Trees and people: relationships between tōtara trees and their environment

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Abstract

This research addresses significant gaps in the literature concerning *Podocarpus totara* (tōtara), a foundational *taonga* species in Aotearoa New Zealand. The study uniquely integrates Western Science techniques alongside Mātauranga Māori (Māori knowledge) to explore the physiology and cultural significance of this key endemic gymnosperm.

The Western Science component involved quantitative measurements of instantaneous leaf gas exchange, photosynthetic response curves to light, CO_2, and vapour pressure deficit (VPD), and analysis of the stable carbon isotopic composition of leaf-respired CO_2 ($\delta^{13}C_{Rl}$). Measurements were conducted on adult tōtara over seven months (August 2024 to March 2025) across two distinct growth environments: individual, fully exposed trees and trees growing in stands of varying densities. Key photosynthetic parameters, including net photosynthetic rate (A), stomatal conductance (g_s), and maximum carboxylation rate (V_{cmax}), were quantified. Physiological results showed that tōtara growing individually exhibited significantly higher net photosynthetic rates than those in stand environments (1.15 µmol CO_2 m^{-2} s^{-1} versus 0.47 µmol CO_2 m^{-2} s^{-1}), likely due to greater irradiance and reduced competition for light. Overall values were low, consistent with other Podocarpaceae species. Analysis of $\delta^{13}C_{Rl}$ provided an integrated signal of carbon-water dynamics, revealing a general trend of values becoming less negative from spring to autumn. This trend is consistent with stomatal closure in response to water limitation and increased VPD during the warmer months (summer drought 2024-2025). No statistically significant difference was found between individual and stand trees over the measurement period. Furthermore, a simple model designed to predict A and g_s failed to accurately correlate with observed field

data, potentially because it was parameterized using data from saplings grown under optimal greenhouse conditions rather than adults subject to field variability.

The Mātauranga Māori component explored tōtara's significance through a cultural lens. In te ao Māori (the Māori world), tōtara is considered paramount and is connected to humans through whakapapa (ancestry/genealogy) as children of Tāne-Mahuta, the god of the forest; tōtara is considered the tuakana (older sibling) to humans. The species has historically been crucial for crafting waka (canoes) and marae carvings, and its attributes, such as wisdom and generosity, are honored in whakataukī (proverbs). Semi-qualitative techniques were used to respectfully 'interview' six adult tōtara, treating each tree as an 'expert' to foster a journey of personal and cultural reconnection for the author. This research highlights the fundamental philosophical contrast between the individualistic, objective nature of Western Science and the holistic, entangled perspective of Te Ao Māori, where humans are part of nature. The approach successfully employed techniques and customs from both knowledge systems side by side, aiming to create new insights while ensuring that the distinct ethics and special character of each worldview are maintained and acknowledged. The study advocates for continued research at this interface to enhance understanding of the interface and foster increased communication and respect in practitioners of both worldviews.

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Table 1: Parameter table including units, definitions and citations.

Symbol	Units	Definition	Citation
A	µmol CO_2 m^{-2} s^{-1}	net photosynthetic rate	(Farquhar & Wong, 1984)
A_{max}	µmol CO_2 m^{-2} s^{-1}	light-saturated photosynthetic rate	(Farquhar & Wong, 1984)
I	µmol m^{-2} s^{-1}	absorbed light	(Farquhar & Wong, 1984)
ϕ	mol/mol	apparent quantum yield	(Farquhar & Wong, 1984)
θ	dimensionless	curvature of the response	(Farquhar & Wong, 1984)
R_{dark}	µmol m^{-2} s^{-1}	dark respiration	(Farquhar & Wong, 1984)
V_{cmax}	µmol m^{-2} s^{-1}	maximum carboxylation rate	(Von Caemmerer & Farquhar, 1981).
C_c	µmol mol^{-1}	chloroplastic CO2 concentration	(Von Caemmerer & Farquhar, 1981).
Γ^*	µmol mol^{-1}	CO2 compensation point	(Von Caemmerer & Farquhar, 1981).
K_c	µmol mol^{-1}	Rubisco Michaelis-Menton constant for CO2	(Von Caemmerer & Farquhar, 1981).
K_o	µmol mol^{-1}	Rubisco Michaelis-Menton constant for O2	(Von Caemmerer & Farquhar, 1981).
O	µmol mol^{-1}	oxygen concentration	(Von Caemmerer & Farquhar, 1981).
R_d	µmol m^{-2} s^{-1}	mitochondrial respiration in the light	(Von Caemmerer & Farquhar, 1981).
J	µmol m^{-2} s^{-1}	electron transport rate	(Von Caemmerer & Farquhar, 1981).
TPU	µmol m^{-2} s^{-1}	triose phosphate utilisation rate	(Von Caemmerer & Farquhar, 1981).
gs	µmol m^{-2} s^{-1}	stomatal conductance to water vapour	(Lohammar et al., 1980)
gsmin	µmol m^{-2} s^{-1}	minimum stomatal conductance	(Lohammar et al., 1980)
VPdL	kPa	leaf-to-air vapor pressure deficit,	(Lohammar et al., 1980)
Dmin	kPa	VPD threshold below which stomatal response does not occur	(Lohammar et al., 1980)
D_0	kPa	scaling parameter controlling sensitivity	(Lohammar et al., 1980)
δ	‰	isotopic composition	(Farquhar et al., 1989)
Δ	dimensionless	isotopic discrimination	(Farquhar et al., 1989)

Chapter One: An introduction to tōtara

1.1 Introduction

The aim of this research is to fill a gap in the literature around *Podocarpus totara* (tōtara), one of the most significant taonga species of Aotearoa New Zealand. The intention of this project is to offer insight into this key species through a range of Western Science techniques in an exploration of this species physiology, and also to examine relationships between trees and people, meeting tōtara through the framework of Mātauranga Māori. The Western Science techniques used in this research include; measurements of instantaneous leaf gas exchange, light and CO_2 response curves, stomatal response to changes in VPD, the stable carbon isotopic composition of respired CO_2 and the formulation of a simple photosynthetic model based off of observed measurements. These methods aim to increase our understanding of the carbon-water dynamics of tōtara, and combined with meeting tōtara through a cultural lens, are an attempt to 'interview' this consequential species, to learn more about it using a range of different techniques through the vehicle of two different worldviews.

This chapter provides a review on the current literature regarding tōtara, from distribution to growth rates to regeneration strategy, and also on the limited amount of information on tōtara's cultural significance. This chapter will also explore the forestry potential and future of tōtara, and lastly will outline the aims and objectives of this research.

1.2 Phylogeny and distribution

Tōtara is the common name for *Podocarpus totara*, or lowland tōtara, and is one of four species that make up the New Zealand tōtara (Simpson, 2017). Tōtara belong to the gymnosperms, a group of plants that evolved earlier than the now dominant angiosperms and that are characterised by producing naked seeds that are not enclosed in an ovary (Simpson, 2017). Gymnosperms are further distinguished by long term survival traits such as relatively coarse leaves, slower overall growth and soft wood. Within the gymnosperms tōtara is a part of the Pinophyta (conifers), an abundant and diverse clade which are characterised by bearing cones and needle- or scale-like leaves (Simpson, 2017).

This endemic species is well-distributed across the country, found all over the North Island, in some parts of the South Island and in a small part of Stewart Island (Figure 1). Tōtara is found everywhere that there are fertile soils that are reasonably well drained but is not usually found above an elevation of 600 meters above sea level (Simpson, 2017).

Figure 1: Generalised distribution of *Podocarpus totara* (green)(Simpson, 2017).

The distribution of tōtara in New Zealand reflects a mix of historical and anthropogenic influences, along with current regional variability in abundance, characteristics, and, therefore, management priorities. This species is now distributed across various environments and habitats in New Zealand. Cown & Bergin (2009) reported that tōtara has a wide distribution across New Zealand and is present at elevations ranging from sea level to 500m. Salekin et al., (2025) also reported planting sites in the North Island in the regions of Northland, Thames, Bay of Plenty, Hawkes Bay, Gisborne, and Taranaki. Quinlan et al. (2011) reported that naturally regenerated tōtara stands are found in many pastoral areas throughout New Zealand, with particularly high vigor in Northland. In addition, the study conducted by Bergin & Kimberley (2014), which focused on the Gisborne Region, reported that there are over 7,000 woody stems per ha of pasture hill country in this area, with tōtara being an important part of this composition.

Unfortunately, significant reductions of past forests have occurred in many of these regions. Miller et al. (2003) noted that Podocarpus spp. forests on alluvial floodplains are under-represented compared to their original extent in Westland. McSweeney (1982) found that the matai/tōtara forest in South Westland declined from perhaps 43,000 ha to about 600 ha, with 25% of the remaining area harvested or cleared within 2 years before the study. Bergin & Kimberley (2012) reported that old-growth tōtara stands were nearly eliminated throughout New Zealand, while Salekin et al. (2025) attributed this loss to extensive land use by European settlers. There are a range of factors that may influence tōtara distribution. Bergin et al. (2014) identified a lack of suitable local seed sources as a major constraint. Cown & Bergin (2009) further reported that tōtara is often seen as a weed on farms, suggesting it is becoming more common in agricultural areas.

1.3 Growth rate and adaptations

Most differences in published tōtara growth rates come from site quality, stand density, and past management, rather than physiological factors. Cown & Bergin, (2009) found that tōtara trees grow slowly at first, but their growth speeds up after about 20 years. Because growth rates change over time, using early data can underestimate long-term productivity, while looking only at older trees may overlook the time needed for them to get established. Cown & Bergin, (2009) found that tōtara can grow quickly in open areas without competition, with trunks reaching over 10 cm in diameter in 10 years. However, since these results are from young trees in open spaces, it is not clear if the same growth happens in dense forests where competition for resources is high. Bergin & Kimberley (2003) also noted that how closely trees are spaced affects their growth and shape. Quinlan et al. (2011) showed that thinning trees from 6,000 per hectare to between 800 and 2,000 per hectare led to much better growth and higher total wood volume. This suggests that competition for resources is the main factor affecting growth rates. The not-thinned plots, which represent natural regeneration, had more competition and slower growth. Further, Bergin & Kimberley (2012) reported slow growth rates (2.8-4.8 mm/yr) in several naturally regenerated stands.

There is conflicting research about the influence of grazing on tōtara regrowth. This variation is likely due to variations in grazing frequency and intensity, along with variability in the types of species grazed. Bergin et al. (2014) found that grazing tōtara creates a short, pastured environment and therefore allows for more photosynthesis from the forest floor. Miller et al. (2003) demonstrated that there was an increase in tall seedling development in grazed environments compared to ungrazed environments. Bergin et al. (2014) and (McSweeney, 1982) both examined the impact of continued grazing by cattle on pastureland; however, both studies had varying degrees of grazing pressure and levels of other plant species present. In contrast, McSweeney et al. (1982) determined that grazing can stunt new regrowth, particularly in matai. There is a possibility that moderate grazing helps reduce competition between seedlings and existing grasses. Bergin et al. (2014) found that tōtara does not regenerate on flat, fertile land with thick grass cover. In these areas, new seedlings cannot compete with established pasture grasses if there is no grazing. Moderate grazing creates gaps in the grass and disturbs the soil enough for seeds to sprout. This explains why tōtara regeneration is often seen in places with less grass cover. However, this does not mean tōtara prefers these sites, but rather that these are the only places where grass competition is low enough for seedlings to grow.

Light levels in the understory of dense herbaceous vegetation are rarely sufficient to support the development of seedlings of light-demanding species such as tōtara and kahikatea. Grazing reduces herbaceous vegetation density, allowing more light into the forest understory. However, overgrazing can remove the protective layer of vegetation (herbaceous) that protects young seedlings from frost damage, drought stress, and/or trampling (McSweeney et al., 1982). Bergin et al. (2014) found that tōtara was a light-demanding species; similarly, Waring (2017) found that kahikatea was a light-demanding species requiring high levels of PAR to succeed. Waring (2017) found that the physiological differences between the two species has important implications for the restoration of kahikatea and tōtara forests. Kahikatea will grow well on very wet sites, whereas tōtara tends to grow on upland, drier sites.

1.4. Growth conditions and forestry

Both direct physiological tolerance to environmental conditions and indirect effects via mycorrhizal associations were found to play a role in the ecological niches occupied by tōtara and kahikatea. The positive association of tōtara with arbuscular mycorrhizal fungi and its negative response to disturbances in mycorrhizal networks suggested that these species have an evolutionary reliance on mycorrhizal relationships to obtain nutrients and water in dry soils, where nutrient availability is limited. The mycorrhizal relationships also provided evidence of phylogenetic constraints on restoration methods. The competitive effects of other species on tōtara and kahikatea differed depending on whether those species were connected through mycorrhizal networks. When they were connected, tōtara competed more strongly and kahikatea benefited (Fabbro, 2018). These competitive effects indicate evolutionary divergence in competitive strategies - tōtara has developed stronger mycorrhizal-mediated resource acquisition, and kahikatea has developed stronger beneficial interactions with nurse plants. Because there is phylogenetic variation in how species interact, there is no single restoration protocol that can be applied to all podocarps; instead, restoration protocols need to be species-specific.

Tōtara has different levels of provenance within its various populations (Bergin & Kimberley, 1992; Hawkins et al., 1991), this leads to an inherent conflict between the two goals of preserving natural population genetic diversity and achieving plantation growth rates or forms that are commercially viable. The use of locally obtained seeds to maintain genetic diversity and local adaptation in restoration ecology (Bergin & Kimberley, 1992; Hawkins et al., 1991) may be in direct contrast to the goals of breeding programs in commercial plantations which seek to select for faster growth and superior form (Bergin & Kimberley, 1992). Therefore, this presents a trade-off between conserving the evolved local adaptations of tōtara populations and gaining genetic improvement through selective breeding. The variation in frost hardness among provenances provides an opportunity to resolve this trade-off. Provenances from higher-altitude areas showed greater frost tolerance (Hawkins et al., 1991), and this was associated with a genetic marker (the Idh-1 allele) indicative of frost tolerance. Therefore, when planting tōtara in frost-prone areas, it would be preferable to choose high-altitude provenances that retain locally adapted genetic variation and may accept slower growth rates. On the other hand, when planting in less frost-prone areas, it would be preferable to choose low-latitude, low-altitude provenances that achieve faster growth rates at the expense of increased frost sensitivity.

The hybridization patterns add further complexity. Extensive hybridization has been reported to occur between tōtara and *Podocarpus spp.* (Wardle, 1972; Webby et al., 1987) resulting in additional genetic variation in tōtara populations not present in pure tōtara populations. Hybrids between tōtara and *Podocarpus spp.* may possess desirable characteristics (e.g., the compact growth habit of *Podocarpus acutifolius* and the timber quality of tōtara). However, the use of hybrids in commercial plantations carries the risk of genetic swamping of pure populations if hybrids are planted adjacent to wild tōtara stands. Therefore, it would be preferable to separate commercial plantations (where hybrid or selected cultivars may be grown) from conservation plantings (which should use locally sourced pure species seed stocks).

1.5 Tōtara and whakapapa

A considerable knowledge gap exists regarding the cultural significance of tōtara within the literature examined; especially since tōtara has long been recognized as culturally important in Māori culture and New Zealand heritage. Cultural value was rarely the focus of the studies that were conducted, which were primarily concerned with the utilization aspects of tōtara (i.e., carvings, waka and timber). Māori culture and tradition are oral based, with information and history passed on in stories and songs. This oral based tradition, coupled with the place-based nature of Mātauranga Māori (Māori knowledge), has meant that few written resources exist for specific species in te ao Māori (the Māori world), although this number is increasing with time. The one resource that has done well at pooling information together on tōtara in a cultural context is the work by Simpson (2017). In his book he acknowledges that tōtara in te ao Māori is considered a part of humans whakapapa (ancestry) due to the fact that both are considered children of the atua (god) of the forest, Tāne-Mahuta. The author goes on to cover the various uses of tōtara in Māori culture, from carvings in marae to waka (canoe), to the inclusion of tōtara in whakataukī (proverbs). Tōtara is paramount in te ao Māori and one of the purposes of this research is to further explore this species through this cultural lens. This exploration will be done respectfully, coming from a place of willingness to learn as a student who has much still to discover about both Western Science and Mātauranga Māori.

1.6 Aims and objectives

There is a gap in the literature around the physiology of podocarps endemic to New Zealand, and especially *Podocarpus totara* (tōtara). There is an even larger gap around the integration of Western Science and Mātauranga Māori as collaborative components in research within the natural sciences. The aim of this research is to help fill these gaps in understanding through tōtara. This research aims to investigate this significant podocarp by using a mixture of quantitative and semi-qualitative techniques. Leaf level gas exchange in tōtara will be measured to quantify photosynthetic capacity and response. The stable carbon isotope composition of leaf-respired CO_2 will be measured to understand past integrated environmental conditions that tōtara has experienced, and the formulation of a simple photosynthetic model based off of observed measurements will be formulated. Finally, the use of semi-qualitative techniques will be employed with the objective to connect with tōtara and with Māori culture. The key objectives of this study are therefore:

1. To investigate the differences in carbon-water dynamics of tōtara growing in distinct growth environments (individually or in stands) through spot measurements of photosynthetic capacity, response to changing conditions and the use of a simple photosynthetic model
2. To further investigate the integrated carbon-water dynamics in tōtara using stable carbon isotope composition of leaf-respired CO_2
3. To connect with tōtara through connection with culture, to facilitate a journey of reconnection

1.7 Thesis layout

This thesis consists of four chapters. Chapter One is a review of the current literature involving tōtara, including the distribution, growth rates and forestry potential of this species. Chapters Two and Three are formatted as research chapters, each with their own introduction, materials and methods, results and discussion. Chapter Two revolves around leaf-level gas exchange in tōtara, where a range of different techniques have been used to understand the photosynthetic physiology of tōtara and where this sits in relation to other species. Chapter Three focuses on the stable carbon isotope composition of leaf-respired CO_2 in tōtara and how this relates to carbon-water dynamics over time. Lastly, Chapter Four is written using semi-qualitative techniques, with a focus on the significance of connection and culture.

Chapter Two: Leaf gas exchange

2.1. Introduction

Quantifying leaf gas exchange dynamics such as rates of photosynthesis (*A*) and stomatal conductance (g_s) is critical to an understanding of the physiology of terrestrial plant species and how they will adapt to their environment over the long term (Givnish, 1988). The net rate of photosynthesis in plants is dependent upon a variety of interrelated biophysical and biochemical limitations associated with the transport of CO_2 through the stomata and into leaf tissue and the enzymatic reactions occurring within the chloroplast, particularly those involving RuBP carboxylase-oxygenase activity (Sharkey et al., 2007; Von Caemmerer & Farquhar, 1981). Instantaneous measures of gas exchange are conventionally made using IRGAs (infrared gas analysers) to provide estimates of stomatal conductance (g_s) and internal CO_2 concentrations (C_i) (Lusk et al., 2003). The interpretation of these dynamic processes can rely heavily on theoretical models with both empirical and evolutionary bases (Medlyn et al., 2011).

The interpretation of plant physiological measurements requires the consideration of the limiting biological and environmental factors influencing them. Photosynthesis is affected by a range of environmental factors including photosynthetically active radiation (PAR), temperature, and vapour pressure deficit (VPD)(Grossiord et al., 2020). Additionally, physiological potential is limited by ontogenic development and resource economics. Mature tree photosynthetic and biochemical potential is documented to differ from that of seedlings (Tissue et al., 2005), a difference often linked to hydraulic constraints that increase with tree size (Whitehead et al., 2011). In addition, there is a decline in photosynthetic capacity with increasing leaf age throughout the canopy (Macinnis-Ng et al., 2017).

In this chapter, leaf gas exchange in tōtara (*Podocarpus totara*) is measured to quantify photosynthetic differences between trees growing *in situ* in distinct growth environments, comparing individuals with complete exposure to sunlight versus individuals competing for resources in dense stands. Data collected during the period of August 2024-March 2025 provide important information to link carbon assimilation and water-use strategies to site-specific environmental and stand structural conditions. The aim of this chapter is to fill a gap in the literature on real-world tōtara leaf gas exchange.

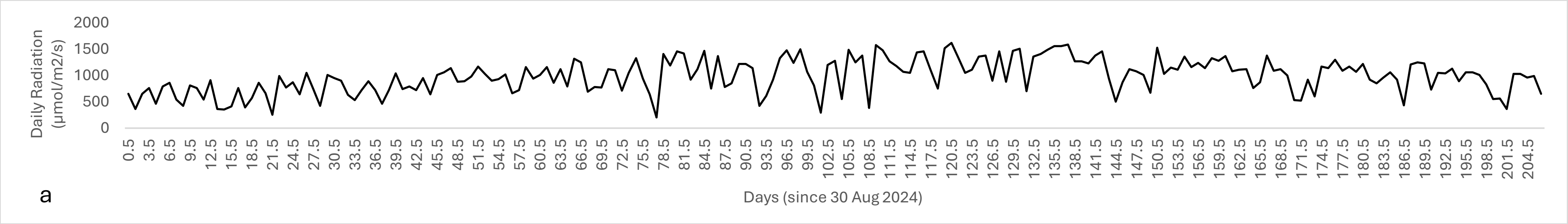
2.2. Materials and methods

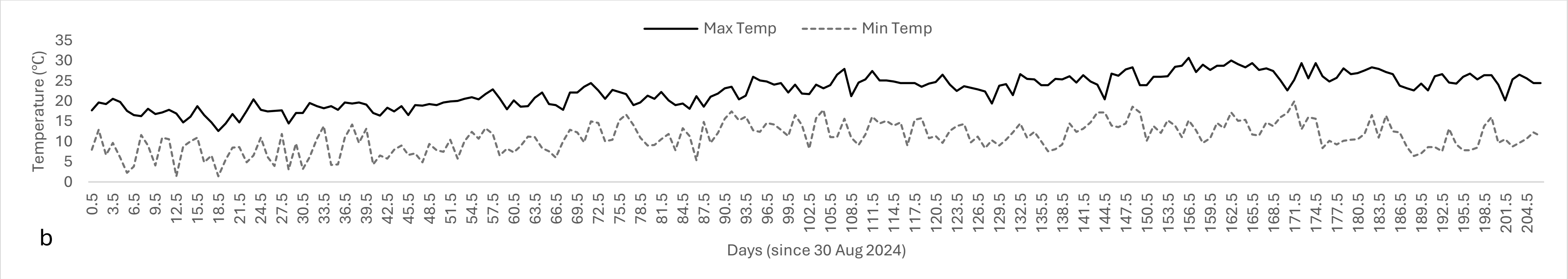
2.2.1. Site and plant material

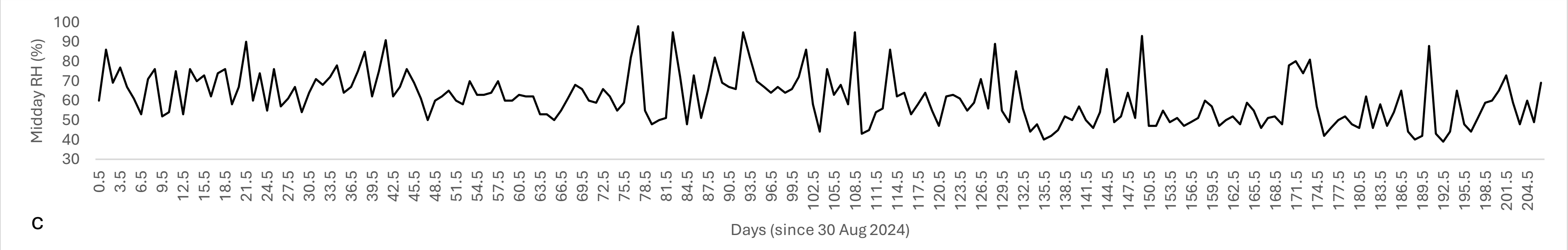
Six adult tōtara were selected to measure *in situ* on the University of Waikato Hamilton Campus from August 2024 until March 2025. These sample trees were selected based on distinct growth environments – three trees were selected because they are growing individually with access to sunlight on all sides, and the remaining three trees were selected because they are growing in stands with other trees (both native and non-native), where access to sunlight was restricted by competition with other trees in the stand (Figure 1). Tree habitat varied; Tree 1 was located on relatively flat ground, with the closest tree approximately 10m away, Tree 2 was located midway down a slope with the closest large tree approximately 7m away, Tree 3 was located near the bottom of a slope with the closest tree approximately 12m away. Tree 4 was located at the top of a slope and was a part of a relatively small stand that included both deciduous and evergreen species, Tree 5 was located in a dip in the surrounding topography in a relatively larger and dense mixed species stand comprised of evergreen species and Tree 6 was located at the top of a slope in a relatively medium sized stand that included both deciduous and evergreen species.

Figure 2: Satellite image map of sampled adult tōtara, Hamilton New Zealand. Grey symbols represent trees in the individual growth environment; black symbols represent trees in the stand growth environment.

2.2.2. Environmental conditions







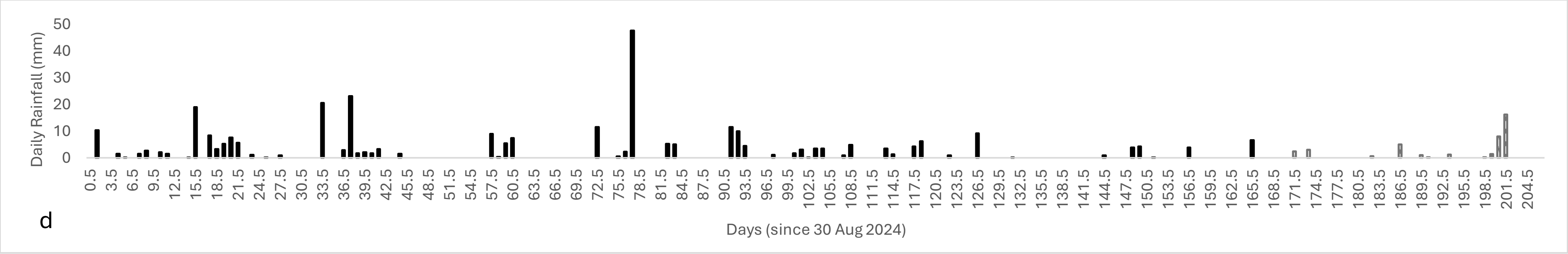


Figure 3: Daily values for environmental conditions across the length of time measurements were taken (a) total radiation at midday, (b) mean maximum and minimum temperature, (c) midday relative humidity, (d) total rainfall. Data sourced from nearby climate station (NIWA).

Daily environmental conditions varied over the 7 months of *in situ* measurements (Figure 3). Daily solar radiation at midday ranged from 203 to 1617μmolm^{-2}s^{-1} with an upward trend observed from late spring to mid-summer, November to January (Figure 3a). Daily maximum temperatures ranged from 12.6 to 30.7°C with the highest max temperatures observed from December to March, while daily minimum temperatures ranged from 1.4 to 19.9°C with the lowest min temperatures observed from August to October (Figure 3b). Relative humidity at midday ranged from 39% to 98% with a downward trend observed in the summer months, January to March (Figure 3c). Daily rainfall ranged from 0 to 47.6mm with the lowest rainfall occurring in the month of January with a total rainfall of 18.4mm over the entire month (Figure 3d).

2.2.3. Leaf gas exchange in distinct growth environments

Lower sunlit branches were selected to measure in trees growing in the individual growth environment (tree 1-3), lower branches were selected to measure in trees growing in the stand environment (tree 4-6)(Givnish, 1988) as sunlit branches were not always available, and the same branches were measured each measurement day. Leaf age of sampled shoots was not consistent for the duration of measurements, leaves from the previous season's growth were measured for the first seven measurement days (August-November 2024), then partway through the growth season a switch was made to leaves of the current season's growth for the remainder of measurements (January 2025-March 2025). One measurement day the previous seasons leaves and current seasons leaves were measured on the same day for comparison (December 2024). Measurements were taken using a portable photosynthesis system with an

LED 2x3cm chamber (Model LI-6400-02B, LI-COR). Measurement days took place twice a month, weather and equipment permitting. Three shoots were selected per tree for measurement each measuring day. Environmental parameters within the chamber such as temperature and PAR were set to match the surrounding conditions at each tree. The concentration of CO_2 in air supplied to the chamber was set at 420ppm, the assumed concentration of atmospheric CO_2 (Friedlingstein et al., 2025). Photosynthetic parameters measured included net photosynthetic rate (*A*, μmol CO_2 $m^{-2}s^{-1}$), stomatal conductance (g_s, mol H_2O m^{-2} s^{-1}) and the concentration of intercellular CO_2 (C_i, ppm). *In situ* net photosynthetic rate was chosen to report over maximum photosynthetic rate as the data collected was linked to measurements of stable C isotope discrimination in tōtara (further information in Chapter 3). Photosynthetic rates were allowed to stabilize before three consecutive measurements were logged for each shoot, each log roughly 10 seconds apart. Average values were calculated across the three logged measurements for key photosynthetic parameters to continue with data analysis.

2.2.4. Photosynthetic response parameters

Four tōtara saplings (approx. 5 years old) that were grown under well-watered greenhouse conditions were selected for measurement. Photosynthetic response curves were generated for changes in light (PAR), CO_2, and vapour pressure deficit (VPD) conditions. The photosynthetic responses of the youngest, fully expanded shoots were measured using a portable photosynthesis unit (Model LI-6400XT, LI-COR) with an LED 2x3cm chamber, to assess photosynthetic parameters such as; maximum carboxylation rate (V_{cmax}), maximum electron transport rate (J), triose phosphate utilization (TPU), apparent quantum yield (ϕ), light compensation point (LCP), maximum photosynthetic rate (A_{max}), curvature (θ) and stomatal conductance to water vapour (g_s) (further detail provided in Chapter 3)(Lohammar et al., 1980; Sharkey et al., 2007). Calculations of gas exchange in both adult tōtara in the field and saplings in the glasshouse required correction for actual leaf area enclosed in the leaf chamber. Shoots were photographed alongside an object of a known length, and images were processed using ImageJ software to ascertain projected leaf area. This process had the potential to introduce human error in the leaf area results, this is important to consider when interpreting the data (Schmiege et al., 2021).

2.2.5. Light response

Six shoots across the four saplings were assessed to ascertain photosynthetic response to changes in light conditions in tōtara, two of the six shoots returned irrational photosynthetic parameter values for C3 plants, and this data was therefore excluded. Initially conditions within the chamber were set to maximum light (1500 $\mu molm^{-2}s^{-1}$ PAR) and zero CO_2 to incentivize the opening of stomata to a suitable level for measurement (stomatal conductance of 0.1 $molm^{-2}s^{-1}$). The concentration of CO_2 in air supplied to the chamber was set at 400ppm, temperature within the chamber was set at ambient temperature (25°C). Light levels began at maximum for the system (1500 $\mu molm^{-2}s^{-1}$ PAR), then reduced in step changes as follows; 1200 1000 800 600 400 200 100 90 80 70 60 55 50 45 40 35 30 25 20 10 0. Measurements were set to log every 120 seconds.

2.2.6. CO_2 response

Eight shoots were sampled across the four saplings to ascertain photosynthetic response to changes in CO_2 conditions in tōtara. Initially conditions within the chamber were set to maximum light (1500 μmolm^{-2}s^{-1} PAR) and zero CO_2 to incentivize the opening of stomata to a suitable level for measurement (stomatal conductance of 0.1 molm^{-2}s^{-1}). Light levels within the chamber were kept at maximum (1500 μmolm^{-2}s^{-1} PAR), temperature within the chamber was set at ambient temperature (25°C). The concentration of CO_2 in air supplied to the chamber was set at 400ppm initially, then adjusted in step changes as follows; 0 25 50 75 100 150 200 300 400 600 800 1000 1500. Measurements were set to log every 120 seconds.

2.2.7. Stomatal response to changes in VPD

Four shoots were sampled across the four saplings to ascertain stomatal response to changes in vapour pressure deficit (VPD) in tōtara. Initially conditions within the chamber were set to maximum light (1500 μmolm^{-2}s^{-1} PAR) and zero CO_2 to cause the opening of stomata to a suitable level for measurement (stomatal conductance of 0.1 molm^{-2}s^{-1}). Light levels within the chamber were set at maximum (1500 μmolm^{-2}s^{-1} PAR), temperature within the chamber was set at room temperature (25°C), and the concentration of CO_2 in air supplied to the chamber was set at 420ppm. Initially air supplied to the chamber bypassed dryerite to reflect ambient RH, then the air flow rate through the water vapour trap was adjusted in stepwise changes at 1 hour intervals until the air entering the leaf chamber was completely dry. Measurements were set to log every 120 seconds.

2.2.8. Data analysis

Data analysis was performed using a combination of two-way analysis of variance (ANOVA) in Microsoft Excel and three distinct statistical photosynthesis models from Sharkey et al., 2007, Lohammar et al., 1980 and Kevin Tu (personal communication) also in Microsoft Excel. The use of processing spreadsheets was employed to calculate photosynthetic parameter values for tōtara using collected gas exchange response data. The parameters for photosynthesis response to changes in light were calculated using the quadratic equation (Farquhar & Wong, 1984):

$$A = \frac{\phi I + A_{max} - \sqrt{(\phi I + A_{max})^2 - 4\theta \phi I A_{max}}}{2\theta} - R_{dark} \tag{1}$$

Where A is the net photosynthetic rate, A_{max} is the light-saturated photosynthetic rate, I is the absorbed light, ϕ is the apparent quantum yield, θ is the curvature of the response and R_{dark} is dark respiration.

The parameters for the photosynthetic response to changes in CO_2 were modelled by the minimum of limitations in the subsequent equations (Von Caemmerer & Farquhar, 1981). Either Rubisco-limited using the following equation:

$$A = V_{cmax} \left[\frac{C_c - \Gamma^*}{C_c + K_c\,(1 + O/K_O)}\right] - R_d \tag{2}$$

Or RuBP-limited using the following equation:

$$A = J\,\frac{C_c - \Gamma^*}{4C_c + 8\Gamma^*} - R_d \tag{3}$$

Or TPU-limited using the following equation:

$$A = 3TPU - R_d \tag{4}$$

Where V_{cmax} is the maximum carboxylation rate, C_{c} is chloroplastic CO_2 concentration, Γ^* is the CO_2 compensation point, K_{c} is the Rubisco Michaelis-Menton constant for CO_2, K_{o} is the Rubisco Michaelis-Menton constant for O_2, O is oxygen concentration, R_{d} is mitochondrial respiration in the light, J is the electron transport rate and TPU is the triose phosphate utilisation rate (Sharkey et al., 2007). During data analysis R_{d} was assumed to be 0.5 of R_{dark} (dark respiration) as has been assumed in previous studies (Faber et al., 2022; Miyazawa et al., 2023).

Stomatal response to changes in VPD was modelled utilising collected gas exchange response data in tōtara saplings and applying the following equation (Lohammar et al., 1980):

$$g_s = g_{smin}\left(1 + \frac{VPdL - D_{\mathrm{min}}}{D_0}\right)^{-1} \tag{5}$$

Where g_s is stomatal conductance to water vapour, g_{smin} is minimum stomatal conductance, VPdL is leaf-to-air vapor pressure deficit, D_{min} is the VPD threshold below which stomatal response does not occur and D_0 is the scaling parameter controlling sensitivity.

2.2.9 A simple photosynthesis model

Data to inform the model was extracted from gas exchange measurements of tōtara saplings grown under well-watered greenhouse conditions. Data from the light and VPd response curves measured on the saplings was used to fit parameters to the Medlyn model (Medlyn et al., 2011), while the CO_2 response curves provided fitted values for V_{cmax} and J in tōtara.

Environmental data (PAR, temperature, CO_2 concentration and VPd) from the time of *in situ* measurements in adult tōtara was extracted from a nearby NIWA climate station to parameterise the Medlyn-coupled leaf level A and g_s model.

Data collected during CO_2 response measurements were excluded to avoid model over-fitting, and only light and VPD response data used. Values for A and g_s were then modelled using a combination of approaches. The Farquhar-von Caemmerer-Berry (FvCB) model (Eqn. 2-4) was used to predict A (Von Caemmerer & Farquhar, 1981), while C_i was solved numerically by coupling g_s and A using the approach proposed by Medlyn et al. (2011):

$$g_s^* \approx g_0 + \left(1 + \frac{g_1}{\sqrt{D}}\right)\frac{A}{C_a} \tag{6}$$

Where g_s^* is optimal stomatal conductance, g0 and g1 are fitted parameters.

The model does not accurately predict A and g_s below the light compensation point, therefore these data points were excluded.

2.3. Results

2.3.1. *In situ* leaf gas exchange in distinct growth environments

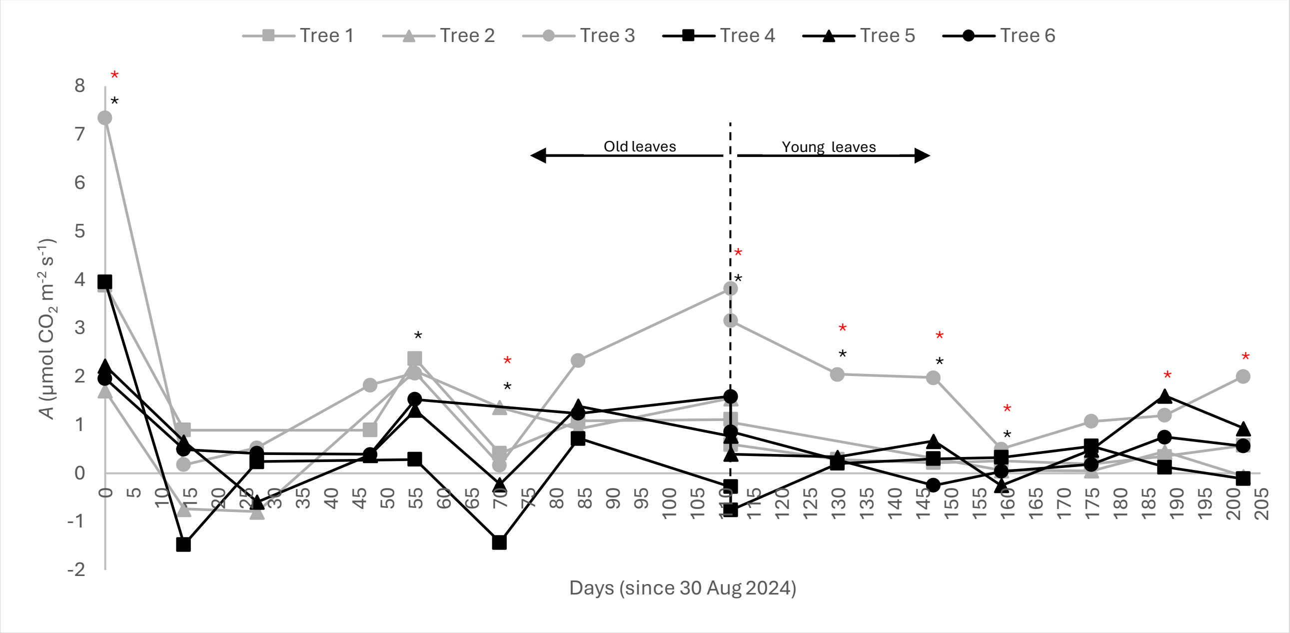


Figure 4: Average in situ *A* (net photosynthetic rate) for *Podocarpus totara* in stand vs. individual growth environments from August 2024 to March 2025, Hamilton New Zealand. Grey denotes individual growth environment, black denotes stand growth environment. Note: * indicates significant differences between each tree, * indicates significant differences between trees in distinct growth environments.

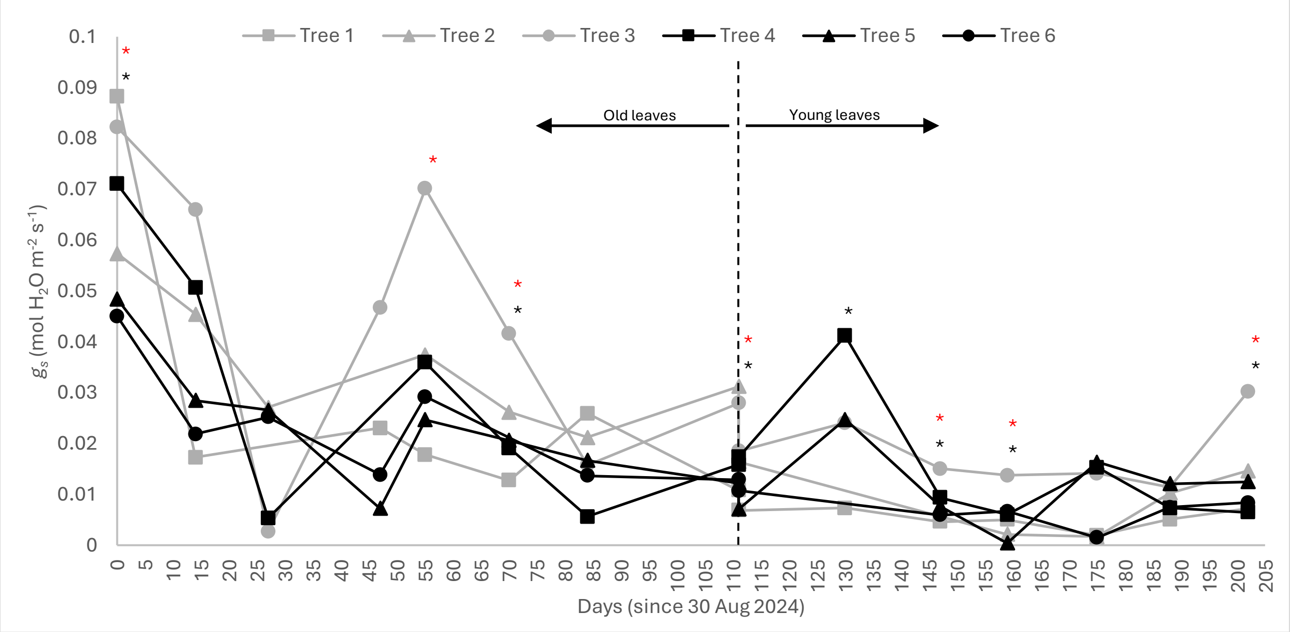


Figure 5: Average in situ g_s (stomatal conductance) for *Podocarpus totara* in stand vs. individual growth environments from August 2024 to March 2025, Hamilton New Zealand. Grey denotes individual growth environment, black denotes stand growth environment. Note: * indicates significant differences between each tree, * indicates significant differences between trees in distinct growth environments.

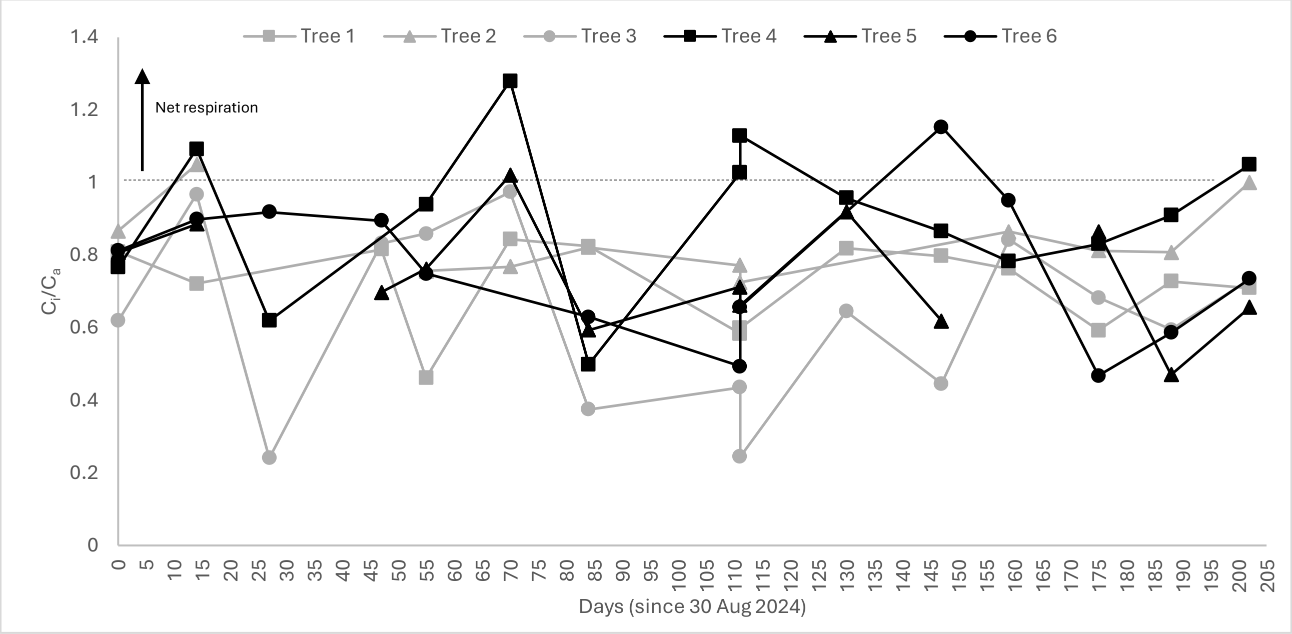


Figure 6: Average in situ C_i/C_a (ratio of intercellular to ambient concentration of CO_2) for *Podocarpus totara* in stand vs. individual growth environments from August 2024 to March 2025, Hamilton New Zealand. Grey denotes individual growth environment, black denotes individual growth environment, black denotes stand growth environment.

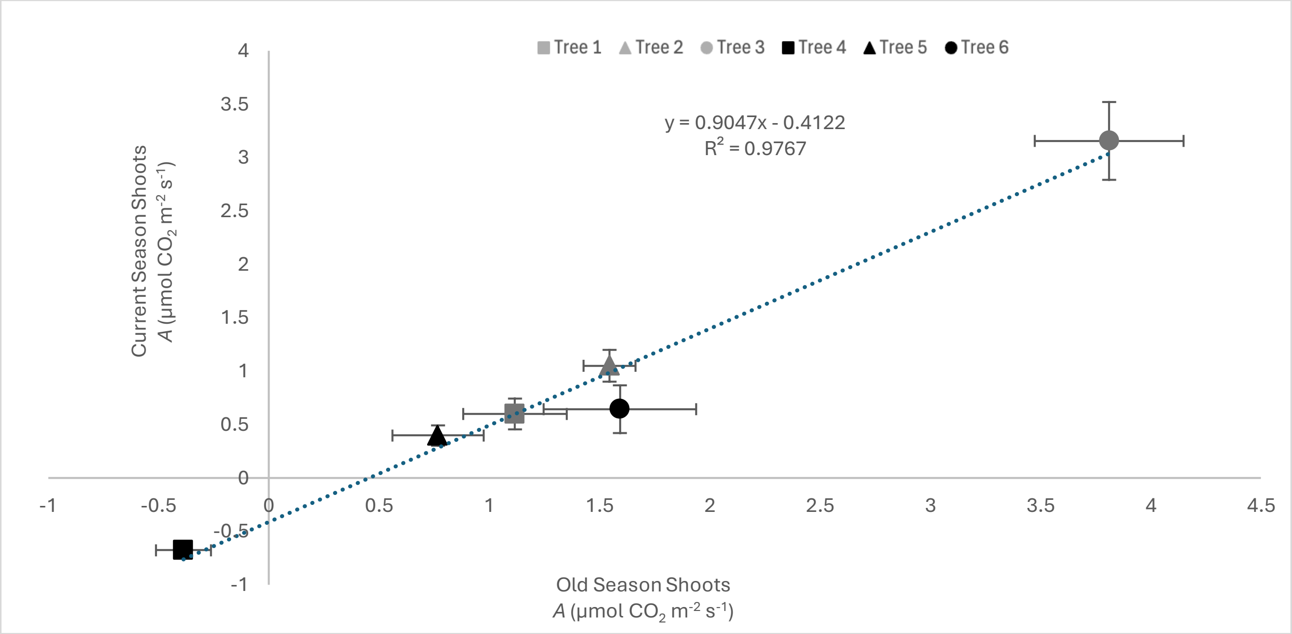


Figure 7: Average measured *A* (net photosynthetic rate) of old season growth vs current season growth shoots for each sampled tōtara on the same measurement day. Grey denotes individual growth environment, black denotes stand growth environment.

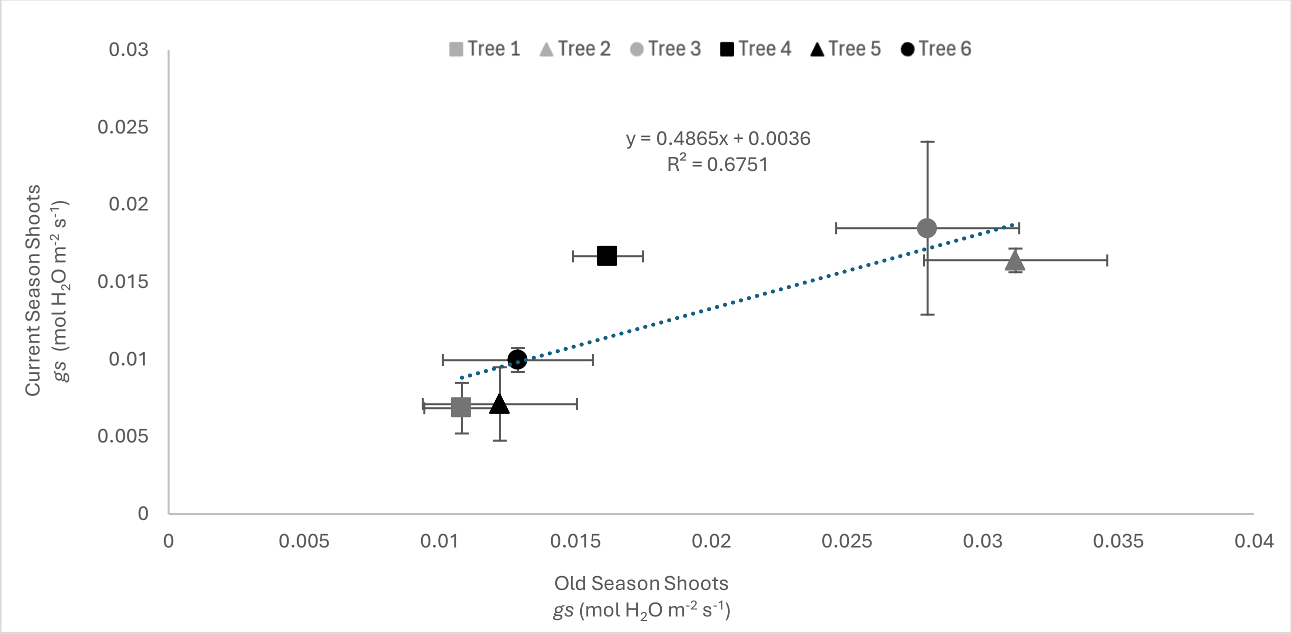


Figure 8: Average measured g_s (stomatal conductance) of old season growth vs young season growth shoots for each sample tōtara on the same day. Grey denotes individual growth environment, black denotes stand growth environment.

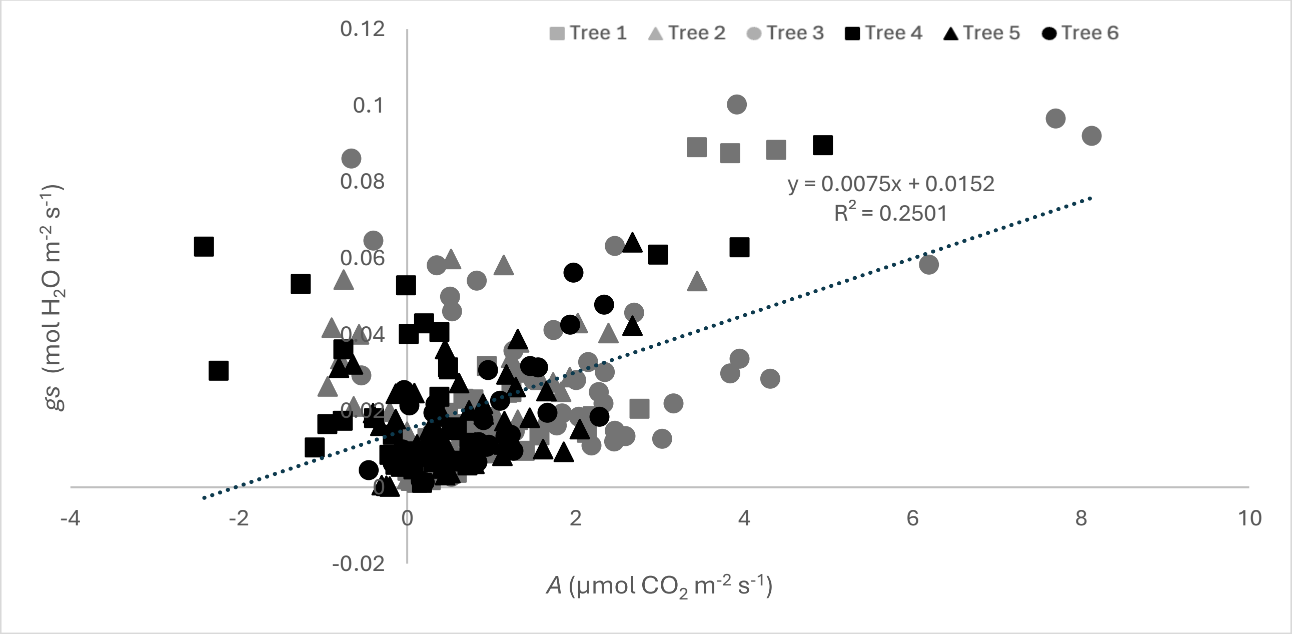


Figure 9: Relationship between average observed g_s (stomatal conductance) and *A* (net photosynthetic rate) in adult tōtara. Grey denotes individual growth environment, black denotes stand growth environment.

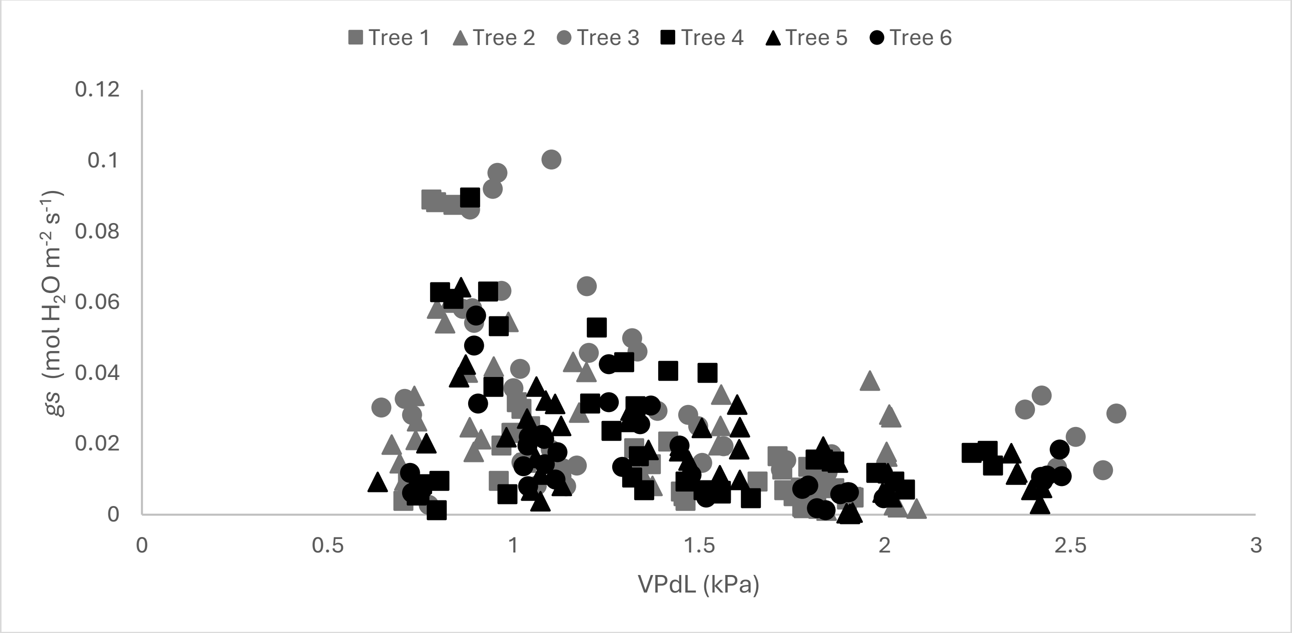


Figure 10: Relationship between average observed g_s (stomatal conductance) and VPdL (leaf-to-air vapor pressure deficit) in adult tōtara. Grey denotes individual growth environment, black denotes stand growth environment.denotes individual growth environment, black denotes stand growth environment.

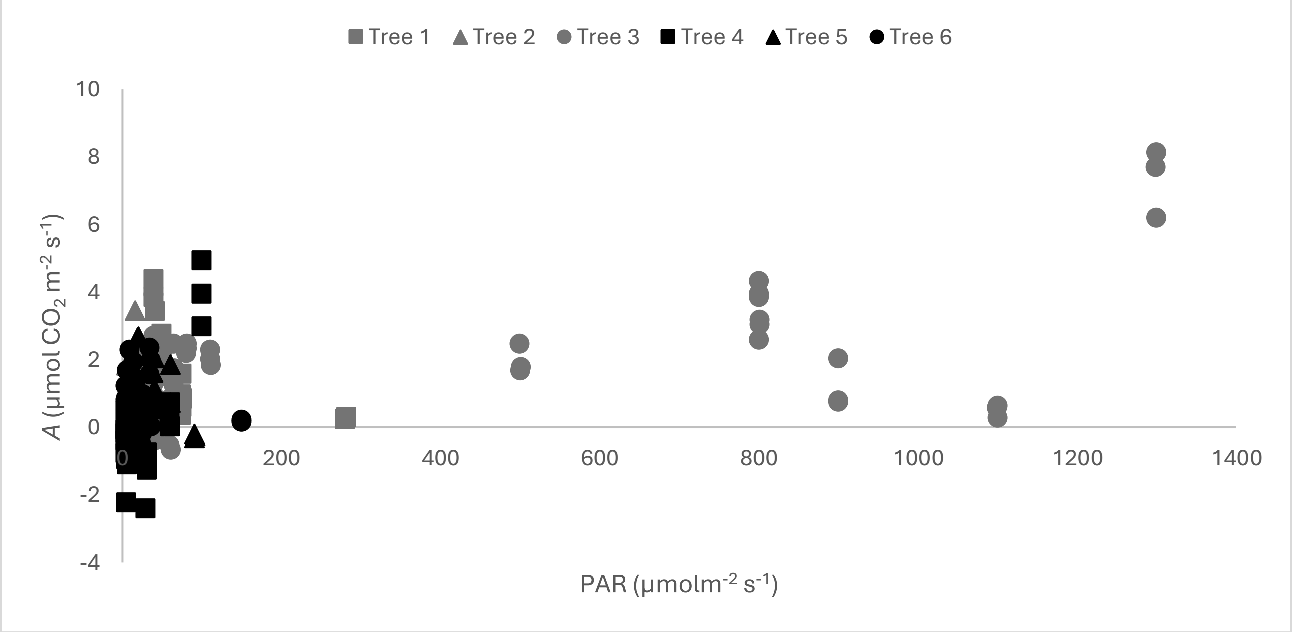


Figure 11: Relationship between average observed *A* (net photosynthetic rate) and PAR (photosynthetically active radiation) in adult tōtara. Grey denotes individual growth environment, black denotes stand growth environment.

Large variability was observed in net photosynthetic rates in the course of *in situ* measurements of the adult tōtara, with the highest recorded rate 7.3 µmol CO_2 m^{-2} s^{-1} and the lowest at net respiration -1.5 µmol CO_2 m^{-2} s^{-1} (Figure 4). The average measured net photosynthetic rates of tōtara in the two distinct growth environments displayed statistically significant differences on seven out of fourteen measurement days, while statistically significant differences in net photosynthetic rates between each of the observed trees was found on eight out of fourteen measurement days. The highest net photosynthetic rates were observed in an individual growth environment tree (Tree 3) and the lowest net photosynthetic rates were observed in a stand growth environment tree (Tree 4).

Low stomatal conductance was observed in the course of *in situ* measurements of the adult tōtara, with the highest recorded conductance 0.088 mol H_2O m^{-2} s^{-1} and the lowest 0.0004 mol H_2O m^{-2} s^{-1} (Figure 4). The average measured stomatal conductance of tōtara in the two distinct growth environments displayed statistically significant differences on seven out of fourteen measurement days, while statistically significant differences in stomatal conductance between each of the observed trees was found on eight out of fourteen measurement days. Consistent with the observed net photosynthetic rates, the highest average stomatal conductance was observed in an individual growth environment tree (Tree 1) and the lowest average stomatal conductance was observed in a stand growth environment tree (Tree 5). Large variability was observed in C_i/C_a values in the course of *in situ* measurements of the adult tōtara, with the highest recorded value 1.28 and the lowest 0.24 (Figure 5). Tree 4 displayed the highest values for C_i/C_a on seven out of fourteen measurement days and displayed net respiration on four measurement days, while Tree 3 displayed the lowest values for C_i/C_a on six out of fourteen measurement days.

A statistically significant difference was observed in average net photosynthetic rate between individual and stand growth environment trees over the course of seven months of measurements, where the individual growth environment trees displayed higher net photosynthetic rates than the stand growth environment trees (A=1.15 µmol CO_2 $m^{-2}s^{-1}$ and A=0.47 µmol CO_2 $m^{-2}s^{-1}$, respectively; p=0.0135). Observed average stomatal conductance was greater in individual growth environment trees than in stand growth environment trees over the same time period, although no statistically significant difference was observed (g_s=0.025 mol H_2O $m^{-2}s^{-1}$ and g_s=0.018 mol H2O $m^{-2}s^{-1}$, respectively; p= 0.2120).

Measurements for net photosynthetic rate were recorded for old season growth and new season growth on the same shoot and on the same measurement day (19 Dec 2024) for each tree (Figure 7). The measured rates showed a very strong positive correlation, with ~98% of variation in net photosynthetic rates of new season growth explained by the net photosynthetic rates observed in old season growth (r^2=0.98, p<0.001). Further, statistically significant differences were observed in net photosynthetic rates between old season growth and new season growth for each tree (p<0.001). Measurements for stomatal conductance were recorded for old season growth and new season growth on the same shoot and on the same measurement day for each tree (Figure 7). The measured stomatal conductance showed a moderate positive correlation, with ~68% of variation in stomatal conductance of new season growth explained by the stomatal conductance observed in old season growth (r^2=0.6751, p<0.05). Further, statistically significant differences were observed in stomatal conductance between old season growth and new season growth for each tree (p<0.001).

A positive relationship was observed between g_s and A in adult tōtara (Figure 8). A negative exponential relationship was observed between g_s and VPdL in adult tōtara (Figure 9), consistent with same relationship observed in tōtara saplings (Figure 11). The same general trend in data was observed between *A* and PAR in adult tōtara as was observed in tōtara sapling response curves (Table 1), although differences between observed trends may be due to the fact that the adults in this study were subject to more environmental variability compared to the saplings which were grown in greenhouse conditions.

2.3.2. Leaf level response to changing conditions

2.3.2.1 Light and CO_2 response

Table 2: Fitted photosynthetic parameters from A/C_i and light response curves of tōtara saplings grown under well-watered greenhouse conditions. Values of maximum carboxylation rate (V_{cmax}), electron transport rate (J), triose phosphate utilization (TPU), apparent quantum yield (ϕ), light compensation point (LCP), maximum photosynthetic rate (A_{max}) and curvature of the response (θ) are presented per shoot and as means (±SE).

Sample	**V_{cmax}**	**J**	**TPU**	**ϕ**	**LCP**	**A_{max}**	**θ**
	μmol $m^{-2}s^{-1}$	μmol $m^{-2}s^{-1}$	μmol $m^{-2}s^{-1}$	mol/mol	μmol $m^{-2}s^{-1}$	μmol $m^{-2}s^{-1}$	------
Leaf 2	36.6	49.9	7.8	0.059	45.9	12.5	0.010
Leaf 3	40.0	83.1	9.4	0.070	36.7	13.3	0.010
Leaf 5				0.091	34.6	10.6	0.430
Leaf 6				0.090	22.1	9.3	0.014
Leaf 1	12.0	21.8	2.9				
Leaf 4	39.3	54.5	9.4				
Leaf 7	28.0	42.8	5.7				
Leaf 8	23.4	39.5	4.5				
Leaf 9	28.1	55.5	9.1				
Leaf 10	49.2	114.3	9.7				
Average	**32.1**	**57.7**	**7.3**	**0.078**	**34.8**	**11.4**	**0.12**
Standard Err.	**4.1**	**10.1**	**0.93**	**0.008**	**4.9**	**0.90**	**0.10**

Large variation was observed in fitted electron transport rate in tōtara saplings (~5 years old) when sapling response to changes in CO_2 conditions was measured, with the highest recorded 114.28 $\mu molm^{-2}s^{-1}$ and the lowest recorded 21.81 $\mu molm^{-2}s^{-1}$ (Table 1). Lower levels of variation were observed in triose phosphate utilisation rate with a maximum of 9.74 $\mu molm^{-2}s^{-1}$ and a minimum of 2.90 $\mu molm^{-2}s^{-1}$, and maximum carboxylation rate with a maximum of 49.18 $\mu molm^{-2}s^{-1}$ and a minimum of 12.04 $\mu molm^{-2}s^{-1}$. Large variation was observed in the fitted light compensation point parameter in tōtara saplings when sapling response to changes in light conditions was measured, with the highest calculated light compensation point 95.50 $\mu molm^{-2}s^{-1}$ and the lowest 7.97 $\mu molm^{-2}s^{-1}$. Little variation was observed in the parameters of apparent quantum yield, maximum net assimilation rate or the curvature of the response. A_{max} was also more consistent, ranging from 9.3 to 13.3 $\mu mol\ m^{-2}s^{-1}$.

2.3.2.2. Stomatal response to changes in VPD

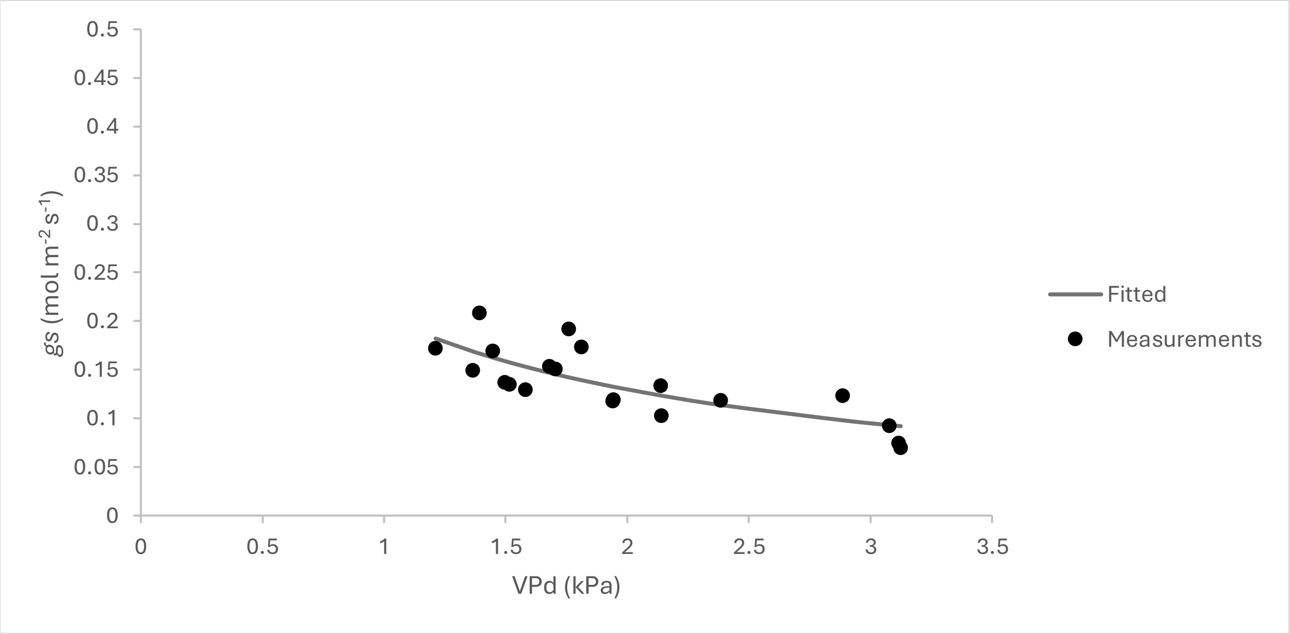


Figure 12: Measured stomatal conductance response to changes in VPD in tōtara saplings grown under greenhouse conditions.

Stomatal response to changes in vapour pressure deficit was measured in tōtara saplings grown under greenhouse conditions (Figure 12). Stomatal conductance decreased nonlinearly with increasing vapour pressure deficit, with the lowest average measured 0.07 molm^{-2}s^{-1} and the highest 0.21 molm^{-2}s^{-1}. Values for response parameters were fitted using Equation 5 (g_{smin}=0.204 mol H_2O m^{-2} s^{-1}, therefore g_{smin}= 0.128 mol CO_2 m^{-2} s^{-1}, D_0=1.74 kPa, D_{min}=1 kPa).

2.3.2.3. A simple photosynthesis model

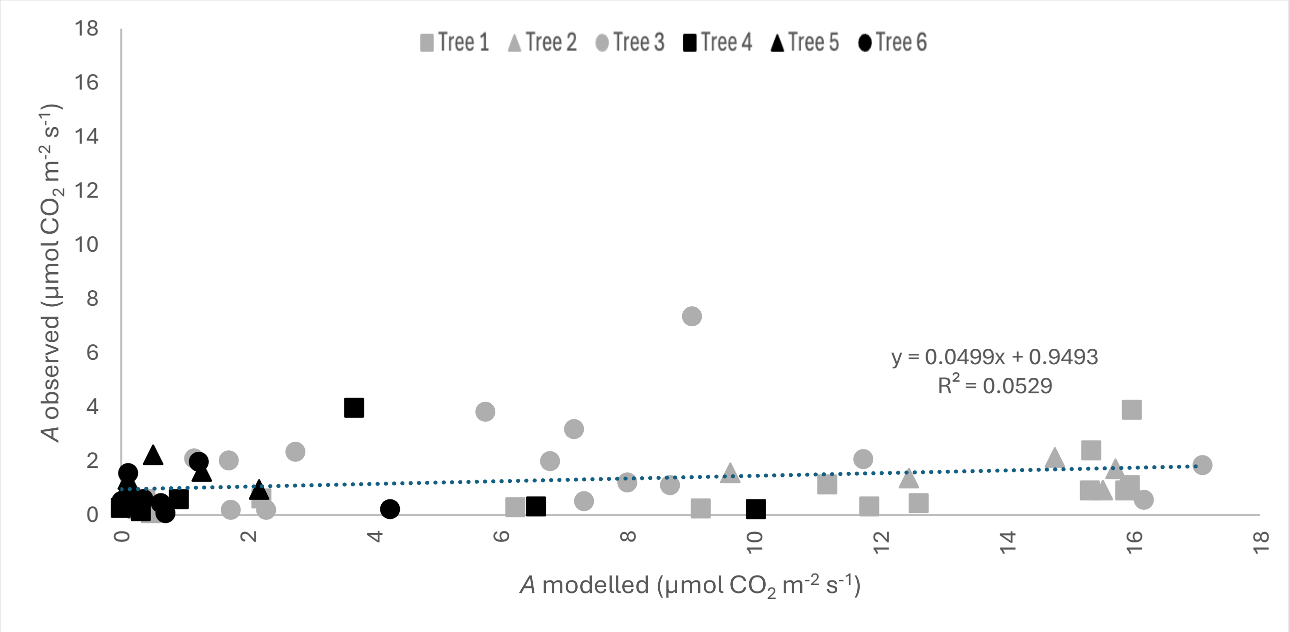


Figure 13: Relationship between observed and modelled values for *A* (net photosynthetic rate) in tōtara. Grey denotes individual growth environment, black denotes stand growth environment.

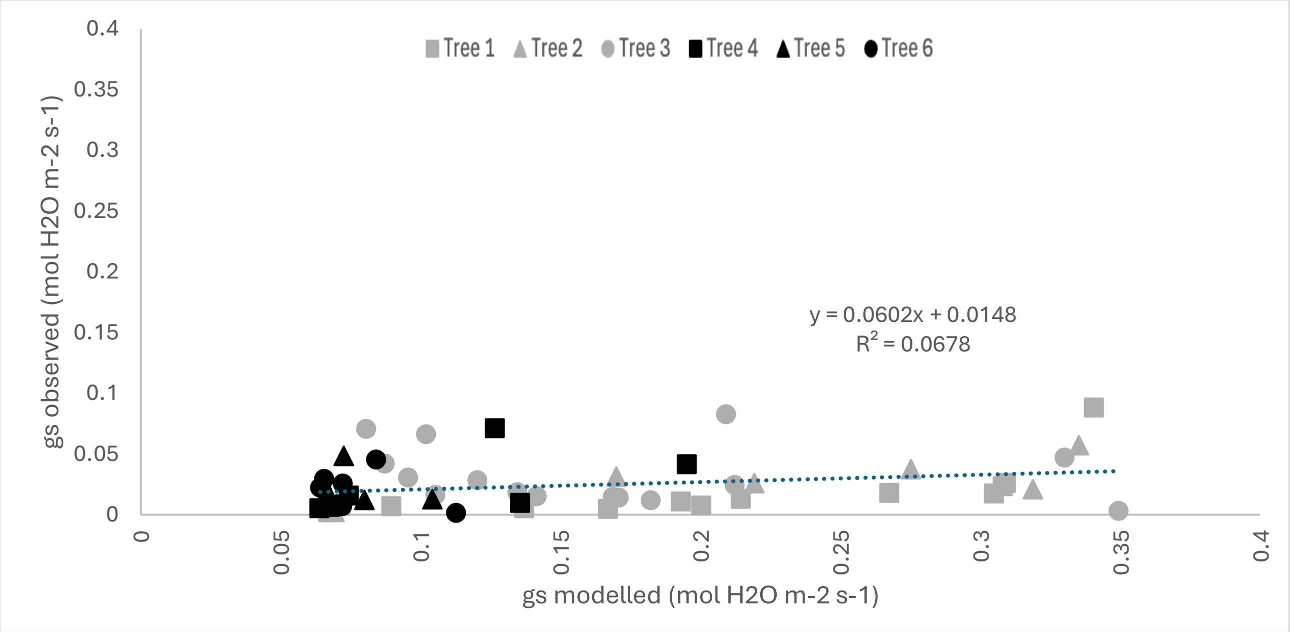


Figure 14: Relationship between observed and modelled values for g_s (stomatal conductance to water vapour) in tōtara. Grey denotes individual growth environment, black denotes stand growth environment.

Overall, there was no statistically significant correlation between modelled and observed values for *A* and g_s in tōtara using the Medlyn approach (p=0.09 and p=0.05, respectively). Large variation was seen in modelled and observed values, with the model generally predicting higher values than observed, especially in the individual growth environment trees (Figure 7 & 8).

2.4. Discussion

2.4.1. *In situ* leaf gas exchange in distinct growth environments

Leaf level gas exchange measurements were carried out in this study with the understanding that there are a multitude of interrelated factors that affect gas exchange in the field, therefore rather than attempting to attribute variations in gas exchange processes in tōtara to one or more variables, this research aims to fill a gap in the literature on real world observational data regarding gas exchange in this ecologically and culturally important species. Observational measurements of adult tōtara revealed a significant difference in net photosynthetic rates between trees growing individually and trees growing in stands ($P<0.05$). While stomatal conductance was greater in trees growing individually, this difference was not statistically significant ($P>0.05$). Although these results are an integration of spot measurements made on adult tōtara over the course of seven months, large variability was observed between measurement days, and statistically significant differences were not necessarily observed every measurement day for net photosynthetic rates. Statistically significant differences were observed in stomatal conductance on seven out of fourteen measurements days (Figures 2 & 3). The ratio of intercellular to ambient concentrations of CO2 (C_i/C_a) is important when considering controls on plant physiological function and is related to the supply of CO2 into the leaf (stomatal conductance, g_s) and the demand for CO_2 from the chloroplasts (photosynthesis, A)(Figure 4)(Palma et al., 2020). As each adult tōtara was growing in slightly different micro-climates, the most obvious control on the observed difference in A is the differences in irradiance experienced by tōtara growing in the individual growth environment and those growing in the stand growth environment. Tōtara growing in the stand growth environment were in competition with other plants surrounding them for light as light interception in the stand growth environment was greater, while the tōtara growing in the individual growth environment experienced self-shading only (Will et al., 2001) and therefore higher levels of irradiance. Higher levels of irradiance drive higher rates of photosynthesis. Out of necessity the lower branches of each tree were measured and for the stand growth environment trees this meant more shaded branches were measured, resulting in potentially lower rates of A than might have been found in the upper canopy where light interception was highest (Bown et al., 2024).

There is limited data available in the literature comparing the physiological responses of adult gymnosperms to differing growth environments such as has been done in this study, and virtually none with a focus on Podocarpaceae. Ebbett & Ogden (1998) investigated the growth of seedlings of five native New Zealand podocarp species under differing light levels, including tōtara, to draw some conclusions regarding the regeneration strategy for each species. The study looked at the seedlings of podocarps *Dacrycarpus dacrydioides* (kahikatea)*, Dacrydium cupressinum* (rimu), *Prumnopitys ferruginea* (miro), and *Prumnopitys taxifolia* (matai) along with tōtara for a period of 15 months, measuring the effect of different light regimes on growth under greenhouse and forest conditions. Previous studies have highlighted that tōtara is relatively light demanding (Bergin & Kimberley, 2014) and therefore the least shade tolerant of the five podocarps and the authors findings supported this conclusion. Tōtara saplings in this study displayed an increase in height and dry weight with increasing light levels, and this response on average was greater than that observed in the other podocarp seedlings. The authors therefore suggest that tōtara employs the use of a catastrophic regeneration strategy and is able to respond to increased light following disturbance in a forest canopy. Although this study did not measure net photosynthetic rate directly, these findings support the proposition that tōtara is relatively sensitive to the levels of irradiance in its growth environment and subsequently supports the findings of the current research.

Bown et al. (2024) explored the effectiveness of using the $\delta^{13}C$ of leaf respired CO_2 to investigate differences in physiology between 20 year old adjacent stands of kahikatea and tōtara under the same environmental conditions. To check the validity of this technique they also carried out measurements of gas exchange at the shoot level, including net photosynthetic rate and stomatal conductance, and evaluated whether these variables changed with canopy height. The authors found that shoot level net photosynthetic rates increased in both species with canopy height and related this to an increase in photosynthetically active radiation with increased canopy height. Higher rates of shoot level net photosynthesis were observed in kahikatea, although the authors suggest that due to nutrient availability and limitation this did not result in higher rates of net canopy photosynthesis when the two stands were compared. The authors found that spot measurements of stomatal conductance in both species did not display the same positive relationship with canopy height. The findings of this study also support the proposition found here that shoot-level net photosynthetic rates in tōtara are affected by variation in light levels, affecting the demand rather than the supply of CO_2 when the tree is not under saturating light.

Another consideration to make when interpreting the data from this research is that each sample tree was growing in locations with differences in topography, therefore, (unquantified) variations in soil moisture and nutrient availability were likely.

2.4.2. Tōtara in relation to Podocarpaceae

Podocarpaceae are a key component of forest structure in Aotearoa New Zealand, but they are also widely distributed elsewhere in the Southern Hemisphere and even in limited locations in the Northern Hemisphere (Simpson, 2017). Comparable values for *in situ* shoot level net photosynthetic rates and stomatal conductance in Podocarpaceae from the literature are limited. The net photosynthetic rates observed in the current research were low, as expected from a gymnosperm (Lucia et al., 2003; Lusk et al., 2003; Palma et al., 2020; Schmiege et al., 2021; Tissue et al., 2005), exhibited considerable variability (-1.47 to 7.34 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$ with an average of 0.8053 $\mu mol\ CO_2\ m^{-2}\ s^{-1}$) and net respiration was observed in at least one of the six trees on nine out of fourteen measurement days (Figure 2). The stomatal conductance observed in the current research were also very low (0.0004 to

0.0882 mol H_2O m^{-2} s^{-1}, average of 0.0216 mol H_2O m^{-2} s^{-1})(Figure 3), as expected from tōtara (Bown et al., 2024). The previously discussed paper by Bown et al. (2024) provides some values for tōtara and another podocarp native to New Zealand (kahikatea) for reference. The authors found that net photosynthetic rates at the shoot level in adult tōtara ranged between ~1-4 µmol m^{-2} s^{-1} at ambient field conditions, while rates in adult kahikatea ranged from ~1-7 µmol m^{-2} s^{-1} at ambient field conditions. Measurements of stomatal conductance made concurrently with those of net photosynthesis in their study ranged from ~0.01-0.04 mol m^{-2} s^{-1} in tōtara, but more variability was observed in kahikatea with values ranging from ~0.02-0.15 mol m^{-2} s^{-1}. Another study investigated constraints on photosynthesis in three species of young angiosperms and three species of young conifer under controlled conditions, with two of these conifers of interest belonging to the Podocarpaceae (rimu and miro) and native to New Zealand (Lucia et al., 2003). Measurements were made at ~20°C, a photon flux density of 500 µmol m^{-2} s^{-1} and a CO_2 concentration of 355ppm. The authors found that the average net photosynthetic rate of rimu was the lowest of the species studied at 5.2 µmol m^{-2} s^{-1} (±1 SD), with average rates in miro also relatively low at 6.8 µmol m^{-2} s^{-1} (±1 SD). The average stomatal conductance measured in this study were 0.0944 mol m^{-2} s^{-1} (±0.024 SD) in rimu and 0.0816 mol m^{-2} s^{-1} (±0.026 SD) in miro.

Lusk et al. (2003) investigated the role of photosynthetic traits in terms of competitive advantage between adult evergreen angiosperms and adult evergreen conifers in North and South America, with two of the studied conifers belonging to the Podocarpaceae (*Podocarpus saligna*, mañío de hojas largas; *Podocarpus nubigena*, mañío macho). The authors observed an average net photosynthetic rate of 6.2 µmol m^{-2} s^{-1} in mañío de hojas largas and an average net photosynthetic rate in mañío macho of 7.9 µmol m^{-2} s^{-1}. In terms of stomatal conductance, the mentioned conifers displayed average values of 0.07 mol m^{-2} s^{-1} and 0.115 mol m^{-2} s^{-1}, respectively. Strobl et al. (2011) investigated the physiology of *Podocarpus falactus* saplings under distinct canopies of exotic and native species in southern Ethiopia. The authors measured a number of different photosynthetic variables in the saplings, including net photosynthetic rates and stomatal conductance at ambient field conditions over the course of two years. The authors reported that typical net photosynthetic rates for the saplings ranged from 0-3 µmol CO_2 m^{-2} s^{-1} over the course of an entire day under native forest canopy, 0-4 µmol CO_2 m^{-2} s^{-1} under a *Pinus* canopy, and 0-3 µmol CO_2 m^{-2} s^{-1} under a *Eucalyptus* canopy on a more overcast day. Typical stomatal conductance under the same conditions was reported at 0-0.06 mol m^{-2} s^{-1} under native forest canopy, 0-0.05 mol m^{-2} s^{-1} under a *Pinus* canopy, and 0-0.03 mol m^{-2} s^{-1} under a *Eucalyptus* canopy.

The values recorded in the current research for net photosynthetic rates and stomatal conductance in adult tōtara appear to be within the range of values from the literature of these photosynthetic variables in Podocarpaceae, both in New Zealand and elsewhere.

2.4.3. Old season and new season growth

Net photosynthetic rate and stomatal conductance for old season and new season shoots of adult tōtara are reported above, where the relationship between net photosynthetic rates in shoots of different ages was very strongly correlated across all six trees (Figure 5). This suggests that the variability observed in new season growth can be explained by that observed in old season growth, and therefore the controls on photosynthetic rate are the same regardless of shoot age (Wong et al., 1985). Concurrent measurements of stomatal conductance revealed a correlation between values in shoots of different ages that is not as strong as for *A* (Figure 6). There is a gap in the current literature around the direct measurement of the effect of leaf age on photosynthetic rates and stomatal conductance in podocarps, although these effects in other conifers are reasonably well represented (Han et al., 2008; Macinnis-Ng et al., 2017; Tissue et al., 2001; Turnbull et al., 1998). It is acknowledged in the literature that in conifers, younger leaves generally display higher photosynthetic rates and stomatal conductance than older leaves, and this has been at least partially attributed to an adjustment of nutrient resource partitioning from old to new growth (Macinnis-Ng et al., 2017). Interestingly, the photosynthetic rates observed in the adult tōtara in this study were consistently higher in the last seasons growth compared to the new season growth. Macinnis-Ng et al. (2017) investigated leaf gas exchange in *Agathis australis* (kauri), another evergreen conifer native to New Zealand, and found that leaf age had a measurable effect on C assimilation rates and stomatal conductance. The authors found that the highest values for both variables were observed in one year old growth, and the lowest values were observed in the current year growth. This pattern was attributed to the fact that the current year growth was not yet fully expanded and hardened at the time of the study (January 2013). The results of this previous study may potentially explain the patterns observed in the effect of leaf age in the current research as well. Although young shoots were measured at a time when they were assumed to be fully expanded and photosynthetically operational (December 2024), they may not have yet been at full capacity.

2.4.4. Leaf level response to changing conditions

2.4.4.1. Light and CO2 response

Tōtara response to changing CO_2 and light conditions was measured in the youngest, fully expanded leaves of saplings grown under well-watered greenhouse conditions (Table 1). Values for maximum carboxylation rate were highly variable and ranged from 12-49.2 µmol

$m^{-2}s^{-1}$ in tōtara, higher than values recorded for other podocarps such as in rimu with a reported range of 9.4–11.9 µmol $m^{-2}s^{-1}$ (Tissue et al., 2005) or in multiple species of podocarps (*Podocarpus neriifolius, Dacrydium elatum, Dacrycarpus imbricatus, Nageia wallichiana*) in Vietnam with a relatively broader range of 10-40 µmol $m^{-2}s^{-1}$ (Schmiege et al., 2021). Values for electron transport rate in tōtara also displayed high variability with a range of 21.8-114.3 µmol $m^{-2}s^{-1}$, a broader range than reported in other podocarps in the previously mentioned studies; 32.3-40.3 µmol $m^{-2}s^{-1}$ in rimu (Tissue et al., 2005) and 20-90 µmol $m^{-2}s^{-1}$ in multiple species of podocarps in Vietnam (Schmiege et al., 2021). Data was unavailable in the literature for comparison of triose-phosphate-utilisation in tōtara to other podocarps, however the average value observed (7.3 µmol $m^{-2}s^{-1}$) appears rational when considering the value reported for temperate evergreen gymnosperms of 6 ± 0.9 µmol $m^{-2}s^{-1}$ (Kumarathunge et al., 2019).

Apparent quantum yield in tōtara ranged from 0.059-0.091 mol/mol with low levels of variation, this range sits at the higher end of the range reported by Schmiege et al. (2021) of 0.02-0.09 mol/mol across multiple species of podocarps. The range of apparent quantum yield in tōtara is also broader than that reported for *Podocarpus falcatus* of 0.065 – 0.077 mol/mol (Fetene & Feleke, 2001). The range of values observed for light compensation point in tōtara were relatively high (22.1-45.9 µmol $m^{-2}s^{-1}$), a marked difference to those reported by Schmiege et al. (2021) of 2-28 µmol $m^{-2}s^{-1}$ across multiple species of podocarps. Values for maximum photosynthetic rate in tōtara were relatively consistent, ranging from 9.3-13.3 µmol $m^{-2}s^{-1}$. These values are at the higher end when compared with values reported in other podocarps in the literature, such as in *Podocarpus guatemalensis* with a range of 2-9 µmol $m^{-2}s^{-1}$ (Dalling et al., 2016) or in *Podocarpus falcatus* with a range of 7-16.4 µmol $m^{-2}s^{-1}$

(Fetene & Feleke, 2001). The range observed in tōtara also sits above that observed by Schmiege et al. (2021) across four species of podocarps with a range of 2-10 µmol $m^{-2}s^{-1}$.

Variation in photosynthetic processes is expected across species, including those within the same family, as demonstrated here for Podocarpaceae. As discussed previously in this chapter, other factors that can influence the photosynthetic variables discussed include environmental conditions and plant age. The tōtara examined for photosynthetic response to changing conditions in this study were saplings grown under well-watered greenhouse conditions. Therefore, direct comparison of their photosynthetic responses with reported values for other podocarps measured in field environments may not always be appropriate, given the substantially greater environmental variability in field settings. This consideration should be kept in mind when interpreting the data presented here. The comparative studies referenced include both field-based (Schmiege et al., 2021; Tissue et al., 2005) and greenhouse-based (Dalling et al., 2016; Fetene & Feleke, 2001) observational studies.

2.4.4.2 Stomatal response to changes in vapour pressure

As expected, stomatal conductance in tōtara remained relatively low throughout the duration of this study. The sensitivity of stomatal response in tōtara to changes in vapour pressure deficit (Leuning, 1995) observed in this study (D_0=1.74 kPa) differed from that observed in tōtara in the study conducted by Bown et al. (2024)(D_0=0.52 kPa). The greater value in this study for the variable D_0 reflects less stomatal sensitivity to vapour pressure deficit than in the previous study. Bown et al. (2024) also reported a D_0 value for another podocarp, kahikatea, and the authors observed D_0=0.32 kPa in this species, or in other words higher stomatal sensitivity to vapour pressure deficit in this species compared to either of the values reported for tōtara. The sampled trees in this previous study were growing outside in the soil and were small trees, not saplings. Therefore, the differences observed in stomatal sensitivity to VPD may be due to tree age. Data on podocarp stomatal sensitivity to VPD is limited, while stomatal sensitivity to VPD appears to be higher in some conifer species and lower in others (Medlyn et al., 2011). In descending order of sensitivity, D_0 values have been reported for the following: *Picea sitchensis* (Sitka spruce A)(D_0=0.35 kPa), *Pinus taeda* (Duke Pine)(D_0=1.15 kPa) and *Picea sitchensis* (Sitka spruce B)(D_0=1.89 kPa). Of the reported values for D_0 from the three conifer species and two podocarp species discussed, only *Picea sitchensis* displayed less stomatal sensitivity to VPD than that observed in tōtara saplings.

2.4.4.3. A simple photosynthesis model

The Medlyn approach used in this simple photosynthesis model was not able to predict trends seen in the observed data from measurements of *A* and g_s in tōtara (Figures 7 & 8). This result may be due to a number of reasons. Firstly, the data used to inform the model was taken from measurements made on tōtara saplings grown under well-watered greenhouse conditions. Values for *A* and g_s in saplings are acknowledged in the literature to be higher than in adults of the same species (Tissue et al., 2005). Additionally, the environmental conditions that the saplings were grown in within the greenhouse were optimal for plant growth in regard to temperature, light and water availability. These optimal conditions were often absent for the observed adult tōtara in this study as observational measurements were taken in the field amongst variable environmental conditions which likely meant (unquantified) water and nutrient limitations . Both of these factors may have caused the model to overestimate values for both *A* and g_s.

Another potential limitation of the unified stomatal model is that it does not include consideration of the effect of the availability of soil water on leaf gas exchange, which has been proven in previous studies to have a measurable effect (Barbour et al., 2007, 2011; G. Farquhar & Wong, 1984; Medlyn et al., 2011).

Chapter Three: C isotope composition

3.1. Introduction

Stable isotopes are atoms of an element with differing numbers of neutrons as the common atom but the same number of protons and electrons, and which don't isotopically decay over time. The difference in neutrons results in these isotopes having a different molecular weight and therefore alters the way they behave in biochemical processes. In the natural world there are two stable isotopes of carbon, with the more common isotope ^{12}C (~98.9%) and the less common ^{13}C (~1.1%)(Farquhar et al., 1989). It has been proven that the lighter isotope (^{12}C) is preferentially used by plants in the process of C_3 photosynthesis, and this preference enables the examination of this ubiquitous process in fine detail. The ratio of ^{12}C to ^{13}C is commonly reported as a difference in carbon isotope composition ($\delta^{13}C$) relative to a standard (in the case of carbon isotopes, commonly Pee Dee belemnite, PDB) while the preference for the lighter isotope in the process of photosynthesis is referred to as carbon isotope discrimination ($\Delta^{13}C$)(Farquhar et al., 1989).

The study of carbon isotope discrimination in plants can provide insights into the conditions experienced by a plant due to the links between stomatal conductance (g_s), photosynthetic rate (*A)* and the ratio of intercellular to ambient CO_2 concentrations (C_i/C_a), which themselves are affected by variables such as maximum carboxylation rate (V_{cmax}), electron transport rate (J), light compensation point (LCP), vapour pressure deficit (VPD), and photosynthetically active radiation (PAR) (Bown et al., 2024; Field, 1983). The following equation (Bown et al., 2024; G. Farquhar et al., 1982) was used to calculate $\Delta^{13}C$:

$$\Delta = \left(\delta^{13}C_a - \delta^{13}C_p\right)/\left(1 + \delta^{13}C_p\right) \tag{7}$$

Where $\delta^{13}C_a$ is the isotopic composition of air (assumed to be -8.5‰, (Bown et al., 2024) and $\delta^{13}C_p$ is the isotopic composition of, in this case, leaf-respired CO_2. Further, the ratio of internal to external partial pressure of CO_2 was calculated using the following equation (Bown et al., 2024):

$$C_i/C_a = (\Delta - a)/(b - a) \tag{8}$$

Where *a* and *b* are the assumed values for diffusional fractionation of CO_2 in air (*a*=4‰) and during the photosynthetic process (*b*=27‰)(Bown et al., 2024; G. Farquhar et al., 1982). Many studies have employed the use of $\delta^{13}C$ in leaf dry matter to investigate plant physiological characteristics and adaptive strategies such as water use efficiency (Dalling et al., 2016; Macinnis-Ng et al., 2017; Strobl et al., 2011). However, a method developed by Barbour, built on previous research on the use of the stable isotope composition of CO_2 respired by leaves ($\delta^{13}C_{Rl}$) provides a high frequency, rapid measurement technique suitable for the purposes of this study (Barbour et al., 2007), that has previously been used for tōtara (Bown et al. 2024).

Rubisco preferentially fixes ^{12}C over ^{13}C during carboxylation in the Calvin cycle (Farquhar et al., 1982), which results in $\delta^{13}C$ of, in this case, leaf-respired CO_2 that is depleted in the heavier isotope when compared to a standard (PDB)(Barbour et al., 2007; Farquhar et al., 1989). Although the lighter isotope is preferred, depending on a range of variables Rubisco does not always have the option to choose ^{12}C over ^{13}C, related to the supply and demand of CO_2 in the leaf and therefore the ratio of C_i/C_a. Supply in this case refers to g_s which allows

CO_2 to enter the leaf, while demand refers to chloroplastic demand, or photosynthesis (A), which takes CO_2 out of the leaf. When g_s is high, C_i is high and therefore Rubisco is able to preferentially select ^{12}C over ^{13}C, while the opposite also remains true. When A is high and therefore C_i is low, Rubisco has a limited resource of C and subsequently fixes relatively more of the heavier isotope, while the opposite also remains true in this case as well. As g_s and A directly affect C_i and therefore $\delta^{13}C$ it is necessary to consider factors that affect these variables. Leaving aside CO_2 for the moment, it is commonly accepted that *A* is affected by environmental factors such as availability of PAR and the availability of H_2O as components of photosynthesis. At the same time g_s is affected by environmental factors such as the availability of soil water, as signals transmit from roots to the stomata when soil water is less than optimal to facilitate stomatal closure and the mitigation of water loss (Comstock, 2002). $\delta^{13}C$ is therefore an integration of past environmental conditions experienced by the plant, although important to note here is that values for $\delta^{13}C$ can suggest that either *A* or g_s has affected C_i but cannot clearly attribute this to one variable or the other.

Complementing the instantaneous gas exchange measurements of the previous chapter, stable isotope composition offers valuable integrative insights. Analysis of the carbon isotope ratio of leaf-respired CO2 ($\delta 13C_{Rl}$), often measured simultaneously with gas exchange (Barbour et al., 2007), can provide an integrative signal related to recent photosynthetic water-use efficiency (Barbour et al., 2011; G. Farquhar et al., 1982).

3.2. Materials and methods

The six adult tōtara on the University of Waikato Hamilton Campus that were sampled for leaf gas exchange measurements (Figure 1) were also sampled to investigate $\delta^{13}C$ of leaf-respired CO_2 in tōtara. Shoot samples were collected that included tissue from the current season and previous seasons growth. These samples were collected on the same days that leaf gas exchange measurements were taken between October 2024 and March 2025.

Following collection, shoot samples were incubated in the absence of light for a minimum of 2 hours (Barbour et al., 2011; Bown et al., 2024), the shoots were then placed in sealed Tedlar bags and ambient air removed from the bags. The Tedlar bags were then filled with different gases dependent on which laser gas analyzer was used for measurement. The use of N gas was employed when using a cavity ring-down spectrometer (CRDS) or, the use of compressed air that was scrubbed of CO_2 with the use of soda lime was employed when using a tunable diode laser (TDL, Barbour et al., 2011) for measurement. The shoots were further incubated for a minimum of 30 minutes in darkness to allow the concentration of respired CO_2 in the sample bags to reach a level conducive to measurement (>1000ppm for the CRDS and between 300 and 500ppm for the TDL). The $\delta^{13}C$ of respired CO_2 was then measured by pumping air from the Tedlar bags through a CRDS or a TDL (TGA100A; Campbell Scientific). Measurements were recorded for data analysis. Data analysis was performed using two-way analysis of variance (ANOVA) in Microsoft Excel, where data was compared between each tree and between trees grouped by distinct growth environments.

3.3. Results

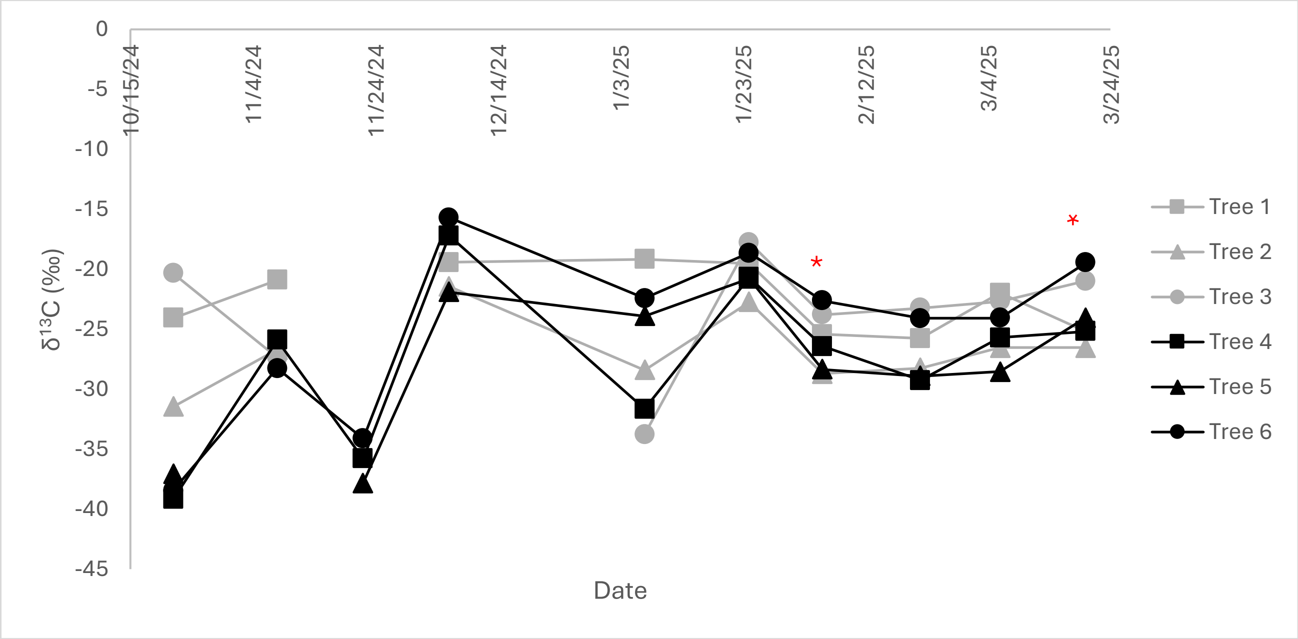


Figure 15: $\delta^{13}C$ of leaf-respired CO_2 from *Podocarpus totara* in individual and stand growth environments from October 2024 to March 2025. Grey denotes individual growth environment, black denotes stand growth environment. Note: * indicates statistically significant differences between each tree.

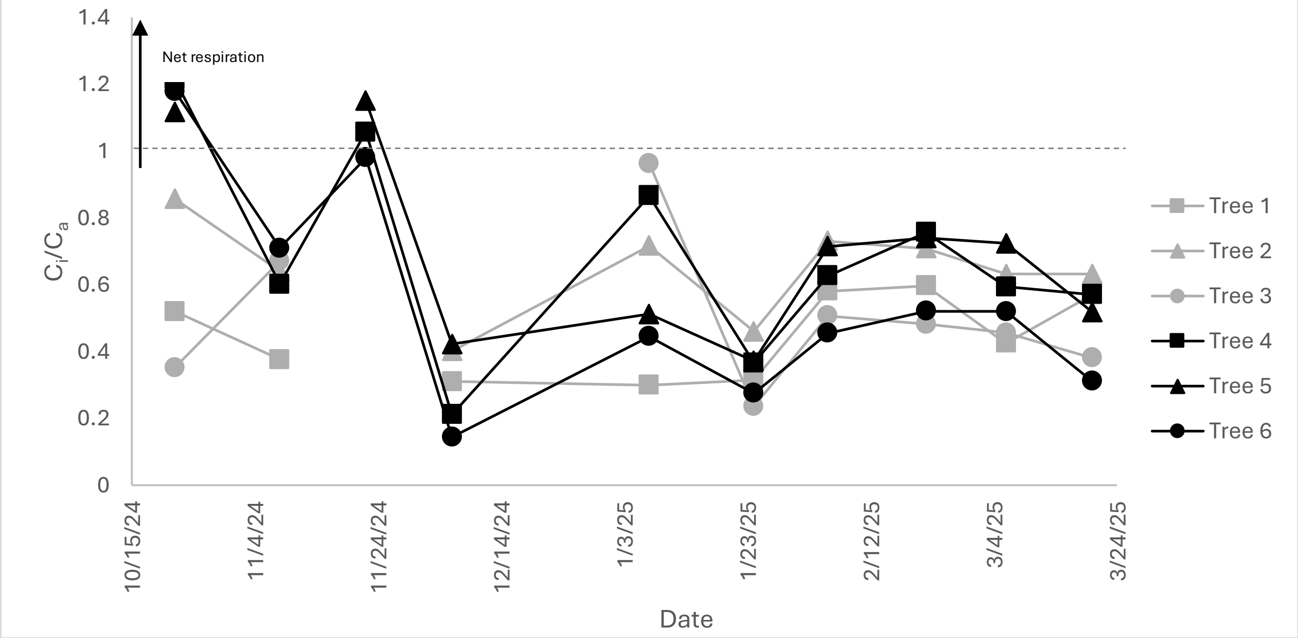


Figure 16: C_i/C_a calculated from $\delta^{13}C$ of leaf-respired CO_2 from *Podocarpus totara* in individual and stand growth environments from October 2024 to March 2025. Grey denotes individual growth environment, black denotes stand growth environment.

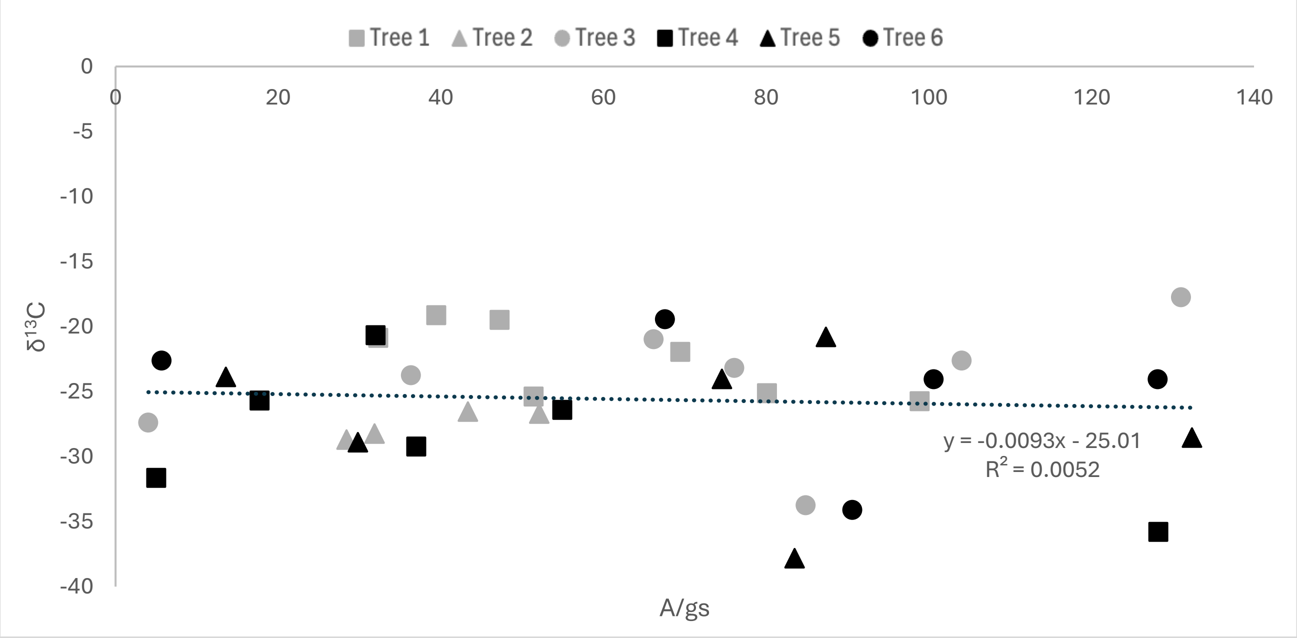


Figure 17: δ^{13}C of leaf-respired CO_2 from *Podocarpus totara* in individual and stand growth environments plotted against observed values of A/g_s from in situ leaf gas exchange measurements from the same trees on the same measurement days. Grey denotes individual growth environment, black denotes stand growth environment.

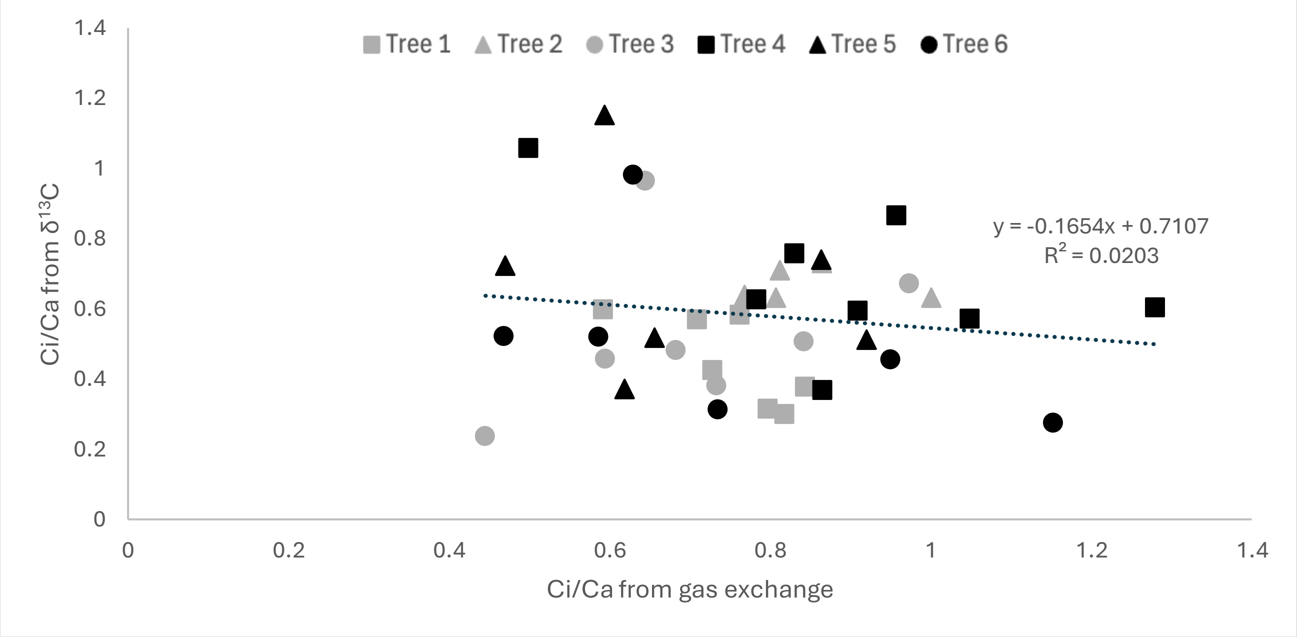


Figure 18: C_i/C_a calculated from measurements of δ^{13}C vs. observed values of C_i/C_a from in situ leaf gas exchange measurements from the same trees on the same measurement days. Grey denotes individual growth environment, black denotes stand growth environment.

Five irrational values of δ^{13}C of leaf-respired CO_2 from adult *Podocarpus totara* were excluded from analysis. The most likely cause of these irrational values was human error in the sampling process resulting in gas leaking from the sample or instrument error. No statistically significant difference was observed in measured $\delta^{13}C$ of leaf-respired CO_2 between each tree over the course of all measurements taken in the five months (Oct 2024 – Mar 2025, Figure 15)(p=0.1542). Focusing in on each measurement day, statistically significant differences in measured $\delta^{13}C$ of leaf-respired CO_2 were found between each tree on two of the measurement days between January and March 2025 (p=0.04 for both)(Figure 15). Measured $\delta^{13}C$ of leaf-respired CO_2 in the stand environment trees displayed more variation (-15.7‰ to -39.2‰) than in $\delta^{13}C$ of leaf-respired CO_2 measured in the individual growth environment trees (-17.8‰ to -33.8‰). The $\delta^{13}C$ of leaf-respired CO_2 measured in the stand growth environment trees was on average more negative than the $\delta^{13}C$ of leaf-respired CO_2 measured in the individual growth environment trees (-26.8‰ and -24.3‰, respectively), however when comparing the difference in $\delta^{13}C$ of leaf-respired CO_2 between samples from the two distinct growth environments the difference was not statistically significant (p>0.18). The least negative $\delta^{13}C$ of leaf-respired CO_2 for all trees was measured on the 06 December 2024, followed by the 24 January 2025. A general trend of less negative $\delta^{13}C$ of leaf-respired CO_2 was observed over the course of measurements, from spring to summer to autumn (Figure 15).

Stand growth environment trees (trees 4-6) displayed the highest values of C_i/C_a on 6 out of 10 measurement days with net respiration calculated in stand growth environment trees on 2 out of 10 measurement days (Figure 16). As this ratio was calculated from measurements of $\delta^{13}C$ of leaf-respired CO_2 the values reported follow the same trends as $\delta^{13}C$, with greater ratio values corresponding with more negative $\delta^{13}C$. No relationship was observed between $\delta^{13}C$ of leaf-respired CO_2 and observed values of A/g_s from *in situ* measurements of leaf gas exchange in tōtara (refer to Chapter 2 for more detail) from the same trees on the same measurement days (Figure 17). No relationship was observed between values of C_i/C_a calculated from $\delta^{13}C$ of leaf-respired CO_2 and observed values of C_i/C_a from *in situ* measurements of leaf gas exchange in tōtara (refer to Chapter 2 for more detail) from the same trees on the same measurement days (Figure 18).

3.4. Discussion

No statistically significant difference was found between $\delta^{13}C$ of leaf-respired CO_2 in adult tōtara growing in distinct growth environments. The general trend of $\delta^{13}C$ becoming less negative over the course of measurements was expected as measurements took place from mid-spring to through to the beginning of autumn. Carbon-water plant dynamics are the key to understanding this pattern.

Over the course of the measurements taken in this study atmospheric concentrations of CO_2 were assumed to have remained relatively consistent, therefore discussion will focus on the C_i component of the C_i/C_a ratio. As previously discussed, g_s controls to a large extent the supply of CO_2 entering the leaf for photosynthesis. At the same time g_s is affected by environmental factors such as the availability of soil water, as signals transmit from roots to the stomata when soil water is less than optimal to facilitate stomatal closure and the mitigation of water loss (G. D. Farquhar & Sharkey, 1982). Taking this into account, the patterns seen over the course of measurements of $\delta^{13}C$ of leaf-respired CO_2 in tōtara begin to make sense. Plants are constantly balancing water loss against C gain (Medlyn et al., 2011), which becomes more difficult in the warmer months as precipitation decreases and temperature and VPD increases. These environmental conditions did take place over the course of leaf gas exchange measurements in tōtara and in fact a drought was officially recognised in the summer of 2024-2025. Under water limitation conditions g_s decreases as plants attempt to mitigate water loss, which therefore leads to a decrease in C_i. This decrease in C_i results in less depleted $\delta^{13}C$ of leaf-respired CO_2 as Rubisco has a limited resource of C and therefore cannot discriminate as much against the heavier isotope. This trend was observed here in the measurements of $\delta^{13}C$ of leaf-respired CO_2 in tōtara (Figure 12).

The range of $\delta^{13}C$ of leaf-respired CO_2 in tōtara found in this research is relatively wide and at the more negative end when compared to other values found in the literature (-15.7‰ to -39.2‰, Figure 12)(Bown et al., 2024; Mortazavi et al., 2012). Bown et al. (2024) also measured $\delta^{13}C$ of leaf-respired CO_2 in tōtara and reported results of approximately -22‰ to -24‰, a range a lot narrower than that reported here. The authors also measured $\delta^{13}C$ of leaf-respired CO_2 in another podocarp, kahikatea, and reported results of -25‰ to -27‰, again a much narrower range than found in the current research. Slightly wider ranges have been reported in *Pinus spp.* (Mortazavi et al., 2012). Mortazavi et al. (2012) measured $\delta^{13}C$ of leaf-respired CO_2 in *Pinus elliottii* and in *Pinus palustris* and reported values of -26 to -32‰ and -23 to -29‰, respectively. Although the results for *Pinus elliottii* were the broadest and most negative $\delta^{13}C$ of leaf-respired CO_2 the variation in values was not as extreme as those measured in the current research. The very depleted values of $\delta^{13}C$ of leaf-respired CO_2 found in tōtara were most likely due to artefacts during sampling or analysis, post-photosynthetic fractionation processes that weren't included in the simple interpretation of $\delta^{13}C$ or the source CO_2 during the period that the carbon was being fixed being more negative than -8.5‰ that was assumed.

No relationship was found between $\delta^{13}C$ of leaf-respired CO_2 and observed values of A/g_s from *in situ* measurements of leaf gas exchange in tōtara (Figure 14), and no relationship was observed between values of C_i/C_a calculated from $\delta^{13}C$ of leaf-respired CO_2 and observed values of C_i/C_a from *in situ* measurements of leaf gas exchange in tōtara (Figure 15). When considering these results, it is important to remember that the *in situ* measurements of leaf gas exchange are a snapshot of gas exchange at one point in time, while $\delta^{13}C$ of leaf-respired CO_2 is an integration of environmental conditions experienced by the plant over time. In fact, research by Bown et al. (2024) supports the results found here. The authors found that there was a 2 day lag in the relationship between C_i/C_a calculated from $\delta^{13}C$ of leaf-respired CO_2 and observed values of C_i/C_a from gas exchange measurements. The authors related this to the possibility of limited abundance of sugars and carbohydrates coupled with low rates of *A* in the canopy (Bown et al., 2024).

The significance of mesophyll conductance (g_m) as a limitation on photosynthesis was intentionally excluded from the main calculations in this study with support from Bown et al. (2024) for this approach. Evidence from other research involving native New Zealand conifer species (Lucia et al., 2003; Veromann-Jürgenson et al., 2020) indicates that values for g_m typically range between 13 and 35 $mmolm^{-2}s^{-1}$, a range that sits within the values measured for g_s in the current study. Mesophyll conductance is recognized as a variable physiological parameter, fluctuating in response to external conditions, including temperature (Shrestha et al., 2019), leaf anatomical and biochemical characteristics (Knauer et al., 2022) and the presence of hydraulic gradients within the canopy structure (Whitehead et al., 2011). While incorporating g_m into photosynthetic analyses is generally necessary to prevent overestimations of water-use efficiency at the canopy scale (Vernay et al., 2020), it was not feasible to perform measurements of g_m for tōtara in the current research. Although including gm was not possible or necessary in this research, this may be a gap in the literature that future research could focus on.

Chapter Four: Mātauranga Māori

4.1. Introduction

Tōtara is considered significant in our understanding of both the human and the more-than-human world, in relation to Mātauranga Māori, the knowledge system of the Indigenous peoples of Aotearoa New Zealand. This significance frames the current thesis, which represents my understanding of tōtara in both contexts: in previous chapters from the perspective of Western Science, and in the following chapter from my limited experience with Mātauranga Māori. At this point, it is important for me to note that I do not pretend to be an expert in mātauranga; rather, my reflections here are offered from a place of curiosity and as a student with much still to learn from both knowledge systems (that is, both Western Science and Mātauranga Māori). As a woman of Māori descent who was raised at a remove from her culture and has studied the natural sciences for five years across two science degrees, the techniques and style of this chapter are not wholly familiar to me. The aim of this chapter is to bring together an exploration of tōtara through both Western Science and Mātauranga Māori, and an exploration of my own identity and experiences in relation to this. In the following pages, my story will be expanded upon, along with tōtara's place in the Māori world, connections between tōtara and others, and a synthesis of my understanding of tōtara in both contexts.

Tēnā koutou katoa,
Ko Maungatautari tōku maunga,
Ko Waikato tōku awa,
Ko Tainui tōku waka,
Ko Ngāti Hauā tōku iwi,

Ko Ngāti Te Oro tōku hapu,

Ko Raungaiti tōku marae,

Ko Mani tōku whanau,

Ko Lomia Quinn tōku ingoa,

No reira tēnā koutou, tēnā koutou, tēnā koutou katoa

Above is my pepeha, a formal introduction of myself in te reo Māori (the Māori language), expressed through a narrative of where I stand in my connections to others. As a fundamental custom of Māori culture, pepeha is a way of acknowledging and honouring one's connection to the land and to one's ancestors. To assist with understanding, included below is the English translation of my pepeha:

Greetings to you all,

Maungatautari is my mountain,

Waikato is my river,

Tainui is my canoe,

Ngāti Hauā is my tribe,

Ngāti Te Oro is my subtribe,

Raungaiti is my marae,

Mani is my family,

Lomia Quinn is my name,

Therefore, greetings, greetings, greetings to you all

4.2. Tōtara in Te Ao Māori

Te ao Māori is the Māori world, or the world as it is understood through a Māori cultural lens. Māori worldviews typically encompass a holistic perspective on the world where everything is connected, from people to the oceans, to the atua (gods), and to the trees. Importantly, in this worldview, humans are connected to the more-than-human, and its expressions and practices are considered non-anthropocentric (Berning et al., 2024; Hikuroa, 2017; Kawharu, 2000). This worldview is based on and expressed through tīkanga, or the customary system of values, practice, custom, and ethics in Māori culture, which includes principles such as manaakitanga (hospitality/generosity), whanaungatanga (relationship/kinship), mana (prestige/authority), and tapu (sacred/restricted) (Hikuroa, 2017; Kawharu, 2000; Mead, 2016). As elucidated in the previous text, there is no direct English translation for the principles of tīkanga, as they possess multi-layered meanings. Another key principle of tīkanga is whakapapa, with two literal translations: genealogy/ancestry, and layering one upon another. Conceptually, whakapapa describes the idea of cause and effect, which links the past, present, and future. Whakapapa also describes connections through the convergence and divergence of causes and effects. Whakapapa is crucial to discuss when considering tōtara. In te ao Māori, the tōtara and humans are closely related through whakapapa, with tōtara being tuakana (older sibling) to humans (teina, younger siblings). Some pūrākau (myths/legends) describe tōtara as the first tree child of Tāne-mahuta and the first woman (Hineahuone), and, as in Māori cosmology, humans are also children of Tāne-mahuta. In this way, this wise tree is deemed our older sibling. When one considers this perspective, the significance of tōtara in te ao Māori begins to take shape.

Māori were once oceanic navigators, sailing between the islands of Polynesia using the stars, winds, and ocean currents as guides, and as such, waka (canoes) were integral to Māori as a people. The story of the carving of the first waka is relevant to mention here, both in terms of the connection to tōtara and to myself, and the following is as it has been recited to me by Dr Tom Roa, a Tainui leader and significant figure in Māori society (Roa, personal communication, August 8, 2025). The first waka was carved pre-Māori by our tupuna (ancestor) Rātā, who felled a breadfruit tree in Hawaiki to carve the Tainui waka. The method by which tohunga (skilled person/chosen expert) judged whether a tree was ready to be felled was by listening to the birds. The birds kākāriki and pohoitere would peck at the wood, and if they made a particular sound, the tohunga knew to leave the tree as it was still growing, but if they made a kind of "*thok-thok*" noise, the tohunga knew that the tree was close to falling naturally and was ripe for felling.

Rātā listened to the birds and heard the distinctive sound indicating that the tree was ready, and decided to cut down the breadfruit tree before it rotted. He felled the tree and that evening went home to sleep. The next morning, after breakfast, he returned to find that the tree was standing back up again. Once more, he chopped the tree down, left to return home and sleep, and came back the next day to find the tree standing back up again. So, a third time he chopped the tree down, but instead of returning home, he hid and watched. And watching, he saw the insects and the birds, and the forest life come together and put the tree that he'd felled back up. Seeing this, Rātā realised he wasn't working with his environment and hadn't reassured the forest life of his intentions in felling the tree, so the next day he returned and recited a karakia (prayer) to affirm the benefits of his actions to the forest life. He asserted to the mana whenua (those whose mana is attached to the land), the forest life, that the felling of this tree would be useful to mankind, who are the younger siblings of the birds and the insects and the other children of Tāne. After his recitation of the karakia, in recognition of tīkanga, the birds and insects of the forest actually came together and helped him to bring the tree down. And from this tree was carved the first waka, the Tainui waka.

Moving forward in time to the history of Māori in Aotearoa and connecting the story of Rātā to tōtara, waka have typically been carved from tōtara since the migration to Aotearoa, along with other prominent carvings such as pou (posts) that marked the significance of a place. Tōtara, with its association with tribal histories, is often a key component of marae carvings, and many important taonga (treasures) have been carved from this tree, such as Uenuku, one of the oldest pou. Particularly significant to me, being of Tainui descent, Uenuku was the atua that protected the Tainui people in times of war, and the spirit of this atua was carried with Tainui families on the waka that transported them to Aotearoa. When my tupuna arrived, they carved a pou from tōtara and placed this spirit into it, and this pou became Uenuku (Simpson, 2017). The attributes of this tree are well respected, and tōtara is often referred to as mighty, chiefly, strong, or wise, and is included in many whakataukī (proverbs). When mentioned in whakataukī, the characteristics further associated with this tree are generosity, vulnerability, usefulness, and beauty. One of the most well-known whakataukī around tōtara follows below:

“Kua hinga te tōtara o Te Waonui a Tāne”

Which translates into English as “A tōtara has fallen in the great forest of Tāne.” This whakataukī is used to acknowledge the passing of a respected community member or leader and to honour a life of indelible effect. Building on this, another significant whakataukī concerning tōtara has guided the current research as follows:

“E kore te tōtara e tū noa i te pārae engari me tū i roto i te wao-nui-a-Tāne”

Which translates in English to “The tōtara tree does not stand alone in the field but stands within the great forest of Tāne”. This whakataukī refers to the fact that strong leaders grow surrounded by others instead of in isolation. These are just a few examples of how tōtara is valued in Māori culture, historically and today.

4.3. Connecting with tōtara

For seven months from August 2024 until March 2025, I spent time with tōtara. When asking for advice and guidance around tōtara in Mātauranga Māori, Pā Ropata (respected rongoā Māori practitioner) advised “get to know the trees and they will tell you what you need to know” (McGowan, personal communication, July 20, 2025). Every fortnight, I visited the six adult tōtara interviewed in my project to ask them the question “How are you today?” and “How have you been since the last time I saw you?” (Barbour et al., 2023). In November-December 2024 and March 2025, I spent time with tōtara saplings in the university greenhouses, asking, “If your environment were to change, how would you experience and respond to this change?” In interviewing these trees, I have done so with the perspective that each tree is considered an ‘expert’ (Barbour et al., 2023). I have spent time with tōtara in winter, spring, summer, and autumn. I have seen the trees dominated by old-season growth; I’ve seen them flushed with bright green new growth, and the adult females fruiting with small, brightly coloured, fleshy receptacles. At an individual level, for each tree I have learnt characteristics that make them distinct and unique, and through this time spent connecting with tōtara, I have come to view them fondly as wise and still sentinels of this fast-paced world we live in.

Tree 1 stands at the front of the university, with a stretch of grass to one side, a driveway, a carpark, and a footpath on the other three. This tree stands proudly alone and exhibits the growth form characteristic of tōtara growing outside stands, which is relatively shorter and with multiple low branches (Bergin, 2000). This tree is a female that possesses short, thick, densely packed leaves and bears many small red fruits in the warmer months. This made her a favourite of tūī and other birds who visited frequently, whose song filled the air on many warm, golden afternoons, while I asked her how she was. Tree 2 stands alone at a bend in a driveway, on a patch of grass situated on a small slope. This tree also exhibits the growth form characteristic of tōtara growing outside stands, with relatively longer, thinner, and more widely spaced leaves. The microclimate surrounding this tree was colder and darker than that of Tree 1, which was often bathed in sunshine. Tree 2 is male, with flexible stems that drape and a section of foliage that appears yellow rather than the usual dark green.

Tree 3 is the most unique of the observed trees in this project. This tree is the only other adult female, grows on a slight incline, stands alone, and exhibits the growth form characteristic of tōtara growing outside stands. Tree 3 possesses dry, brittle stems that break easily and short, thick, densely packed leaves. This tree dropped its old-growth foliage the earliest of all observed adult trees and appeared to rely on new-season growth relatively early for photosynthesis. Interestingly, although this tree appeared the least 'healthy' of the six adults in terms of brittleness and bare branches, when 'interviewing' this tree, it was doing the best in some regards, comparatively to the others, with the highest photosynthetic rates recorded. Tree 4 is situated within a stand of tōtara and other mixed species and grows at the top of a slight slope. This male tree possesses the most sharply tipped leaves of all the observed adults, and this is something I experienced first-hand when the tips of his needles pierced my skin each time I interviewed him. Tree 4 appears to be the youngest of the adults in this study and has comparatively flexible stems and dark, glossy leaves that are thinner, longer, and more widely spaced.

Tree 5 is the tallest of the six adult trees and grows in a dense stand, at least partially dominated by other tōtara, situated in a dip in the surrounding topography. This tree exhibits most clearly the growth form of adult tōtara growing in stands, with a relatively straight trunk with few branches close to ground level, making it a little difficult to measure. The foliage of this male close to ground level was sparse, with many stems that only possessed old-season growth and did not flush with new growth during the growing season. The final tree, Tree 6, grows in a stand of tōtara and other mixed species at the top of a slope. This male tree possesses comparatively flexible stems and thin, long, and widely spaced leaves. The most unique characteristic of this tree is its branching pattern, which forms almost curtain-like arrangements of stems to orient leaves in the most advantageous way towards available sunlight.

Spending this time getting to know and connecting with these trees throughout this project was done with the understanding that we, as humans, are part of nature rather than separate from it. These ‘interviews’ were conducted using Western scientific techniques to ask questions of tōtara and record their answers in the language of what is important to them: sunlight and water availability, and the processes associated with these, such as photosynthesis.

4.4. A journey of reconnection

I am one of many Māori who have grown up disconnected from our culture, a product of colonialism in Aotearoa New Zealand. For most of my formative years, I was raised by my mum (of Māori and Samoan descent) and my stepdad (of Māori and European descent), although I did spend two years as a teenager with my biological father (of Scottish and Irish descent) and my stepmother (of Māori and Samoan descent). As a child, my parents travelled often for work, taking my siblings and me with them. By the time I was eighteen, I had lived in eleven different towns and cities around Aotearoa, from the northernmost city of Whangārei to the southernmost city of Invercargill. This meant growing up away from my marae, my whenua (land), and my whānau (family). However, to really understand the depth of the disconnection from culture realised in myself, we have to consider the intergenerational suppression of culture suffered historically through my whakapapa, and specifically my nana in this context.

My nana (my mum's mother) was raised in Waharoa, in the Waikato District of Aotearoa, with her 10 siblings. She was raised on a farmstead with no electricity and attended the local school in Waharoa, which was run by Europeans. Growing up, she experienced a form of cultural colonisation, where at school she wasn't allowed to speak te reo Māori. As such, she never learnt to speak the language, only to understand it, as that was what her mother and father spoke at home. Negative associations with te reo Māori developed as she grew up in two worlds: the almost bygone Māori world and the new European world. To get a job and make a living, you had to learn English because there were no Māori who were hiring and no support for te reo Māori in communities like there is today. She grew up on the whenua, down the road from our marae Raungaiti, and used her English name instead of her Māori given name when not amongst her whānau, as non-Māori struggled to pronounce it. As an adult, she married my grandfather on the marae, who had moved to Aotearoa from Samoa, and they had five children together. The oldest of these children was my mum, Leata Mani.

Moving forward in time to my mum's generation, growing up with a Samoan father and a mother who could not speak te reo Māori, she naturally did not learn te reo as it was not spoken at home. Mum grew up on the marae and was therefore raised in tīkanga, although she didn't necessarily know the technical terms of the customs she followed. She remembers falling asleep to the sound of the kaumātua and the kuia (elders) reminiscing, talking, and laughing around the body during a tangihanga (funeral). She grew up with a deep connection to her marae, and even though she drifted away after having her first child in her early twenties, she always knew it was there. She knew it would always be there for generations to come. In conversation, she has spoken about how, when she was younger, fragments of our culture remained, seemingly dormant. However, in the current day, our culture seems to be coming back, with many people, even in our own whānau, reconnecting with te reo Māori. The experience of my whānau, which may or may not ring true for others, has been that if one is raised on the marae, then one is raised in tīkanga and is connected and immersed in culture, but if one was raised away from the marae and did not learn te reo Māori, there is an absence there where connection should reside.

This absence of connection has had a significant impact on my life, my understanding of my place in the world, and my sense of self. My siblings and I grew up with our immediate family, not surrounded by our greater whānau, which, in Māori culture, is the natural way of life. Whānau is so important and integral in Māoritanga (Māori culture/way of life) that when assessing the hauora (health) of an individual, hauora practitioners will take into consideration whānau connections and obligations due to the understanding of the effect these have on the individual. When considering myself in relation to other members of my whānau, I have felt that others have seemed grounded and connected, while I have always been searching for that sense of belonging. Where my cousins have always known everyone in our whānau, I often feel like an outsider looking in at my own culture. As I have matured, I have come to the realisation that this disconnection is something I would like to resolve, and that it is within my power to do so. This, of course, comes with its own trials and challenges, as many of us who are disconnected feel shame or guilt around our lack of knowledge. However, as a respected kuia once told me, “Remember, colonisation is not your fault.” And so began a journey of reconnection.

Studying at the University of Waikato has provided me with opportunities to learn more about my culture through both resources and people, and, importantly, it has highlighted to me that the experience I believed to be individual was shared. As the first in my immediate family to attend university and having observed the underrepresentation of Māori in the natural sciences, it was encouraging to hear stories of other Māori students who had used their tertiary studies as a vehicle to reconnect with their culture. Working on this project has been a further exploration of reconnection for me, with one of the key realisations centred around karakia.

Near the end of my project, after I had collected all my data for my previous chapters, I realised that, in accordance with tīkanga, karakia should have been recited before I began my data collection. Further to this, I was honoured to korero (talk/speak) with Dr Tom Roa, as discussed previously, with the hope of learning from his wisdom on tīkanga and karakia. After telling him the guilt I felt around missing this important tīkanga in my project, Matua Tom reassured me that our tupuna never used karakia to beg, but rather to assert to the environment the value of the action being taken (Roa, personal communication, August 8, 2025). He reminded me that our tupuna Rātā also did not use karakia at first when felling the tree for the carving of the Tainui waka, and that he amended this over time. Matua Tom then offered to me the karakia recited by our tupuna Rātā, which I gratefully accepted and is subsequently outlined below:

Kākāriki! Pōwhoitere!

Kotia te pū-waiho i konei!

Kotia te kāuru - waiho i konā!

E ai hoki rā ko te umu a Te Tuhi

Kihai i tae ki ngā pukenga;

Ki ngā wānanga; ki ngā tauira!

Patua a-kuru! Patua ā-whao!

Patua te toki a Taiharuru;

Piki ake nei au

I te whare hukahuka nui o Tangaroa

I huakina ia a Nukutaimaroro

Nukutaimaroro, pērā hoki rā

Ko au ko Hinetuahoanga

E kimi ana e hahau ana

I te whānau a Rāta

Rātā i mate atu i Pikopiko-i-whiti

Mate! Maranga mai!

Ko Whiti-nuku te tatauranga -

Whano! Whano!

Hara mai te toki -

Haumi e!

Hui e!

Taiki e!

4.5. Two views of tōtara

As I understand it, one of the key differences between Western-centric culture and Māori culture is the contrast in perspective on connection, interrelatedness, and entanglement. Here, I define entanglement as the foundational, inseparable connectedness between all things; however, please see Karen Barad's work on agential realism for a more fully developed and nuanced definition of entanglement (Barad, 2007). Western culture is dominated by individualism, and Western scientific methods further promote this independent approach by testing causation and effects in isolation, attempting to detach the scientist as the objective observer and the subject as the separate observed. The natural sciences are clearly partitioned into disciplines such as geology, ecology, hydrology, and meteorology (to name a few), even though it is well known that the Earth system as a whole is interconnected and that changes in one sphere will affect another. By contrast, in Te Ao Māori, everything is connected through whakapapa, and humans are understood to be part of nature rather than separate from it. The term whānau therefore applies to other humans, but also to the more-than-human, such as our tuakana tōtara. This perspective necessitates a way of thinking that considers the object in its interrelatedness with others, an understanding not only of the existence of these connections but also of their significance.

This difference in perspective makes work at the interface between the two knowledge systems an interesting place to be, with a natural stretch in perspective occurring as the two worldviews challenge ideas and routines held by the other. My work with tōtara has been a journey, at times a strenuous one, that has explored this chiefly tree through attempts to interview tōtara and record the answers in the language of what is important to trees: sunlight, water availability, and the processes associated with these. This work has initiated my reconnection to my culture through the exploration of the entanglement between tōtara, Te

Ao Māori, and me. Here, I define entanglement as the fundamental nature of connections between all things physical and non-physical that define existence (Barad, 2007). Please refer to Karen Barad's work for a more fully developed and nuanced definition of entanglement. Similar to Mark Twain's "Two Ways of Seeing a River," where he tells the story of getting to know the Mississippi River as a romantic youth and then later as a practical steamboat pilot, I have approached and come to know this tree as an aspiring Western-trained scientist and also as a woman of Māori descent.

Throughout this work, I have tried to the best of my ability to acknowledge and preserve the values of both Mātauranga Māori and Western Science, although, as stated in the beginning, I am not yet an expert in either. In my kōrero with Matua Tom Roa, he talked about the words of the first Māori king, Pōtatau Te Wherowhero, who made the statement as king that there is but "one eye of the needle through which must pass the red thread, the white thread and the black thread" to symbolise unity in the Kīngitanga movement. Matua Tom expanded upon this:

> "I've been saying for a number of years now, and I hear other people saying it now too, that when those threads pass through the eye of the needle, they actually create something new. But in that creation, each of the threads maintain their own ethic. So, I compare that to Western Science and Mātauranga Māori and other sciences and other understandings from wherever, coming through that eye of the needle, they maintain their own ethic. It's really important that each one is recognized, acknowledged and appreciated for its own ethic. And I think that, too often today, Mātauranga Māori is expected to blend with Western Science. So, my assertion is that

> it’s not a case of blending, it’s a case of both working together to create something new but, in that creation, they maintain their own special character.”

In this work, I have attempted to create something new by exploring the mighty tōtara using techniques and customs from both Mātauranga Māori and Western Science, side by side. I have attempted to be the eye of the needle in the metaphor from the first Māori king, bringing these threads together while also aligning with Matua Tom Roa's perspective on maintaining the ethics and special character of each knowledge system. It is my hope that this work serves as further encouragement for research at the interface of these two knowledge systems, which are both equally consequential in contemporary Aotearoa New Zealand.

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