.02
IP-C231	4.003	5.13	4.001	5.15	4.005	5.13	5.14	0.01
IP-D49	4.006	4.92	4.000	4.90	4.003	4.94	4.92	0.02
IP-D103	4.001	4.79	4.001	4.91	4.003	4.93	4.88	0.08
IP-D173	4.001	5.87	4.000	5.91	4.001	5.89	5.89	0.02
IP-D203	4.003	5.15	4.005	5.14	4.000	5.14	5.14	0.01

Soil pH – Asymptomatic Tairua site

Tree code	Soil weight (g)	pH reading 1	Soil weight (g)	pH reading 2	Soil weight (g)	pH reading 3	Mean pH	± SD
WRC AUT tree 1	4.000	4.44	4.005	4.39	4.001	4.36	4.40	0.04
WRC AUT tree 2	4.001	4.59	4.000	4.45	4.003	4.52	4.52	0.07
AUT tree 3	4.005	4.80	4.002	4.92	4.000	4.70	4.81	0.11
AUT tree 4	4.006	4.44	4.000	4.58	4.000	4.51	4.51	0.07
AUT tree 5	4.004	4.49	4.000	4.54	4.001	4.62	4.55	0.07
AUT tree 6	4.006	4.91	4.005	4.99	4.004	4.95	4.95	0.04
AUT tree 7	4.000	4.61	4.004	4.64	4.003	4.56	4.60	0.04
AUT tree 8	4.002	4.60	4.002	4.60	4.004	4.63	4.61	0.02
AUT tree 9	4.001	4.79	4.003	4.71	4.004	4.76	4.75	0.04
AUT tree 10	4.007	5.08	4.003	5.00	4.000	5.17	5.08	0.09
AUT tree 11	4.002	4.88	4.000	4.64	4.006	4.55	4.69	0.17
AUT tree 12	4.005	4.54	4.003	4.55	4.005	4.54	4.54	0.01
AUT tree 13	4.004	4.79	4.007	4.71	4.003	4.68	4.73	0.06
AUT tree 14	4.005	4.84	4.000	4.73	4.005	4.72	4.76	0.07
AUT tree 15	4.006	4.93	4.003	4.87	4.002	4.88	4.89	0.03

Soil pH – Symptomatic Whangapoua site

Tree code	Soil weight (g)	pH reading 1	Soil weight (g)	pH reading 2	Soil weight (g)	pH reading 3	Mean pH	± SD
G1	4.000	4.73	4.001	4.69	4.001	4.70	4.71	0.02
G2	4.002	5.00	4.005	4.91	4.001	4.98	4.96	0.05
G3	4.001	4.96	4.002	5.00	4.006	5.00	4.99	0.02
G4	4.007	5.26	4.007	5.29	4.004	5.32	5.29	0.03
G5	4.006	4.65	4.005	4.62	4.002	4.63	4.63	0.02
G6	4.000	4.44	4.005	4.41	4.002	4.42	4.42	0.02
G7	4.000	4.20	4.005	4.14	4.001	4.14	4.16	0.03
G8	4.002	4.24	4.000	4.22	4.002	4.24	4.23	0.01

Electrical conductivity – Asymptomatic Cascade site

Tree code	EC	Temperature	EC	Temperature	EC	Temperature	Mean EC	± SD
	reading		reading		reading			
	1		2		3			
	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(µS/cm)
UC-A43	65.8	24.6	63.0	24.6	64.2	24.6	64.3	1.4
UC-A68	85.1	24.6	78.0	24.6	70.7	24.6	77.9	7.2
UC-A86	78.5	24.7	76.0	24.7	86.6	24.6	80.4	5.5
UC-A94	113.6	24.6	120.6	24.6	112.2	24.6	115.5	4.5
UC-B70	150.2	25.0	137.8	25.0	136.5	25.0	141.5	7.6
UC-B128	60.7	25.2	67.3	25.2	69.3	25.2	65.8	4.5
UC-B134	59.6	25.3	58.7	25.4	59.6	25.2	59.3	0.5
UC-C1	78.5	25.1	79.3	25.0	76.0	25.1	77.9	1.7
UC-C62	90.4	25.1	88.3	25.1	95.3	25.1	91.3	3.6
UC-C134	98.4	25.1	106.4	25.1	107.1	25.2	104.0	4.8
UC-C137	173.9	25.3	165.0	25.7	166.2	25.1	168.4	4.8
UC-C180	52.1	25.3	51.6	25.5	55.6	25.4	53.1	2.2
UC-D2	98.3	24.6	94.5	24.6	95.4	24.6	96.1	2.0
UC-D29	104.2	24.6	104.8	24.6	107.7	24.6	105.6	1.9
UC-D45	94.3	24.6	94.9	24.6	94.9	24.6	94.7	0.3
UC-D81	101.2	24.6	98.5	24.6	97.3	24.6	99.0	2.0

Electrical conductivity – Symptomatic Cascade site

Tree code	EC	Temperature	EC	Temperature	EC	Temperature	Mean EC	± SD
	reading		reading		reading			
	1		2		3			
	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(µS/cm)
IC-A26	157.3	22.7	150.3	22.3	144.8	22.1	150.8	6.3
IC-A107	151.4	22.1	143.0	22.2	152.0	22.2	148.8	5.0
IC-A143	147.5	22.2	145.9	22.2	152.0	22.2	148.5	3.2
IC-A172	166.5	22.4	171.0	22.3	162.6	22.1	166.7	4.2
IC-B84	164.0	22.1	162.0	22.2	166.2	22.2	164.1	2.1
IC-B126	139.2	22.3	142.5	22.1	144.3	22.3	142.0	2.6
IC-B191	153.6	22.3	164.3	22.3	152.7	22.3	156.9	6.5
IC-B314	165.7	22.3	169.9	22.3	157.5	22.3	164.4	6.3
IC-C2	148.8	22.1	164.5	22.2	150.6	22.2	154.6	8.6
IC-C39	163.5	22.1	162.4	22.2	165.4	22.3	163.8	1.5
IC-C93	166.7	21.5	173.0	21.5	172.7	21.5	170.8	3.6
IC-C141	140.8	21.6	139.0	21.6	137.4	21.6	139.1	1.7
IC-D1	152.9	21.5	158.2	21.5	157.5	21.5	156.2	2.9
IC-D63	161.1	21.7	163.6	21.7	161.6	21.5	162.1	1.3
IC-D126	153.5	21.7	153.8	21.7	156.8	21.7	154.7	1.8
IC-D154	158.0	21.8	159.9	21.9	160.4	22.0	159.4	1.3

Electrical conductivity – Asymptomatic Huia site

Tree code	EC	Temperature	EC	Temperature	EC	Temperature	Mean EC	± SD
	reading		reading		reading			
	1		2		3			
	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(µS/cm)
UH-A1	128.2	21.9	136.9	21.9	143.7	21.9	136.3	7.8
UH-A2	88.7	23.1	75.0	23.1	85.7	23.1	83.1	7.2
UH-A3	91.6	23.1	82.2	23.1	86.8	23.1	86.9	4.7
UH-A4	47.3	23.1	47.8	23.1	50.0	23.1	48.4	1.4
UH-B3	108.5	23.1	112.2	23.1	116.3	23.1	112.3	3.9
UH-B9	72.4	23.1	71.2	23.0	71.7	23.1	71.8	0.6
UH-B15	47.2	23.1	47.9	23.1	50.5	23.0	48.5	1.7
UH-B22	57.4	23.0	50.4	23.0	58.9	23.0	55.6	4.5
UH-C1	80.0	23.9	68.1	23.9	68.2	23.9	72.1	6.8
UH-C4	90.5	23.9	94.4	23.9	100.0	24.0	95.0	4.8
UH-C11	70.8	24.2	64.2	24.1	66.9	24.1	67.3	3.3
UH-C17	94.2	24.2	83.8	24.2	98.5	24.2	92.2	7.6
UH-D3	112.8	25.2	101.6	25.0	108.8	24.9	107.7	5.7
UH-D12	102.7	25.1	93.5	25.1	86.3	25.2	94.2	8.2
UH-D17	84.7	24.9	91.6	25.1	93.8	25.1	90.0	4.7
UH-D25	116.4	25.3	123.3	25.0	115.0	25.1	118.2	4.4

Electrical conductivity – Symptomatic Huia site

Tree code	EC	Temperature	EC	Temperature	EC	Temperature	Mean EC	± SD
	reading		reading		reading			
	1		2		3			
	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(µS/cm)
IH-A6	73.1	23.0	65.4	22.9	66.9	22.8	68.5	4.1
IH-A39	75.5	22.9	70.1	22.9	67.9	22.8	71.2	3.9
IH-A90	57.6	22.8	60.6	22.9	58.0	22.8	58.7	1.6
IH-A123	59.1	22.9	63.2	22.9	56.6	22.9	59.6	3.3
IH-B41	99.4	23.0	96.3	22.9	93.0	22.9	96.2	3.2
IH-B53	83.1	23.0	92.8	23.0	91.4	22.9	89.1	5.2
IH-B86	74.3	22.9	73.2	22.9	70.0	22.9	72.5	2.2
IH-B96	75.1	23.0	73.1	22.9	64.6	22.9	70.9	5.6
IH-C19	61.9	23.5	60.1	23.5	57.5	23.5	59.8	2.2
IH-C75	95.2	23.5	83.6	23.5	85.6	23.5	88.1	6.2
IH-C114	90.0	23.5	95.5	23.5	91.0	23.5	92.2	2.9
IH-C131	88.9	23.5	88.6	23.5	87.2	23.5	88.2	0.9
IH-D26	57.5	23.5	55.3	23.5	56.7	23.5	56.5	1.1
IH-D89	221.0	23.2	224.0	23.4	216.2	23.5	220.4	3.9
IH-D107	86.1	23.5	82.0	23.5	74.0	23.4	80.7	6.2
IH-D142	61.1	23.4	61.2	23.5	62.3	23.5	61.5	0.7

Electrical conductivity – Asymptomatic Piha site

Tree code	EC	Temperature	EC	Temperature	EC	Temperature	Mean EC	± SD
	reading		reading		reading			
	1		2		3			
	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(µS/cm)
UP-A4	82.9	23.1	76.1	23.2	79.3	23.3	79.4	3.4
UP-A117	162.1	21.8	151.5	21.8	148.5	21.9	154.0	7.1
UP-A186	93.2	23.1	99.9	23.1	91.7	23.1	94.9	4.4
UP-A282	208.1	23.2	212.4	23.1	205.7	23.1	208.7	3.4
UP-B22	93.5	23.1	100.3	23.1	95.7	23.0	96.5	3.5
UP-B138	116.1	23.0	121.6	23.0	130.1	23.1	122.6	7.1
UP-B171	89.8	23.1	84.8	23.1	89.2	23.1	87.9	2.7
UP-B284	105.0	23.0	119.2	23.1	117.3	23.1	113.8	7.7
UP-C10	104.2	23.8	91.3	23.8	94.5	23.8	96.7	6.7
UP-C79	63.8	23.8	63.3	23.8	54.0	23.8	60.4	5.5
UP-C158	106.4	23.8	119.7	23.8	106.1	23.8	110.7	7.8
UP-C239	111.2	23.8	109.5	23.8	119.1	23.8	113.3	5.1
UP-D37	124.7	23.7	135.7	23.7	117.8	23.7	126.1	9.0
UP-D124	101.9	23.8	91.7	23.8	103.4	23.8	99.0	6.4
UP-D228	116.0	21.8	106.1	21.9	115.2	21.8	112.4	5.5
UP-D1044	96.5	21.5	90.7	21.6	95.1	21.6	94.1	3.0

Electrical conductivity – Symptomatic Piha site

Tree code	EC	Temperature	EC	Temperature	EC	Temperature	Mean EC	± SD
	reading		reading		reading			
	1		2		3			
	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(µS/cm)
IP-A26	125.9	21.7	126.7	21.7	129.0	21.9	127.2	1.6
IP-A71	79.5	21.9	91.9	21.9	94.8	21.9	88.7	8.1
IP-A129	162.6	21.7	151.5	21.7	153.2	21.7	155.8	6.0
IP-A211	101.1	22.2	112.7	22.2	105.0	22.1	106.3	5.9
IP-B10	104.1	22.0	105.8	22.0	101.7	22.0	103.9	2.1
IP-B72	89.4	22.0	93.7	22.1	101.6	22.0	94.9	6.2
IP-B123	102.1	22.1	112.0	22.0	102.0	22.0	105.4	5.7
IP-B185	88.8	21.8	81.1	21.8	80.9	21.9	83.6	4.5
IP-C5	97.7	21.6	105.5	21.6	101.5	21.6	101.6	3.9
IP-C117	75.0	21.5	78.3	21.6	80.3	21.6	77.9	2.7
IP-C147	157.8	21.5	142.0	221.5	152.5	21.5	150.8	8.0
IP-C231	142.3	21.3	147.4	21.4	148.8	21.5	146.2	3.4
IP-D49	102.0	21.2	119.2	21.3	107.3	21.4	109.5	8.8
IP-D103	127.3	21.6	124.0	21.6	129.0	21.6	126.8	2.5
IP-D173	94.3	21.5	106.4	21.3	106.7	21.3	102.5	7.1
IP-D203	91.1	21.7	97.4	21.7	88.1	21.8	92.2	4.7

Electrical conductivity – Asymptomatic Tairua site

Tree code	EC	Temperature	EC	Temperature	EC	Temperature	Mean EC	± SD
	reading		reading		reading			
	1		2		3			
	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(µS/cm)
WRC AUT tree 1	227.0	25.1	218.4	25.2	221.0	25.2	222.1	4.4
WRC AUT tree 2	121.6	25.0	138.8	24.7	128.4	25.0	129.6	8.7
AUT tree 3	74.0	24.7	67.1	24.6	65.2	24.4	68.8	4.6
AUT tree 4	72.3	24.6	67.2	24.6	77.9	24.6	72.5	5.4
AUT tree 5	74.5	25.3	79.7	25.3	67.4	25.1	73.9	6.2
AUT tree 6	115.0	25.2	122.0	25.4	114.7	25.3	117.2	4.1
AUT tree 7	81.1	25.5	71.8	25.7	85.1	25.5	79.3	6.8
AUT tree 8	169.3	25.6	164.9	25.7	156.8	25.7	163.7	6.3
AUT tree 9	71.3	25.3	83.4	25.3	67.0	25.5	73.9	8.5
AUT tree 10	44.6	25.8	58.3	25.7	47.8	25.6	50.2	7.2
AUT tree 11	39.3	25.7	47.8	25.5	55.6	25.5	47.6	8.2
AUT tree 12	42.7	25.7	44.0	25.7	47.6	25.6	44.8	2.5
AUT tree 13	70.5	25.9	73.3	25.3	72.9	25.3	72.2	1.5
AUT tree 14	74.4	25.0	74.3	25.0	77.0	24.7	75.2	1.5
AUT tree 15	65.3	23.8	53.3	24.5	61.7	23.7	60.1	6.2

Electrical conductivity – Symptomatic Whangapoua site

Tree code	EC	Temperature	EC	Temperature	EC	Temperature	Mean EC	± SD
	reading		reading		reading			
	1		2		3			
	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(°C)	(µS/cm)	(µS/cm)
G1	147.5	23.1	150.4	23.2	154.0	23.3	150.6	3.3
G2	89.8	23.5	95.1	23.8	96.9	23.8	93.9	3.7
G3	116.0	23.8	106.8	24.0	115.8	24.2	112.9	5.3
G4	76.3	24.2	79.9	24.3	80.2	24.3	78.8	2.2
G5	124.8	24.3	131.0	24.3	135.5	24.6	130.4	5.4
G6	155.4	23.5	151.6	23.5	146.4	23.6	151.1	4.5
G7	122.5	23.8	129.8	23.8	130.0	23.8	127.4	4.3
G8	127.8	23.6	129.2	23.5	131.1	23.8	129.4	1.7

Elemental analyser – Asymptomatic Cascade site

Tree code	TC	Mean	± SD	TN	Mean	± SD	C:N	TH	Mean	± SD
sample	reading	TC		reading	TN		Ratio	reading	TH	
triplicate	(%)	(%)	(%)	(%)	(%)	(%)		(%)	(%)	(%)
UC-A43-1	15.63	15.42	0.22	0.70	0.70	0.01	22.18	2.91	2.96	0.07
UC-A43-2	15.46			0.68				3.04		
UC-A43-3	15.19			0.70				2.92		
UC-A68-1	11.36	11.51	0.14	0.55	0.53	0.02	21.70	2.59	2.57	0.04
UC-A68-2	11.56			0.52				2.60		
UC-A68-3	11.62			0.52				2.53		
UC-A86-1	22.04	22.21	0.15	0.78	0.78	0.01	28.33	3.55	3.52	0.04
UC-A86-2	22.33			0.80				3.53		
UC-A68-3	22.24			0.78				3.47		
UC-A94-1	0.53	39.74	0.14	-0.12	1.20	0.76	33.02	-0.20	4.48	2.74
UC-A94-2	39.64			1.22				4.94		
UC-A94-3	39.84			1.18				4.03		
UC-B70-1	34.99	35.08	0.12	0.97	0.98	0.66	35.85	4.42	4.42	2.64
UC-B70-2	0.39			-0.17				-0.15		
UC-B70-3	35.17			0.98				4.42		
UC-B128-1	10.46	10.54	0.10	0.56	0.57	0.01	18.64	2.28	2.32	0.06
UC-B128-2	10.52			0.56				2.32		
UC-B128-3	10.61			0.57				2.36		
UC-B134-1	9.56	9.42	0.14	0.49	0.50	0.00	18.97	2.21	2.19	0.02
UC-B134-2	9.41			0.50				2.19		
UC-B134-3	9.29			0.50				2.17		
UC-C1-1	12.60	12.63	0.06	0.63	0.63	0.01	20.12	2.60	2.61	0.02
UC-C1-2	12.69			0.62				2.63		
UC-C1-3	12.58			0.63				2.61		
UC-C62-1	13.68	13.71	0.05	0.64	0.62	0.03	21.95	2.70	2.67	0.03
UC-C62-2	13.70			0.59				2.65		
UC-C62-3	13.77			0.65				2.66		
UC-C134-1	19.55	18.88	0.62	0.73	0.73	0.00	25.73	3.15	3.08	0.06
UC-C134-2	18.78			0.73				3.05		
UC-C134-3	18.32			0.74				3.02		
UC-C137-1	26.28	24.16	2.24	0.96	0.90	0.06	26.90	3.64	3.49	0.16
UC-C137-2	21.82			0.84				3.31		
UC-C137-3	24.38			0.89				3.52		
UC-C180-1	9.06	9.12	0.05	0.47	0.47	0.00	19.24	2.19	2.20	0.02
UC-C180-2	9.13			0.47				2.18		
UC-C180-3	9.16			0.48				2.22		
UC-D2-1	11.97	11.86	0.34	0.62	0.61	0.02	19.58	2.51	2.48	0.03
UC-D2-2	12.13			0.60				2.48		
UC-D2-3	11.48			0.60				2.46		
UC-D29-1	16.40	16.66	0.40	0.76	0.76	0.00	21.82	2.86	2.87	0.03
UC-D29-2	16.46			0.77				2.86		
UC-D29-3	17.12			0.76				2.90		
UC-D45-1	13.23	13.37	0.16	0.66	0.67	0.01	19.90	2.57	2.57	0.01
UC-D45-2	13.54			0.67				2.58		
UC-D45-3	13.34			0.68				2.56		
UC-D81-1	17.44	17.82	0.77	0.70	0.70	0.00	25.60	2.86	2.89	0.06
UC-D81-2	17.31			0.70				2.86		
UC-D81-3	18.70			0.70				2.97		

Erroneous outliers disregarded.

Elemental analyser – Symptomatic Cascade site

Tree code	TC	Mean	± SD	TN	Mean	± SD	C:N	TH	Mean	± SD
sample	reading	TC		reading	TN		Ratio	reading	TH	
triplicate	(%)	(%)	(%)	(%)	(%)	(%)		(%)	(%)	(%)
IC-A26-1	17.82	17.03	0.68	0.70	0.69	0.01	24.83	3.04	3.05	0.01
IC-A26-2	16.64			0.68				3.06		
IC-A26-3	16.64			0.67				3.06		
IC-A107-1	13.23	13.26	0.18	0.53	0.54	0.01	24.68	2.76	2.74	0.03
IC-A107-2	13.10			0.53				2.76		
IC-A107-3	13.45			0.55				2.70		
IC-A143-1	12.18	11.89	0.37	0.47	0.46	0.01	25.62	2.57	2.59	0.06
IC-A143-2	12.01			0.47				2.66		
IC-A143-3	11.48			0.45				2.54		
IC-A172-1	14.98	15.05	0.11	0.54	0.53	0.02	28.56	2.85	2.83	0.02
IC-A172-2	15.18			0.51				2.82		
IC-A172-3	14.99			0.54				2.82		
IC-B84-1	9.54	9.50	0.11	0.47	0.47	0.01	20.39	2.34	2.32	0.02
IC-B84-2	9.58			0.47				2.32		
IC-B84-3	9.37			0.46				2.31		
IC-B126-1	11.57	11.58	0.02	0.54	0.54	0.01	21.26	2.45	2.47	0.03
IC-B126-2	11.49			0.53				2.44		
IC-B126-3	11.60			0.55				2.50		
IC-B191-1	9.83	9.92	0.19	0.47	0.46	0.01	21.64	2.35	2.34	0.01
IC-B191-2	9.79			0.45				2.33		
IC-B191-3	10.14			0.46				2.35		
IC-B314-1	9.46	9.48	0.04	0.44	0.44	0.00	21.76	2.31	2.32	0.01
IC-B314-2	9.53			0.43				2.33		
IC-B314-3	9.45			0.44				2.32		
IC-C2-1	13.09	13.25	0.28	0.60	0.60	0.00	21.91	2.67	2.68	0.02
IC-C2-2	13.09			0.61				2.66		
IC-C2-3	13.57			0.61				2.70		
IC-C39-1	9.41	9.17	0.21	0.49	0.48	0.01	19.13	2.28	2.26	0.02
IC-C39-2	9.10			0.48				2.24		
IC-C39-3	9.01			0.47				2.25		
IC-93-1	13.22	13.24	0.06	0.58	0.59	0.01	22.63	2.60	2.61	0.01
IC-93-2	13.20			0.58				2.62		
IC-93-3	13.31			0.60				2.60		
IC-C141-1	7.23	7.20	0.12	0.40	0.40	0.01	18.01	2.12	2.11	0.01
IC-C141-2	7.32			0.39				2.11		
IC-C141-3	7.07			0.41				2.10		
IC-D1-1	17.34	17.35	0.01	0.73	0.73	0.00	23.69	3.10	3.11	0.01
IC-D1-2	17.35			0.74				3.12		
IC-D1-3	17.36			0.73				3.11		
IC-D63-1	12.13	12.27	0.31	0.54	0.56	0.02	22.06	2.54	2.53	0.01
IC-D63-2	12.63			0.56				2.54		
IC-D63-3	12.05			0.57				2.52		
IC-D126-1	9.34	9.36	0.04	0.51	0.50	0.01	18.56	2.25	2.25	0.01
IC-D126-2	9.33			0.49				2.26		
IC-D126-3	9.40			0.51				2.25		
IC-D154-1	10.93	10.81	0.15	0.45	0.45	0.01	24.27	2.37	2.36	0.02
IC-D154-2	10.85			0.44				2.37		
IC-D154-3	10.64			0.45				2.34		

Elemental analyser – Asymptomatic Huia site

Tree code	TC	Mean	± SD	TN	Mean	± SD	C:N	TH	Mean	± SD
sample	reading	TC		reading	TN		Ratio	reading	TH	
triplicate	(%)	(%)	(%)	(%)	(%)	(%)		(%)	(%)	(%)
UH-A1-1	10.12	10.18	0.18	0.59	0.58	0.01	17.63	2.28	2.33	0.05
UH-A1-2	10.04			0.58				2.32		
UH-A1-3	10.38			0.56				2.38		
UH-A2-1	9.14	8.80	0.41	0.43	0.42	0.01	21.16	2.21	2.22	0.05
UH-A2-2	8.35			0.41				2.19		
UH-A2-3	8.92			0.41				2.28		
UH-A3-1	10.30	10.75	0.48	0.61	0.63	0.02	17.13	2.31	2.36	0.05
UH-A3-2	10.69			0.62				2.37		
UH-A3-3	11.26			0.65				2.41		
UH-A4-1	7.87	7.95	0.22	0.49	0.51	0.02	15.63	1.91	1.87	0.05
UH-A4-2	7.78			0.52				1.82		
UH-A4-3	8.19			0.52				1.88		
UH-B3-1	14.44	15.02	0.53	0.66	0.69	0.02	21.85	2.54	2.58	0.04
UH-B3-2	15.16			0.69				2.57		
UH-B3-3	15.47			0.71				2.63		
UH-B9-1	11.79	11.72	0.10	0.61	0.60	0.01	19.46	2.18	2.19	0.01
UH-B9-2	11.90			0.60				2.22		
UH-B9-3	11.64			0.60				2.19		
UH-B15-1	9.04	8.85	0.17	0.51	0.48	0.03	18.33	1.93	1.89	0.06
UH-B15-2	8.79			0.46				1.92		
UH-B15-3	8.72			0.48				1.82		
HU-B22-1	9.98	10.23	0.46	0.50	0.52	0.02	19.80	2.02	2.02	0.04
UH-B22-2	9.95			0.53				1.98		
UH-B22-3	10.75			0.52				2.06		
UH-C1-1	9.58	10.35	0.96	0.47	0.48	0.01	21.65	2.07	2.16	0.12
UH-C1-2	10.05			0.48				2.11		
UH-C1-3	11.43			0.48				2.30		
UH-C4-1	8.79	8.83	0.34	0.43	0.43	0.01	20.73	1.84	1.83	0.04
UH-C4-2	8.50			0.42				1.79		
UH-C4-3	9.19			0.43				1.87		
UH-C11-1	8.70	9.09	0.38	0.45	0.46	0.01	19.62	1.74	1.79	0.06
UH-C11-2	9.46			0.47				1.85		
UH-C11-3	9.11			0.47				1.77		
UH-C17-1	13.12	13.39	0.31	0.53	0.57	0.03	23.61	2.30	2.35	0.06
UH-C17-2	13.32			0.57				2.33		
UH-C17-3	13.74			0.59				2.41		
UH-D3-1	14.67	14.90	0.86	0.54	0.55	0.01	27.22	2.66	2.68	0.05
UH-D3-2	15.86			0.56				2.74		
UH-D3-3	14.19			0.54				2.63		
UH-D12-1	7.28	7.37	0.38	0.35	0.35	0.01	21.01	1.55	1.55	0.03
UH-D12-2	7.79			0.36				1.58		
UH-D12-3	7.05			0.34				1.51		
UH-D17-1	9.94	10.42	0.47	0.46	0.45	0.02	22.96	1.99	2.04	0.05
UH-D17-2	10.88			0.47				2.09		
UH-D17-3	10.44			0.44				2.03		
UH-D25-1	12.20	11.59	0.59	0.57	0.54	0.03	21.55	2.32	2.25	0.07
UH-D25-2	11.52			0.52				2.24		
UH-D25-3	11.04			0.53				2.19		

Elemental analyser – Symptomatic Huia site

Tree code	TC	Mean	± SD	TN	Mean	± SD	C:N	TH	Mean	± SD
sample	reading	TC		reading	TN		Ratio	reading	TH	
triplicate	(%)	(%)	(%)	(%)	(%)	(%)		(%)	(%)	(%)
IH-A6-1	9.03	9.14	0.10	0.43	0.43	0.01	21.07	2.13	2.20	0.06
IH-A6-2	9.21			0.43				2.23		
IH-A6-3	9.20			0.44				2.23		
IH-A39-1	9.45	9.65	0.52	0.43	0.45	0.02	21.64	2.20	2.25	0.07
IH-A39-2	10.24			0.47				2.33		
IH-A39-3	9.26			0.43				2.22		
IH-A90-1	11.74	11.53	0.36	0.47	0.45	0.01	25.35	2.56	2.55	0.03
IH-A90-2	11.12			0.45				2.52		
IH-A90-3	11.73			0.45				2.58		
IH-A123-1	8.66	8.59	0.15	0.37	0.38	0.01	22.89	2.18	2.17	0.01
IH-A123-2	8.42			0.38				2.17		
IH-A123-3	8.70			0.38				2.18		
IH-B41-1	10.01	10.61	0.53	0.42	0.43	0.00	24.96	2.28	2.28	0.03
IH-B41-2	10.97			0.43				2.31		
IH-B41-3	10.86			0.42				2.26		
IH-B53-1	15.55	15.87	0.44	0.56	0.57	0.01	27.99	2.81	2.82	0.02
IH-B53-2	15.75			0.53				2.83		
IH-B53-3	16.18			0.58				2.83		
IH-B86-1	16.78	17.40	0.57	0.60	0.61	0.00	28.75	2.79	2.87	0.07
IH-B86-2	17.90			0.61				2.93		
IH-B86-3	17.51			0.61				2.89		
IH-B96-1	12.65	12.74	0.08	0.50	0.51	0.03	25.08	2.29	2.29	0.01
IH-B96-2	12.78			0.48				2.30		
IH-B96-3	12.80			0.54				2.28		
IH-C19-1	10.03	9.86	0.18	0.48	0.47	0.02	20.98	2.14	2.12	0.02
IH-C19-2	9.68			0.45				2.10		
IH-C19-3	9.88			0.48				2.13		
IH-C75-1	14.76	15.47	0.63	0.57	0.59	0.02	26.34	2.56	2.62	0.05
IH-C75-2	15.72			0.61				2.63		
IH-C85-3	15.94			0.58				2.66		
IH-C114-1	20.08	19.50	0.54	0.75	0.76	0.01	25.81	2.90	2.91	0.04
IH-C114-2	19.01			0.75				2.87		
IH-C114-3	19.41			0.77				2.94		
IH-C131-1	16.10	15.84	0.63	0.69	0.67	0.02	23.67	2.62	2.59	0.06
IH-C131-2	16.31			0.68				2.63		
IH-C131-3	15.12			0.64				2.51		
IH-D26-1	11.59	11.38	0.38	0.52	0.51	0.01	22.32	2.39	2.31	0.10
IH-D26-2	11.60			0.51				2.34		
IH-D26-3	10.94			0.49				2.20		
IH-D89-1	30.54	30.11	0.82	0.97	0.96	0.01	31.43	3.80	3.78	0.07
IH-D89-2	29.17			0.95				3.70		
IH-D89-3	30.62			0.95				3.85		
IH-D107-1	11.51	11.92	0.37	0.49	0.49	0.01	24.54	2.06	2.09	0.03
IH-D107-2	12.04			0.48				2.10		
IH-D107-3	12.22			0.49				2.12		
IH-D142-1	7.63	7.52	0.12	0.42	0.40	0.02	18.63	1.90	1.89	0.01
IH-D142-2	7.54			0.41				1.88		
IH-D142-3	7.38			0.38				1.89		

Elemental analyser – Asymptomatic Piha site

Tree code	TC	Mean	± SD	TN	Mean	± SD	C:N	TH	Mean	± SD
sample	reading	TC		reading	TN		Ratio	reading	TH	
triplicate	(%)	(%)	(%)	(%)	(%)	(%)		(%)	(%)	(%)
UP-A4-1	8.94	9.02	0.20	0.40	0.40	0.00	22.66	2.19	2.18	0.04
UP-A4-2	8.87			0.39				2.13		
UP-A4-3	9.25			0.40				2.22		
UP-A117-1	10.69	10.74	0.08	0.46	0.47	0.01	23.08	2.40	2.38	0.04
UP-A117-2	10.71			0.48				2.40		
UP-A17-3	10.83			0.46				2.34		
UP-A186-1	10.26	10.23	0.03	0.43	0.44	0.01	23.50	2.33	2.32	0.01
UP-A186-2	10.22			0.43				2.32		
UP-A186-3	10.20			0.44				2.31		
UP-A282-1	20.06	20.47	0.46	0.62	0.63	0.02	32.42	3.12	3.16	0.03
UP-A282-2	20.39			0.63				3.18		
UP-A828-3	20.96			0.65				3.18		
UP-B22-1	7.35	7.69	0.30	0.34	0.35	0.01	22.22	2.03	2.06	0.02
UP-B22-2	7.91			0.35				2.08		
UP-B22-3	7.80			0.35				2.06		
UP-B138-1	14.33	13.81	0.73	0.46	0.46	0.00	29.80	2.65	2.62	0.04
UP-B138-2	13.82			0.47				2.64		
UP-B138-3	13.30			0.46				2.59		
UP-B171-1	9.27	8.94	0.29	0.39	0.39	0.01	22.77	2.16	2.12	0.03
UP-B171-2	8.72			0.40				2.11		
UP-B171-3	8.84			0.38				2.10		
UP-B284-1	14.23	14.80	0.50	0.51	0.54	0.03	27.64	2.60	2.66	0.05
UP-B284-2	15.13			0.54				2.69		
UP-B284-3	15.05			0.56				2.68		
UP-C10-1	8.57	8.51	0.08	0.42	0.42	0.00	20.11	2.02	2.01	0.02
UP-C10-2	8.42			0.42				2.01		
UP-C10-3	8.52			0.43				1.99		
UP-C79-1	6.24	6.10	0.20	0.30	0.30	0.01	20.40	1.93	1.92	0.02
UP-C79-2	5.86			0.30				1.90		
UP-C79-3	6.19			0.29				1.94		
UP-C158-1	8.10	8.36	0.30	0.35	0.35	0.00	23.82	2.09	2.12	0.04
UP-C158-2	8.69			0.35				2.16		
UP-C158-3	8.28			0.35				2.11		
UP-C239-1	9.62	9.79	0.61	0.38	0.38	0.01	25.66	2.21	2.21	0.06
UP-C239-2	10.47			0.39				2.28		
UP-C239-3	9.28			0.37				2.15		
UP-D37-1	8.40	8.47	0.19	0.38	0.38	0.01	22.47	2.04	2.04	0.02
UP-D37-2	8.69			0.38				2.06		
UP-D37-3	8.32			0.37				2.01		
UP-D124-1	10.49	10.38	0.19	0.49	0.48	0.01	21.46	2.20	2.20	0.01
UP-D124-2	10.49			0.48				2.20		
UP-D124-3	10.16			0.49				2.19		
UP-D228-1	10.14	10.16	0.03	0.44	0.44	0.01	23.04	2.23	2.24	0.01
UP-D228-2	10.16			0.45				2.23		
UP-D-228-3	10.20			0.43				2.25		
UP-D1044-1	9.02	8.72	0.35	0.39	0.39	0.00	22.49	2.16	2.12	0.04
UP-D1044-2	8.33			0.39				2.07		
UP-D1044-3	8.82			0.39			2.14			

Elemental analyser – Symptomatic Piha site

Tree code	TC	Mean	± SD	TN	Mean	± SD	C:N	TH	Mean	± SD
sample	reading	TC		reading	TN		Ratio	reading	TH	
triplicate	(%)	(%)	(%)	(%)	(%)	(%)		(%)	(%)	(%)
IP-A26-1	10.70	10.42	0.40	0.54	0.53	0.01	19.76	2.51	2.47	0.04
IP-A26-2	10.60			0.53				2.46		
IP-A26-3	9.96			0.51				2.43		
IP-A71-1	7.06	7.02	0.04	0.39	0.39	0.01	17.84	1.94	1.97	0.05
IP-A71-2	7.00			0.40				2.03		
IP-A71-3	6.98			0.39				1.94		
IP-A129-1	16.49	16.12	0.38	0.69	0.68	0.01	23.82	2.93	2.88	0.05
IP-A129-2	16.15			0.68				2.87		
IP-A129-3	15.73			0.66				2.83		
IP-A211-1	12.60	12.78	0.49	0.54	0.55	0.01	23.17	2.61	2.60	0.04
IP-A211-2	13.34			0.57				2.64		
IP-A211-3	12.41			0.55				2.56		
IP-B10-1	8.94	9.20	0.85	0.42	0.43	0.04	21.59	2.16	2.19	0.10
IP-B10-2	8.51			0.39				2.11		
IP-B10-3	10.14			0.47				2.30		
IP-B72-1	11.05	11.31	0.38	0.58	0.60	0.02	18.96	2.22	2.25	0.03
IP-B72-2	11.30			0.58				2.25		
IP-B72-3	11.58			0.61				2.27		
IP-B123-1	11.14	11.28	0.47	0.57	0.59	0.02	19.07	2.22	2.22	0.06
IP-B123-2	11.80			0.61				2.29		
IP-B123-3	10.89			0.60				2.16		
IP-B185-1	9.61	9.96	0.68	0.55	0.54	0.01	18.46	2.14	2.15	0.07
IP-B185-2	10.74			0.54				2.23		
IP-B185-3	9.53			0.53				2.09		
IP-C5-1	7.90	8.43	0.57	0.54	0.54	0.01	15.67	1.95	1.98	0.05
IP-C5-2	8.36			0.53				1.96		
IP-C5-3	9.04			0.55				2.04		
IP-C117-1	8.20	8.20	0.50	0.55	0.54	0.03	15.15	1.89	1.87	0.09
IP-C117-2	7.70			0.50				1.78		
IP-C117-3	8.69			0.57				1.95		
IP-C147-1	16.11	15.43	1.08	0.79	0.77	0.03	20.05	2.56	2.50	0.10
IP-C147-2	16.01			0.78				2.55		
IP-C147-3	14.18			0.74				2.39		
IP-C231-1	10.66	10.33	0.30	0.60	0.59	0.01	17.59	2.19	2.18	0.02
IP-C123-2	10.25			0.59				2.16		
IP-C123-3	10.07			0.57				2.18		
IP-D49-1	7.55	7.24	0.30	0.54	0.53	0.01	13.69	1.89	1.85	0.04
IP-D49-2	7.20			0.51				1.82		
IP-D49-3	6.96			0.53				1.83		
IP-D103-1	9.49	9.36	0.27	0.61	0.63	0.02	14.90	1.98	1.97	0.04
IP-D103-2	9.55			0.64				2.00		
IP-D103-3	9.04			0.64				1.92		
IP-D173-1	8.82	8.83	0.09	0.70	0.72	0.03	12.32	1.80	1.80	0.01
IP-D173-2	8.74			0.69				1.78		
IP-D173-3	8.91			0.75				1.81		
IP-D203-1	8.48	9.21	0.68	0.71	0.76	0.05	12.15	1.89	1.97	0.07
IP-D203-2	9.82			0.77				2.02		
IP-D203-3	9.34			0.79				2.00		

Elemental analyser – Asymptomatic Tairua site

Tree code	TC	Mean	± SD	TN	Mean	± SD	C:N	TH	Mean	± SD
sample	reading	TC		reading	TN		Ratio	reading	TH	
triplicate	(%)	(%)	(%)	(%)	(%)	(%)		(%)	(%)	(%)
AUTT1-1	21.03	21.08	0.07	0.68	0.70	0.02	30.16	2.95	2.97	0.04
AUTT1-2	21.06			0.70				2.94		
AUTT1-3	21.16			0.71				3.02		
AUTT2-1	19.50	19.68	0.16	0.61	0.62	0.01	31.96	3.11	3.13	0.04
AUTT2-2	19.82			0.61				3.11		
AUTT2-3	19.71			0.63				3.17		
AUTT3-1	13.20	13.16	0.04	0.56	0.56	0.00	23.42	2.28	2.24	0.04
AUTT3-2	13.11			0.56				2.20		
AUTT3-3	13.18			0.56				2.24		
AUTT4-1	9.33	9.34	0.15	0.38	0.38	0.01	24.67	1.89	1.87	0.02
AUTT4-2	9.20			0.39				1.85		
AUTT4-3	9.49			0.37				1.88		
AUTT5-1	17.98	17.51	0.65	0.62	0.62	0.02	28.14	2.81	2.77	0.10
AUTT5-2	17.79			0.64				2.84		
AUTT5-3	16.76			0.61				2.66		
AUTT6-1	15.97	15.77	0.27	0.55	0.54	0.01	29.37	2.50	2.49	0.01
AUTT6-2	16.28			0.56				2.57		
AUTT6-3	15.58			0.53				2.49		
AUTT7-1	9.45	10.07	0.56	0.31	0.34	0.02	30.04	2.11	2.21	0.09
AUTT7-2	10.22			0.34				2.25		
AUTT7-3	10.54			0.35				2.28		
AUTT8-1	15.34	15.95	0.61	0.53	0.54	0.01	29.38	2.50	2.60	0.10
AUTT8-2	16.55			0.55				2.69		
AUTT8-3	15.96			0.55				2.61		
AUTT9-1	13.09	12.82	0.25	0.46	0.45	0.02	28.71	2.30	2.25	0.05
AUTT9-2	12.62			0.43				2.20		
AUTT9-3	12.74			0.45				2.24		
AUTT10-1	10.96	11.17	0.26	0.41	0.41	0.01	27.11	2.10	2.14	0.06
AUTT10-2	11.46			0.42				2.21		
AUTT10-3	11.09			0.41				2.13		
AUTT11-1	10.38	10.36	0.35	0.37	0.38	0.01	27.29	1.88	1.91	0.06
AUTT11-2	10.71			0.39				1.98		
AUTT11-3	10.00			0.37				1.88		
AUTT12-1	10.92	11.10	0.36	0.42	0.42	0.01	26.47	1.68	1.68	0.04
AUTT12-2	11.51			0.41				1.71		
AUTT12-3	10.86			0.42				1.64		
AUTT13-1	9.31	9.21	0.37	0.47	0.47	0.02	19.65	1.92	1.90	0.08
AUTT13-2	8.80			0.45				1.81		
AUTT13-3	9.51			0.49				1.96		
AUTT14-1	11.24	11.25	0.12	0.40	0.42	0.02	26.47	2.12	2.11	0.01
AUTT14-2	11.13			0.45				2.11		
AUTT14-3	11.37			0.42				2.11		
AUTT15-1	10.88	10.92	0.32	0.56	0.56	0.02	19.56	2.18	2.17	0.03
AUTT15-2	10.63			0.53				2.14		
AUTT15-3	11.27			0.58				2.19		

Elemental analyser – Symptomatic Whangapoua site

Tree code	TC	Mean	± SD	TN	Mean	± SD	C:N	TH	Mean	± SD
sample	reading	TC		reading	TN		Ratio	reading	TH	
triplicate	(%)	(%)	(%)	(%)	(%)	(%)		(%)	(%)	(%)
G1-1	31.06	31.41	0.39	1.13	1.16	0.03	27.08	3.76	3.87	0.09
G1-2	31.34			1.16				3.91		
G1-3	31.83			1.19				3.92		
G2-1	18.15	18.08	0.09	0.68	0.67	0.01	27.09	2.92	2.85	0.06
G2-2	17.97			0.66				2.80		
G2-3	18.12			0.66				2.82		
G3-1	21.58	20.80	0.68	0.71	0.72	0.01	29.00	3.02	2.93	0.08
G3-2	20.40			0.71				2.90		
G3-3	20.42			0.73				2.87		
G4-1	9.07	9.21	0.12	0.38	0.40	0.02	23.02	1.75	1.76	0.01
G4-2	9.23			0.41				1.76		
G4-3	9.32			0.41				1.77		
G5-1	19.18	18.49	1.22	0.67	0.65	0.05	28.65	2.83	2.81	0.06
G5-2	19.21			0.68				2.85		
G5-3	17.09			0.59				2.74		
G6-1	20.28	18.70	2.23	0.69	0.64	0.07	29.30	2.96	2.86	0.14
G6-2	17.41			0.62				2.79		
G6-3	17.12			0.59				2.76		
G7-1	16.91	17.06	0.44	0.60	0.61	0.01	28.07	2.81	2.81	0.04
G7-2	16.71			0.61				2.78		
G7-3	17.56			0.62				2.85		
G8-1	21.89	22.42	0.51	0.73	0.75	0.02	29.88	3.19	3.26	0.06
G8-2	22.91			0.76				3.31		
G8-3	22.48			0.76				3.27		