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Growth and water use dynamics of New Zealand indigenous and exotic tree species in the Wairarapa – a case study

A thesis
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of the requirements for the degree
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Abstract

Little is known about the effect of New Zealand indigenous tree species on the forest hydrological cycle and there are limited quantitative growth and transpiration data for New Zealand indigenous tree species, particularly in a plantation setting. This thesis aims to compare growth and transpiration responses of indigenous and exotic tree species to weather conditions in a plantation setting over a two-year study period (Year 1 = 21/06/2022-21/06/2023, Year 2 = 22/06/2023-21/06/2024). This thesis also aims to assess the suitability of electronic point dendrometers as alternatives to the widely used but expensive and invasive sap flow meters for estimating tree and forest level transpiration.

To achieve our aims, eight study species were selected for this thesis including three indigenous Nothofagaceae species, *Fuscospora fusca*, *F. solandri*, and *Lophozonia menziesii*, two indigenous Podocarpaceae species, *Podocarpus totara* and *Prumnopitys taxifolia*, one exotic angiosperm species, *Eucalyptus fastigata* (Myrtaceae), and two exotic conifer species, *Pinus radiata* (Pinaceae) and *Sequoia sempervirens* (Cupressaceae). Rewanui Forest Park (Wairarapa region) was selected for this thesis as it is a rare example of a forestry trial including both indigenous and exotic species.

Electronic point dendrometer measurements revealed that only one of the exotic study species, *S. sempervirens*, had a faster growth rate than the native species during the study period, despite the much larger size of the exotic species. The other two exotic species, *E. fastigata* and *P. radiata*, were limited by canopy closure and wet microsite conditions respectively. Modelling growing season duration using the Gompertz equation highlighted the role of species-traits and the impact of weather conditions on growth. For example, *F. fusca* and *L. menziesii* demonstrated high instantaneous growth rates but a short growing season duration, particularly under drier weather conditions, suggesting that these were the most climate sensitive of the study species. Notably, all study species were modelled to cease growing on the last day of Year 1 which was wetter than Year 2. This result suggests that all study species were able to continue growing at a rate within the model parameters until the winter solstice (21st June 2023), likely due to higher than normal rainfall in late summer and early autumn of Year 1. Differences in weather also affected the other dendrometer variables.

Notably, one of the shrinkage variables, tree water deficit (TWD), was low in Year 1 but exhibited a large summer peak in Year 2 for all study species. Microsite conditions appeared to affect TWD. For example, the high TWD peak for *E. fastigata* was likely driven by dry microsite conditions, large tree size and high sap flux densities causing increased soil water depletion and stem shrinkage in this species.

The large size and likely high leaf area of *E. fastigata* also appeared to drive higher rates of sap flux density compared to the indigenous species, as revealed by heat ratio method sap flow meter measurements. Larger stem sizes appeared to drive higher rates of total water use for all three of the exotic species compared to the indigenous species. The effects of weather and climate on sap flux density were generally species specific. For example, little sap flux density variation was explained by the climate variables for *P. taxifolia*, which consistently ranked low for all measured and calculated variables.

Maximum daily shrinkage (MDS), emerged as the best overall dendrometer variable for predicting sap flux density, with higher correlation and prediction strength for most of the study species. However, under the drier conditions of Year 2, TWD emerged as a stronger predictor for some of the indigenous species, namely, *F. solandri*, *L. menziesii*, *P. totara*, and *P. taxifolia*. Most of these species were, in some way, restricted by soil water conditions. *Fuscospora solandri* had low soil volumetric water content at the study site, *L. menziesii* is considered to be naturally adapted to wetter conditions than at our study site, and *P. totara* had high competition for soil water due to high planting density at the study site. Including climate variables helped to improve prediction strength of the dendrometer variables across all species.

Together these results highlight the role of microsite conditions, stem size, leaf area, and species-traits on the impacts of trees on components of the forest hydrological cycle such as transpiration. These results also highlight the importance of species selection for afforestation projects. This work advances our understanding of water use and growth dynamics of New Zealand indigenous species that have been previously understudied, and how those dynamics compare to exotic plantation tree species.

Keywords: Electronic point dendrometer, GRO, TWD, MDS, heat ratio sap flow meter, sap flux density, transpiration, planted forests, forest hydrology, New Zealand.

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Chapter 1: Introduction

Climate change has led to a global push for afforestation to offset greenhouse gas emissions. For example, the New Zealand Government established the One Billion Trees Programme with the aim of planting that number of trees to target climate change as well as addressing environmental, social, and financial issues (Ministry for Primary Industries, 2025). Environmental issues include erosion control, habitat provision for native species, enhancing natural landscapes, improvement of soil and water quality, moderating high river flows, and the provision of jobs and diversified income streams (Ministry for Primary Industries, 2025). One of the key schemes for the New Zealand Government to reduce and offset greenhouse gas emissions is the Emission Trading Scheme (ETS). Within the ETS, carbon credits can be earned for planting trees, thereby providing another incentive for afforestation.

Despite the push for afforestation, there are controversies and currently unanswered questions surrounding the effects of afforestation. For example, there are concerns about the loss of land for food production. To target this, as of October 2025, limitations on the conversion of farmed land to exotic plantation within the ETS have been put in place ("Climate Change Response Amendment Act 2025," 2025). There are also concerns about the effects of afforestation on local hydrology (Meason et al., 2019); specifically, the conversion of pastoral farmland to forest could reduce water availability in areas set to become more drought prone due to climate change. However, there has been limited research on the effects of different species on catchment hydrology in New Zealand.

In order for afforestation projects to be successful, the most appropriate species need to be selected for site-specific conditions and to meet project-specific goals.

Traditionally, afforestation projects in New Zealand have favoured exotic species.

Shorter rotation species, particularly *Pinus radiata* D.Don., have been favoured in the forestry sector (New Zealand Forest Owners Association, 2023). *Pinus radiata* makes up 91 % of the planted forest area in New Zealand with an average rotation of 28 years (New Zealand Forest Owners Association, 2023). Fast growing *Salix* and *Populus* species have been favoured for erosion control due to faster growth rates and superior root development in the first few years of growth compared to both fast and slow growing

native species (Phillips et al., 2015). While exotic species may achieve short-term goals, there are increasing incentives for planting indigenous species. For example, pine farming for carbon credits is set to become less profitable, incentivising the planting of other species (Upton, 2025). Erosion and debris flows from shorter-rotation forestry sites during recent storm events have also led to calls for different approaches to afforestation. The October 2025 ETS amendment did not restrict the conversion of farmed land to permanent or harvestable indigenous forest within the scheme.

In order for afforestation projects to be successful, detailed growth, survival, tolerance to dry and wet climate conditions, and tree water use for the appropriate species need to be considered. However, there is a lack of such data for New Zealand indigenous tree species in a range of settings (Upton, 2025). These settings include afforestation for both restoration and forestry purposes (Upton, 2025). Water use measurements have been limited to sap flow measurements of dominant trees within old growth forests (Barbour et al., 2005; Bowman et al., 2005; Cranston, 2022; Kostner et al., 1992; Zhao et al., 2020). These sap flow measurements have only been taken on a few species (Barbour et al., 2005; Bowman et al., 2005; Cranston, 2022; Kostner et al., 1992; Zhao et al., 2020).

1.1 Forest hydrology

The aim of forest hydrology is to assess the effects of forest watersheds on the movement (flux) and retention (stores) of water (Amatya et al., 2016). Forest hydrology integrates hydrology, soil science, forestry, and plant physiology because water interacts with vegetation, soils, and the atmosphere across multiple spatial and temporal scales (Amatya et al., 2016). The forest hydrological cycle is made up of several inputs, outputs, and fluxes of water (Figure 1.1; Levia et al., 2011).

Water enters the cycle through precipitation and is partitioned into stores including canopy interception, soil water, groundwater storage, and surface water bodies. These stores regulate the length of time water remains in the system and how quickly it becomes available for hydrological processes. Water moves between stores through fluxes, which represent directional flows of water. Aboveground fluxes include throughfall, sap flow, and surface runoff, while belowground fluxes include infiltration, percolation, lateral subsurface flow, and groundwater discharge. Water exits the

system through streamflow, groundwater recharge, and evapotranspiration, which is the sum of transpiration and evaporation, including water intercepted by plant canopies before it reaches the ground (Levia et al., 2011). Evapotranspiration (ET) is an important component of the global hydrological cycle, and plays a key role in energy, water and carbon balances within forest stands (Amatya et al., 2016). Approximately 60-70 % of mean global annual precipitation is accounted for by ET (Teuling et al., 2009). Land use changes that alter the vegetation can therefore affect ET and subsequently the catchment water balance and stream flows (Boggs et al., 2016).

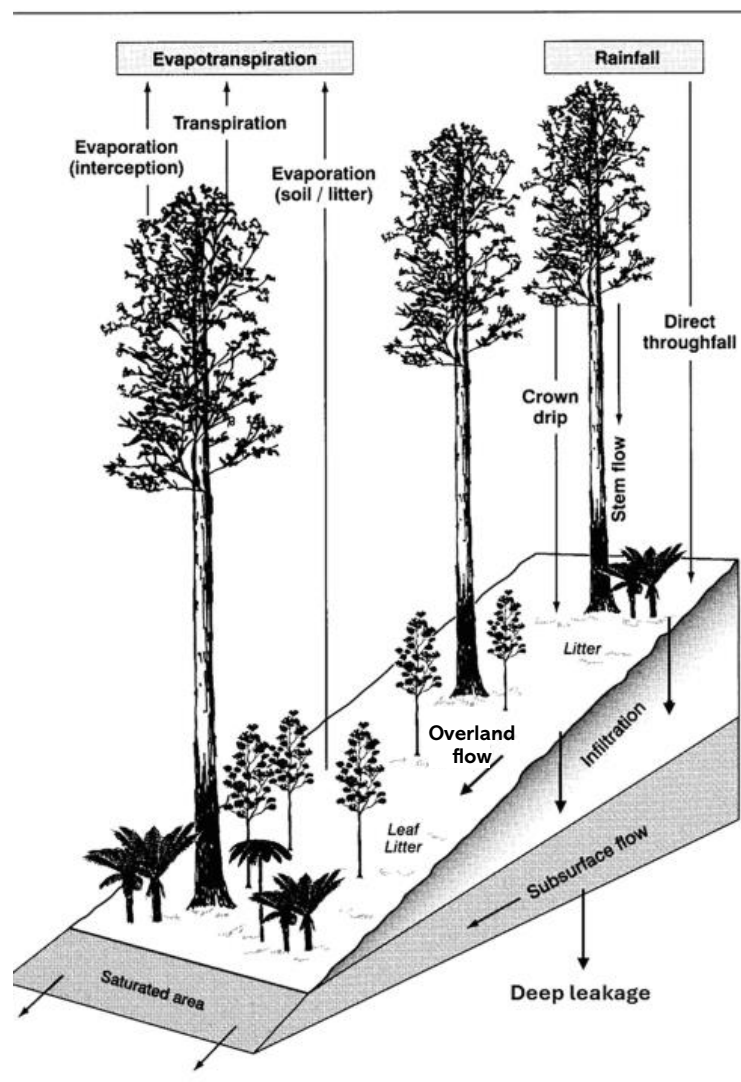


Figure 1.1: The forest hydrological cycle. Source: Bruijnzeel et al. (2025)

The forest hydrological cycle is affected by a range of variables including ecosystem type and species traits. For example, a study in Australia found differences in ET, surface flows, interception, runoff, and soil water content between woodland savanna

in the Northern Territory and eucalyptus forest in New South Wales (Kang et al., 2021). In the eucalyptus forest, the litter layer, larger canopy, and deeper rooting depth affected components of the forest hydrological cycle. The litter layer increased soil water storage and decreased surface flows; the larger canopy increased interception and ET, and reduced runoff; and the deeper rooting depth resulted in more fluctuations in soil water content at deeper depths. In the woodland savanna, lower ET was observed during the distinct dry season due to reduced precipitation and soil water content (Kang et al., 2021).

Forest hydrology has traditionally been studied using catchment scale methods. Paired catchment studies are commonly used in forest hydrology and are useful for determining the effect of changes in vegetation on water yield and streamflow (Brown et al., 2005). Previous paired catchment studies have found that deforestation results in increased groundwater discharge, while afforestation results in decreases in groundwater discharge (Cheng et al., 2017). These changes in groundwater discharge also affect streamflow, however this effect is catchment dependent (Cheng et al., 2017). Previous paired catchment studies have also found that there can be a lag in changes to annual streamflow following vegetation changes, for example, between 3 and 10 years (Zhao et al., 2012).

A disadvantage of paired catchment studies is the difficulty of determining the mechanisms for those effects; for example, ET and transpiration are not directly measured in many forest hydrology studies (Meason et al., 2019). Catchment responses are often the result of the complex interplay of hillslope hydrology, subsurface flow paths, and vegetation water-use (McDonnell et al., 2021). Catchment water balance methods infer plant water use indirectly from the difference between rainfall and stream discharge (Mohajerani et al., 2021). These methods can mask the separate contributions of evaporation, interception, and transpiration (Mohajerani et al., 2021). Measuring evapotranspiration and transpiration directly gives insight into species and tree-level water use and responses to environmental conditions not discernible with an inferred water balance approach (e.g. White et al., 2021).

Planted forests generally have higher annual ET than pasture, dry-land crops (Zhang et al., 2001), and even natural forests, with differences often most pronounced at water-

limited sites (Lima et al., 1990). Expansion of planted forests can lead to reductions in streamflow which may be more pronounced in some catchments, for example reductions in streamflow may be more pronounced in catchments with ephemeral streams compared to catchments with perennial streams (Zhang et al., 2012). Research on *Pinus* and *Eucalyptus* plantations highlights their strong impacts on local hydrology. In central Chile, *P. radiata* plantations have been shown to reduce catchment streamflow, increase water use (Little et al., 2009), and exhibit higher annual evapotranspiration than indigenous forests (White et al., 2021). Similarly, *Eucalyptus globulus* Labill. plantations had elevated evapotranspiration compared with the indigenous forests, driven by higher transpiration rates and distinct water-use strategies (White et al., 2021).

There is evidence that indigenous forest catchments use less water than exotic forests (e.g. Lima et al., 1990). However, there have been limited measurements of tree level contributions to the forest hydrological cycle, including interception and transpiration (Meason et al., 2019). For example, the aforementioned Little et al. (2009) study did not measure transpiration directly. Changes in catchment water yields during natural forest regeneration have been linked to the changing effects of the trees on interception, transpiration and evaporation (Vertessy et al., 1996). Compared to old growth forest, regenerating *Eucalyptus regnans* F.Muell. forest after fire resulted in lower runoff, reduced water yields, higher interception and transpiration due to higher leaf area, and reduced evaporation from the understory (Vertessy et al., 1996). These results highlight the impact of fast growth rates and high leaf area on the forest hydrological cycle.

Regional governing bodies within New Zealand have concerns with afforestation due to the increased interception and evapotranspiration, particularly in catchments with existing low water yields and/or high water demand (Meason et al., 2019). New Zealand studies have shown that planting *P. radiata* forest on pasture or tussock land reduces the annual water yield by 20 to 50 %, depending on the catchment (Davie & Fahey, 2005), and it is assumed from the water balance approach that the reduction is from increased evapotranspiration. Afforestation tends to reduce total annual yield, however, the effects on seasonal yields are less clear. It is well known that forests can have beneficial effects on catchment hydrology by mitigating peak stream flows

following high rainfall, and maintaining higher minimum stream flows and better water quality during dry periods (Amatya et al., 2016). Overall, afforestation of pasture or tussock land in New Zealand is associated with reductions in annual catchment water yield, and variable or inconclusive effects on seasonal yields (Meason et al., 2019). However, a recent New Zealand study found that *P. radiata* plantations across the country used less water than initially thought by the public and less water compared to estimates from previous paired catchment studies from the 1970s (Meason et al., 2025). Forest hydrological studies in New Zealand have been largely focused on paired catchment studies on *P. radiata* forest in comparison with pasture (e.g. Duncan, 1995), with few measuring sap flow directly (e.g. Fahey et al., 2001). More information is needed regarding the effects of indigenous forests in comparison to exotic forest or pasture under similar conditions including soil, weather, climate, and topography. Fluxes of water, including transpiration which is a key component of the forest hydrological cycle in indigenous forests, also remain largely unquantified.

1.2 Transpiration and water transport in trees

Transpiration is one of the key outputs of water from the forest hydrological cycle, accounting for approximately 61 % of total global evapotranspiration (Schlesinger & Jasechko, 2014). Transpiration is also a major component of the plant level water cycle as plants lose approximately 90 % of the water taken up by the roots via transpiration (Kramer & Boyer, 1995). Transpiration represents the final step in the soil-plant-atmosphere continuum, where water is taken up by the roots, moves through the plant via the xylem, and is released to the atmosphere as vapour through the stomata and cuticle (Avril & Barten, 2007; Kumagai, 2011).

Global datasets demonstrate that transpiration rates vary widely between species and systems, and highlight the importance of measuring transpiration rates for a range of species, sites, and weather conditions (Aguadé et al., 2021). Transpiration rate is affected by a range of variables such as tree height and age, leaf area, xylem resistance to cavitation, stomatal conductance, sapwood area, growth rate, and seasonal phenology (Amatya et al., 2016). External factors such as climate, competition, topography, soil type, and soil water availability can also affect transpiration rates (Amatya et al., 2015; Feng et al., 2018).

At the tree level, transpiration is influenced by stomatal behaviour, particularly short-term and highly dynamic changes in transpiration (Canny, 1998). Stomata open to allow the uptake of carbon dioxide for photosynthesis and growth, resulting in the loss of water, creating a trade-off between carbon gain and water loss (Avril & Barten, 2007). Stomata respond to changes in VPD. Reductions in stomatal conductance can prevent further increases in transpiration, minimise stress, and reduce internal tensions (Jarvis, 1976). In theory, stomata can respond to both evaporative demand and the hydraulic supply of water from the roots in a way that optimises water use for a given species under the current conditions (Avril & Barten, 2007). Increases in VPD and a reduction in the availability of soil water can cause stomata to close in response to changes in leaf and soil water potentials (Jarvis, 1976). The response of the stomata to these hydraulic signals provides a link between the potential for photosynthesis and growth, and the properties of the water supply system of the tree (the 'hydraulic architecture').

Sapwood area, leaf area, and the ratio between the two are key components of hydraulic architecture. Sapwood area determines the amount of water that can be supplied to the leaves for transpiration. Leaf area determines the demand for water; higher leaf area means more surface area for transpiration (Amatya et al., 2016). The ratio of cross-sectional sapwood area to leaf area is known as the Huber value (H_v ; Mencuccini et al., 2019). The H_v describes the investment of stem tissue per unit leaf area (Tyree & Ewers, 1991). Plants with a high H_v may be able to compensate for vulnerable xylem due to reduced water potential gradients (Mencuccini et al., 2019).

1.2.1 Water transport in trees

Water is transported through the xylem via a passive process explained by the widely accepted cohesion-tension theory (Dixon & Joly, 1894). This passive process is driven by pressure gradients and negative hydrostatic pressures (tension). Tension can lead to the introduction of air bubbles (cavitation), which can block the passage of water (embolism), and can result in xylem conduit implosion, hydraulic failure, and in extreme cases the death of the plant (Hacke & Sperry, 2001).

In the Ohm's law analogy (Figure 1.2), pressure gradients are equated to the difference in water potential between the leaves and the soil (Tyree & Zimmermann, 2002). The conductance (k) of the system and each segment, including the roots, stem, and leaves,

can be measured to give an idea of the efficiency of water transport. Water can also move radially in and out of bark tissues and xylem parenchyma due to water storage, or capacitance (C) (Tyree & Ewers, 1991). Capacitance can cause variation in the timing and amount of sap flow observed at different positions within the tree, as water moves in or out of storage along the transpiration pathway on a daily basis, or over longer time scales during periods of drought (Macinnis-Ng et al., 2016; Meinzer et al., 2004; Phillips et al., 2009).

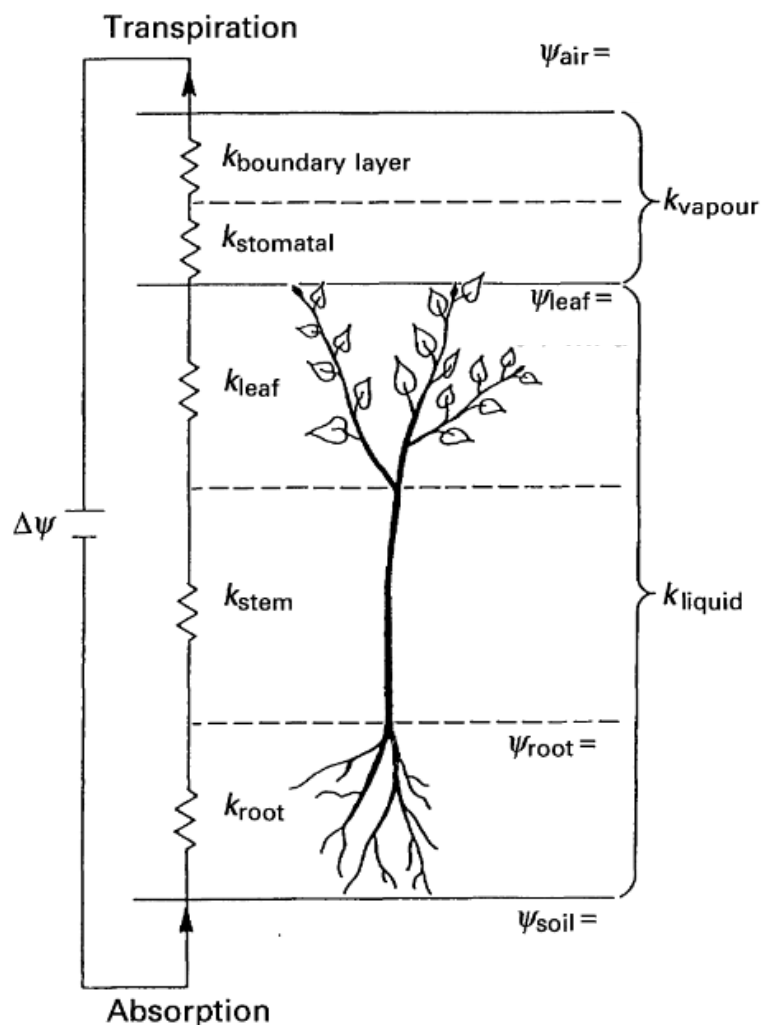


Figure 1.2: The Ohm's law analogy. Water movement is affected by a gradient in water potential (Ψ), and hydraulic conductance (k) of the parts in the system. Source: Ewers and Cruiziat (1990).

1.2.2 Angiosperm and conifer species differences

Angiosperm and conifer species differ in their hydraulic architecture and rates of transpiration. The xylem is made up of a series of conduits and pits (Hacke & Sperry,

2001). Conduits are found in two forms, tracheids and vessels. Conifer xylem contains tracheids only, while angiosperm xylem generally contains a combination of the two. Conduit cell walls are lignified. Pits allow water to pass between conduits. Angiosperm xylem also contains xylem fibres to provide structural support (Hacke & Sperry, 2001). Pits have evolved to minimise the spread of embolism. Heterogeneous torus-margo pits can be found in conifer xylem and act as valves to prevent the spread of embolism. The high efficiency of heterogeneous pits compensates for the narrow diameter of tracheids compared to vessels and allows conifers to remain competitive under specific environmental conditions (Pittermann et al., 2005). In contrast, angiosperm vessels have homogeneous pits that lack an air-sealing mechanism, creating a more direct trade-off between hydraulic efficiency and safety.

Angiosperm xylem has higher maximum transport efficiency but may be more vulnerable to cavitation. In comparison, conifer xylem may have lower maximum transport efficiency and rates of leaf gas exchange, although there is a wide range of overlap in the ranges of drought resistance and productivity when comparing the two groups (Hacke & Sperry, 2001). One way of measuring xylem vulnerability is to measure the xylem water potential at which 50 % of hydraulic conductivity is lost due to embolism (P_{50} ; Delzon, 2015). The less negative a P_{50} , the more vulnerable the xylem (Delzon, 2015). Generally, angiosperm species have less negative P_{50} compared to conifer species (e.g. Laughlin et al., 2020). However, this is species and environment dependent. As soil water depletes under hot and dry conditions, tension increases and turgor decreases, resulting in stomatal closure to avoid excessive dehydration and embolism (Buckley, 2019). Species with xylem that is more vulnerable to drought may close their stomata earlier than species with less vulnerable xylem (Hacke & Sperry, 2001). As angiosperm species tend to have more efficient and more vulnerable xylem, it could be expected that angiosperm species exhibit higher instantaneous transpiration or sap flow rates but earlier stomatal closure than conifer species. Earlier stomatal closure could also affect the cumulative amount of water transpired between these two groups.

A global analysis found that angiosperm species tend to have higher maximum transpiration rates compared to gymnosperm species. However, the angiosperm species also tend to have higher sensitivity to vapour pressure deficit (VPD), decreasing

their water use more quickly in response to increased VPD (Flo et al., 2021). A Chilean study comparing water use and transpiration of exotic plantation species, *P. radiata* and *E. globulus*, with indigenous *Nothofagus* forest found higher transpiration in the exotic species (White et al., 2021). These results were driven by differences in phenology and hydraulic architecture. The *Nothofagus* species in that study were deciduous, resulting in later spring growth and water use initiation compared to the exotic species. *Pinus radiata* had high sapwood and leaf area but low capacity for transpiration per unit leaf area, while *E. globulus* had moderate sapwood and leaf area and instead had higher rates of photosynthesis and transpiration in spring. Overall, the indigenous species had higher sap flux density than *P. radiata*, but the exotic species had higher transpiration efficiency than the indigenous species (White et al., 2021).

1.2.3 Transpiration in New Zealand native species

There are few studies assessing transpiration, water use, stomatal behaviour, and hydraulic architecture for New Zealand indigenous species, such as Nothofagaceae species, *Dacrycarpus dacrydioides* (A.Rich.) de Laub., and *Podocarpus totara* G.Benn. ex D.Don var. *totara*, especially in comparison with exotic species (e.g. Bannister & Kissel, 1986; Bown et al., 2024; Kelliher et al., 1992). Observationally, indigenous species grow more slowly than exotic species, suggesting differences in hydraulic architecture, leaf area, photosynthesis and stomatal conductance between the two types of forest. It is likely that transpiration also differs between indigenous and exotic species when planted in the same environment; however, this has yet to be tested.

1.3 Sap flow estimates of tree water use

Thermal sap flow measurements are widely accepted as the key method for estimating transpiration in plants (Poyatos et al., 2016). The use of heat as a tracer to measure the velocity of sap in xylem tissue was first developed by Huber (1932). Marshall (1958) developed the subsequent theoretical framework. There are a range of methods that can be separated into families based on how heat is applied and sapwood temperature is measured (Wullschleger et al., 1998). These sap flow measurement families include heat balance, heat dissipation, and heat pulse methods (Wullschleger et al., 1998).

Methods within the heat balance family measure the energy balance across a section of heated stem (Smith & Allen, 1996). This family includes stem heat balance (Daum, 1967) and trunk heat balance methods (Čermák et al., 1973). These two methods use external heating which reduces the issue of wounding effects (Smith & Allen, 1996). However, these methods require zero-flow determination, which can be difficult to obtain, and the resulting errors can lead to over- or underestimated sap flow (Smith & Allen, 1996).

Methods within the heat dissipation family measure the dissipation of heat from a heated probe inserted into the sapwood and compare this to a reference probe that is not heated (Do & Rocheteau, 2002; Granier, 1985). This family includes thermal dissipation (Granier, 1985) and transient thermal dissipation methods (Do & Rocheteau, 2002). An issue with this method is that the original empirical calibration equation, developed by Granier (1985), was derived based on a small number of species. Species-specific calibration may be needed due to the wide range of species-specific variation in xylem anatomy and wood thermal properties, and this method also requires measurements during periods of known zero flow (Fuchs et al., 2017).

Methods within the heat pulse family apply pulses of heat and measure thermal convection and conduction driven temperature changes (Flo et al., 2019). This family includes a number of methods including compensation heat pulse (Swanson & Whitfield, 1981), T-max (Cohen et al., 1981), heat ratio (Burgess et al., 2001), calibrated average gradient (Testi & Villalobos, 2009), sapflow+ (Vandegehuchte & Steppe, 2012a), dual heat pulse (Pearsall et al., 2014), and single probe heat pulse methods (López-Bernal et al., 2017). Historically the compensation heat pulse method, developed by Swanson and Whitfield (1981), was the most widely used (Edwards et al., 1997). However, based on Marshall's original 1958 framework, Burgess et al. (2001) developed the heat ratio method to improve on the insensitivity of the compensation heat pulse method to low and reverse flows. The heat ratio method is known for effectively measuring low and reverse rates but not high rates of sap flow (Lopez et al., 2021; Vandegehuchte & Steppe, 2012b). The heat ratio method was used for this thesis to best capture the range of sap flow rates expected from our study species.

Sap flow meters are known to be prone to errors and variable results, even when utilised according to recommended protocols (Flo et al., 2019). These devices are complex to install, delicate, and expensive. Errors introduced by improper installation, calibration issues, frequent maintenance, and wounding effects can lead to variable results, which increases the need for high levels of replication. Together, these issues make sap flow meters impractical for long-term monitoring and for use outside specialist research teams. Cheaper and more practical variants of thermal sap flow methods have been proposed, such as the external heat pulse method (Clearwater et al., 2009). However, these alternatives are not without limitations, leaving room for other alternatives to allow for routine monitoring of crop or forest water use.

1.4 Measuring growth

Growth is relevant to the forest hydrological cycle because transpiration is required for photosynthesis, and larger trees are known to transpire more water than smaller trees (Butz et al., 2018; Kaptein et al., 2023). Therefore, it is possible that species with faster growth rates will have higher water use, when compared to trees of the same age of slower growing species. The growth rate of trees can be estimated by measuring changes in stem radius. New cells in tree stems are formed in the cambium and differentiate primarily into xylem and phloem (Schweingruber, 1996). The building of new cells results in irreversible increases in stem radius (Drew et al., 2010). The rate of these stem radial increases is influenced by turgor, the supply of photosynthates for growth, and water potential conditions in the cambium (Steppe et al., 2006).

Water-related processes can also cause temporary or reversible changes in stem radius, and are driven by water potential gradients in the tree (Steppe et al., 2012). These gradients are mainly induced by transpiration and are affected by factors such as soil water availability (Steppe et al., 2012). Transpiration during the day results in the shrinkage of stems (Zweifel et al., 2016). When water potentials are low, water is lost from the bark, cambium and immature xylem (Zweifel et al., 2014). The lack of transpiration at night results in expansion of the stems as they refill with water (Zweifel et al., 2016). There is a lag between transpiration rate, leaf water potential and changes in tree stem size (Drew et al., 2008). This lag can range from minutes to hours depending on tree size and may be due to the time it takes for water to be released

from storage (Phillips et al., 1997; Phillips et al., 2003; Zweifel et al., 2001; Zweifel et al., 2006).

Dendrometers that make contact with the stem have been used since the 19th century to measure changes in stem diameter (Drew & Downes, 2009; Friedrichs, 1897). There are two main types, point and band dendrometers (Neher, 1993; Sevanto, 2003). Point dendrometers measure stem size changes at either a single radius or across the diameter of the stem (Drew & Downes, 2009). Band dendrometers measure stem diameter changes in the circumference of the stem at a particular height and have been commonly used in forest-based research (Drew & Downes, 2009). However, band dendrometers are less sensitive than point dendrometers at detecting small diurnal changes in the stem (Francon et al., 2024) and are often read manually. Manually read dendrometers offer low temporal resolution and require the researcher to visually read the output at select times (Fritts, 1972). Thus, point dendrometers, especially electronic devices that monitor stem diameter changes continuously, are increasingly used to measure stem diameter changes (Mencuccini et al., 2017). Continuous dendrometers offer high temporal resolution and allow for the recording of remote readings (Phipps & Yater, 1974). Based on these advantages, continuous electronic point dendrometers were selected for use in this thesis.

Raw dendrometer data can be used to calculate growth and shrinkage variables, including irreversible stem growth (GRO), tree water deficit (TWD) and maximum daily shrinkage (MDS). GRO, TWD, and MDS have been popularised by Zweifel et al. (2016). GRO refers to stem diameter increases due to cell expansion and elongation (Zweifel et al., 2016). TWD and MDS both represent reversible changes in stem diameter. TWD reflects the difference between water lost through transpiration and soil water uptake, over timescales longer than one day; high TWD may indicate longer term water or drought stress, because the decrease in diameter is not reversed within 24 hours (Zweifel et al., 2016). There are currently unanswered questions and issues with the Zweifel et al. (2016) method of calculating GRO and TWD. The Zweifel et al. (2016) method assumes that no GRO occurs when TWD is occurring, meaning that a proportion of GRO could be included in TWD calculations. However, there have not been direct tests as to what these variables are actually measuring. MDS reflects a tree's response to current air and soil conditions on a daily scale (Güney et al., 2020). A

small MDS indicates either a day with closed stomata and low transpiration or a large difference between water demand and supply with low tissue saturation. A large MDS indicates a large but reversible daily change in stem diameter caused by a high rate of transpiration and water withdrawal and recharge from and to the elastic tissues that contribute to hydraulic capacitance (Güney et al., 2020).

The shrinkage variables are therefore linked with transpiration, meaning there is a potential for dendrometers to be used as cost-effective alternatives to sap flow meters for estimating transpiration. The benefits of using dendrometers as an alternative to sap flow meters include lower cost, less complexity in their instrumentation and installation, increased reliability, easier manufacturing, and reduced risk of wound effects. However, the dendrometer signal is difficult to interpret, and questions remain regarding the differences between what sap flow meters and dendrometers are measuring. Essentially, sap flow meters are measuring a signal generated by the axial flux of water in the xylem, while dendrometers are measuring the effect of the pressure gradients that drive the axial flux on stem water content. There have been a small number of studies testing the effectiveness of dendrometers as alternatives to sap flow meters. Many of these studies have tested MDS as an alternative to sap flow for irrigation scheduling in an orchard setting (e.g. Biel et al., 2012; Conejero et al., 2007). Fewer studies have been conducted in a forest setting (Donfack et al., 2024; Tian et al., 2019). Based on these limited studies and the potential for cheaper alternatives, there exists a need to test the effectiveness of dendrometer-obtained variables as alternatives to sap flow measurements on a range of species and under different weather conditions.

1.5 Study Species

There are well-documented differences in growth and transpiration between angiosperm and conifer species, and similar differences are expected between exotic and indigenous New Zealand tree species based on observed variation in growth rates. However, little is known about the water use of indigenous species and there is a lack of measured growth data (Upton, 2025). To further explore these differences, a range of species is included in this thesis, introduced below.

1.5.1 Exotic Species

Since the early twentieth century, *P. radiata* has been the most common plantation species in New Zealand due to its fast growth rates at a wide range of planting sites (Upton, 2025). These fast growth rates under a range of conditions have led to short rotation cycles of 25 to 30 years (Woollons & Manley, 2011), compared to 80 to 130 year rotations of other plantation species in Europe (e.g. Kellomäki et al., 2023). Fast growth rates and short rotation cycles of *P. radiata* have led to alternative species, such as indigenous species, being deemed unproductive for wood or fibre production in New Zealand, despite having growth rates considered economically viable in other countries.

The growth rates that *P. radiata* achieves in New Zealand are faster than those achieved in this species' natural range, likely due to highly favourable conditions. *Pinus radiata* occurs naturally in the coastal areas of central California, USA, and some Mexican islands where temperatures are mild, humidity is high, and annual rainfall is low to moderate (Roy, 1990). This species generally grows between 300-1100 metres above sea level (m a.s.l.), on low fertility soils (Roy, 1990). While *P. radiata* is the most common plantation species in New Zealand, other exotic species are also grown for their unique wood properties and species traits, including *Eucalyptus fastigata* H.Deane & Maiden and *Sequoia sempervirens* (D.Don) Endl.

Sequoia sempervirens occurs naturally in coastal areas of central and northern California, USA, where annual rainfall is moderate to high, and the climate is mild but humid (Burns, 1990). This species occurs between sea level and 760 m a.s.l. in moderate fertility soils (Burns, 1990). *Sequoia sempervirens* reaches the tallest heights of all tree species in the world. Reaching these tall heights has been linked to the humid natural environment for this conifer species, as well as increased reliance on water from coastal fog with increasing height (Burgess & Dawson, 2004; Dawson, 1998).

High drought tolerance has been reported for the two exotic conifer species, with P_{50} values of -3.94 MPa for *P. radiata* (Choat et al., 2012) and -6.30 MPa to -12.40 MPa for *S. sempervirens* depending on tree height (Ambrose et al., 2009). *Pinus radiata* is known to have generally shallow roots with a combination of tap and lateral roots (Roy,

1990). *Sequoia sempervirens* is known to have shallow but wide-spreading root systems (Burns, 1990).

Eucalyptus fastigata occurs naturally in New South Wales and Victoria, Australia, between 700-1200 m a.s.l., in moderate rainfall areas, on moist, well-drained, fertile soils (Eldridge et al., 1993). While no P_{50} values have been reported for *E. fastigata*, a range of values from -2.11 to -6.40 MPa have been reported for a range of *Eucalyptus* species, including -4.98 MPa for the closely related *E. regnans*, which occurs in a similar climate niche to *E. fastigata* (Pan et al., 2026), potentially indicating moderate drought tolerance for *E. fastigata*. *Eucalypts* are known to have a combination of tap and lateral roots, potentially providing access to deep soil water during periods of drought (Knight, 1999).

1.5.2 Indigenous species

Nothofagaceae species in New Zealand dominate one of two main zonal forest types in New Zealand, southern beech forest. Southern beech forest occurs in temperate rainforest at cooler, higher altitude sites, typically on less fertile soils (Wardle, 1984). The New Zealand southern beeches are classified into two genera including *Fuscospora* and *Lophozonia* (Heenan & Smissen, 2013). There are five representatives in New Zealand, three of which have been included in this thesis, *Fuscospora fusca* (Hook.f.) Heenan et Smissen, *F. solandri* (Hook.f.) Heenan et Smissen, and *Lophozonia menziesii* (Hook.f.) Heenan et Smissen.

Fuscospora fusca is generally considered to be the fastest growing and the least tolerant of unfavourable conditions of the New Zealand beeches (Smale et al., 2012). This species occurs up to approximately 1000 m a.s.l., with a preference for well-drained, fertile soils. *Fuscospora solandri* is considered to have a slightly slower growth rate than *F. fusca*. This species occurs in lowland areas and on lower mountain slopes up to approximately 750 m a.s.l. and can tolerate poor soils with low soil moisture and low rainfall, about 750 mm yr⁻¹. *Lophozonia menziesii* is considered the slowest growing of the New Zealand beeches. This species occurs in montane and subalpine areas up to 1200 m a.s.l. and is tolerant of a range of soil types and high rainfall, but has the highest rainfall across its distribution compared to the other New Zealand beeches (Smale et al., 2012). These three species have shallow root systems (Smale et

al., 2012) and have low drought tolerance with a P_{50} of -2.30 MPa for *F. fusca*, -2.76 MPa for *F. solandri*, and -2.37 MPa for *L. menziesii* (Laughlin et al., 2020). These three beeches all demonstrated high timber quality with differing properties including excellent stability for *F. fusca*, rot resistance but inconsistent properties for *F. solandri*, and high consistency of properties but low durability for *L. menziesii* (Smale et al., 2012).

The Podocarpaceae is the dominant conifer family in New Zealand. Podocarpaceae species are an important component of the other zonal forest type in New Zealand, mixed conifer and angiosperm forest, commonly referred to as conifer-broadleaf forest. Podocarpaceae species are also known to be unique in their hydraulic architecture, frequently exhibiting high cavitation resistance and hydraulic safety margins, despite inhabiting relatively wet environments (Laughlin et al., 2020; Pittermann et al., 2006). For this thesis, two Podocarpaceae species were selected, *P. totara* and *Prumnopitys taxifolia* (D.Don) de Laub.

Podocarpus totara and *P. taxifolia* are both lowland species, with *P. totara* occurring up to approximately 480 m a.s.l. (Dawson et al., 2012), and *P. taxifolia* occurring up to approximately 760 m a.s.l. (Barton, n.d.). Both species favour well-drained alluvial and fertile soils (Dawson et al., 2012). *Podocarpus totara* is intolerant of wet and waterlogged soils (Dawson et al., 2012). High drought tolerance has been reported for the indigenous conifer species with P_{50} values of -4.90 MPa for *P. totara* and -5.26 MPa for *P. taxifolia* (Laughlin et al., 2020). *Podocarpus totara* is known to have a combination of tap and lateral roots, while *P. taxifolia* is known to have shallow roots only (Marden et al., 2018). *Podocarpus totara* shows promise as a candidate for timber production due to relatively fast growth and high-quality timber (Bergin, 2001). *Prumnopitys taxifolia* timber is also of high wood quality but lacks durability and fast growth rates (McSweeney, 1982).

1.6 Study site

Rewanui Forest Park, located in the Wairarapa region, was a farm that was purchased in 2004 by the Montfort Trimble Foundation for afforestation. The site includes a forestry trial with fifteen indigenous and eleven exotic species, planted in a replicated design between 2006 and 2008 (Meason et al., 2020). The forestry trial was established

to identify viable alternatives to radiata pine and provide long-term data on suitable species for various microsites. A range of indigenous species were planted including New Zealand southern beech and Podocarpaceae species. A minimum of one plot was established for each of the indigenous species; for many species this included plots in different locations, providing contrasts in microsite conditions. Survival and growth were variable for the indigenous species, with the most successful plots occurring in locations with potentially higher soil moisture during the drier months (Meason et al., 2020). Rewanui Forest Park was selected for this thesis as very few sites with a replicated planting design exist for New Zealand indigenous species. The survival and growth of the original plantings limited the choice of species that could be used for this study.

1.7 Summary and conclusions

This literature review presented general information regarding transpiration and growth of trees. Informed decision-making for species selection in afforestation requires an understanding of the potential impacts on local hydrology and a range of performance measures. Potential impacts on local hydrology include reduced streamflow and water yields, due in part to increased transpiration. Alongside transpiration, tree performance measures include growth and shrinkage; all of these performance measures are likely to be affected by changes in environmental conditions as well as species-specific traits. It is also important to understand the physiology of the currently understudied indigenous species, their water use, responses to the environment, and ability to tolerate drier conditions. Sap flow meters and dendrometers are widely accepted as the key methods for measuring estimates of transpiration and both growth and shrinkage, respectively. However, there is a gap in the global dataset for New Zealand indigenous tree species, with a small number of species in a select number of environments being studied previously. Growth rates, transpiration rates, and water-use strategies differ across species; therefore, for afforestation projects to successfully meet their goals and desired outcomes, there is a need for this research to investigate differences in growth and transpiration of New Zealand indigenous trees in comparison with exotic plantation species.

1.8 Research aims and thesis outline

The aims of this thesis were to compare growth and transpiration responses of our study species to the environment, especially water availability and evaporative demand, and to assess the utility of electronic point dendrometers as an alternative to sap flow meters for estimating forest transpiration.

Species selection was a central component of our experimental design. We chose eight species from a range of taxonomic groups that had the potential to be selected for future afforestation projects. We expected contrasting results among the groups of species, including between indigenous and exotic species, and between angiosperm and conifer species. We also expected that our results would provide valuable insight into appropriate species selection for future afforestation projects.

Chapter 2 - Comparison of growth rate and growing season duration between exotic and indigenous planted trees

The aim of this chapter was to measure and compare growth and shrinkage dynamics of our study species to gain an understanding of growth strategies, tree water status, and responses to environmental conditions, particularly of species not commonly researched in a plantation setting. This was achieved by installing electronic point dendrometers over a two-year study period to measure stem radius fluctuations. Growth and shrinkage variables were extracted using the Zweifel et al. (2016) method, and MDS was calculated using the standard method. The Gompertz equation was used to model growing season duration for each species in both of our study years. Generalised additive models (GAMs) were then used to model the effects of climate variables. The key hypothesis for this chapter was that the exotic species would exhibit faster growth rates than the indigenous species due to larger stem sizes at the start of the study period. We expected results from Chapter 2 to give valuable insight into the timeframes in which each study species could achieve afforestation project goals.

Chapter 3 - Comparison of sap flow between exotic and indigenous planted trees

The aim of this chapter was to measure and compare estimates of transpiration of our study species using heat ratio method sap flow meters to gain an understanding of water-use strategies and responses to environmental conditions, particularly of species

not commonly researched in a plantation setting. Raw data was converted to sap flow rate, sap flux density (flow rate per unit sapwood area), and total water transpired. The effect of climate variables was also tested using GAMs. The key hypothesis for this objective was that the exotic species would have higher estimated transpiration than the indigenous species due to larger leaf and sapwood area. We expected results from Chapter 3 to give valuable insight into the potential effects of each study species on the local watershed of afforestation sites.

Chapter 4 - Can electronic point dendrometers be used as cost-effective alternatives to sap flow meters for estimating transpiration?

The aim of this chapter was to test statistically whether dendrometer variables could be used as a more low-cost and practical alternative to sap flow meters for estimating transpiration. All three of the dendrometer variables, GRO, TWD, and MDS, were tested as potential proxy measurements for sap flux density using linear mixed effects models. One of the key hypotheses for this chapter was that MDS would be more tightly correlated with sap flux density than the other dendrometer variables, and that this relationship would vary with species. The other key hypothesis for this chapter was that the inclusion of climate variables would result in a higher proportion of sap flux density variation being explained by the models.

Chapter 5 - Synthesis

The results and conclusions from each chapter are synthesised, and the direction of possible future work is described.

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Chapter 2: Comparison of growth rate, shrinkage, and growing season duration between exotic and indigenous planted trees

2.1 Introduction

The threat of climate change has led to policy reform, scientific research, and a range of afforestation projects across New Zealand (Gluckman et al., 2017; Ministry for the Environment, 2016; Ministry for the Environment & Ministry for Primary Industries, 2018; New Zealand Government, 2014). For afforestation projects to be successful, the most appropriate species for the project goals need to be selected. New Zealand indigenous trees have been understudied and historically overlooked for afforestation. Shorter rotation and faster growing species, particularly *Pinus radiata*, have been favoured in the forestry sector, with *P. radiata* making up 91 % of the planted forest area in New Zealand (New Zealand Forest Owners Association, 2023). While exotic species may be more suitable for fast-growing timber production, there is increasing incentive for planting indigenous species. For example, pine farming for carbon credits is set to become less profitable, incentivising the planting of other species (Upton, 2025). Other species, such as *Sequoia sempervirens*, have been proposed as alternatives to *P. radiata* due to higher productivity over longer periods of time and greater resilience to stressors (Watt et al., 2021). Alongside *S. sempervirens*, indigenous *Podocarpus totara* is also being considered an option for long-term carbon sequestration goals (Salekin et al., 2024). However, detailed growth rate and survival data for a range of alternatives, particularly indigenous species, from different sites and forestry regimes across New Zealand are missing (Upton, 2025). Currently, indigenous species data is based primarily on ecological distribution maps and quantitative data on the tolerance of each species to differing climatic conditions, such as wet versus dry conditions, is missing.

Growth rate is affected by a range of intrinsic and extrinsic factors including climate and species traits. A modelling study in New Zealand found that age and stocking density were the most important predictors of diameter at breast height for the exotic

species, including *S. sempervirens* (Lin et al., 2022). In contrast, stocking density, aspect, altitude, and slope were the most important predictors of diameter changes for the indigenous species, including *P. totara*, reflecting differences in the ecology and growth plasticity of the indigenous species (Lin et al., 2022).

Climate and weather drivers, including temperature, precipitation, soil moisture, and atmospheric demand (vapour pressure deficit; VPD), affect tree growth rates and the timing and length of the growing season. Warmer late-winter and spring temperatures generally advance growth onset (Basler & Körner, 2014), but warming often interacts with soil drying so that early starts can be offset by reduced annual radial growth under summer drought (Bose et al., 2025; Qiao et al., 2023). Soil moisture and precipitation modulate site productivity and growing-season length; wetter sites (or years with higher precipitation) tend to show earlier onset, later cessation and greater cumulative growth, while increasing growth sensitivity to precipitation has been documented across recent studies (Larson et al., 2024; Li et al., 2024a). Atmospheric demand can independently suppress carbon uptake and growth even when temperatures are favourable, because higher VPD drives stomatal closure, reduces photosynthesis and accelerates soil drying (Gauthey & Gardner, 2024; Middleby et al., 2024). Extreme events, such as droughts and heatwaves, frequently shorten the number of effective growing days and reduce productivity, with strong, species-dependent responses (Jiang et al., 2024; Matula et al., 2023; Zhang et al., 2024b). Fast-growing species have been shown to suffer larger proportional declines in productivity (Matula et al., 2023).

Species-specific traits, such as growth strategy, xylem anatomy, hydraulic efficiency, and phenology, play pivotal roles in shaping tree growth rates and the duration of the growing season. Fast-growing species typically exhibit higher hydraulic conductivity and larger xylem conduits, facilitating efficient water transport and enabling rapid growth (Wang et al., 2024a). These species often prioritise carbon assimilation during favourable conditions but may be more susceptible to hydraulic failure under drought stress (Tao et al., 2024). In contrast, slow-growing species often possess denser wood and smaller conduits, enhancing drought resistance but potentially limiting growth rates (Hu et al., 2024). Phenological traits, such as leaf-out timing and cambial activity, also influence the growing season's length and productivity (Wang et al., 2025). Key differences in anatomy, stomatal behaviour, and drought tolerance underpin contrasts

in growth rates and growing season duration between angiosperm and conifer species. Conifer species are generally considered more drought tolerant due to their hydraulically resistant xylem (Hacke & Sperry, 2001), with some conifer xylem described as being “overbuilt” for the climates in which these species occur (Laughlin et al., 2020). The greater hydraulic resistance associated with narrower conduits and smaller pit structures results in lower water transport efficiency and, consequently, slower growth rates compared with angiosperm species (Hacke & Sperry, 2001). However, this reduced hydraulic efficiency confers greater resistance to hydraulic failure, allowing conifer species to maintain physiological function and extend their growing season duration under late-season water stress (Hacke & Sperry, 2001).

Tree age, stem size, and stocking density are pivotal factors influencing tree growth rates and the duration of the growing season. As trees age, their growth rates typically decline due to factors such as reduced photosynthetic capacity and the transition of sapwood to heartwood (Thurner et al., 2025). Larger stem sizes, often associated with older trees, can enhance growth by providing greater structural support and access to resources. However, high stocking densities can lead to increased competition for light, water, and nutrients, potentially reducing individual tree growth rates (Li et al., 2025). Conversely, optimal stocking densities can mitigate competition, allowing for improved growth and extended growing seasons (Li et al., 2024b). Recent studies have highlighted that managing these factors effectively can enhance tree growth and productivity, underscoring the importance of considering tree age, stem size, and stocking density in forest management practices (Forrester et al., 2025).

Tree growth responses to climate, weather, and site factors can be quantified with high temporal resolution using electronic dendrometers, which track changes in stem radius over time (Drew & Downes, 2009). Raw dendrometer data allow calculation of key growth and water-related variables, including irreversible stem growth (GRO), maximum daily shrinkage (MDS), and tree water deficit (TWD; Zweifel et al., 2016). Irreversible growth reflects true stem expansion due to cell elongation and division and is calculated as the current stem radius reading minus the previous maximum when the current day’s average exceeds that maximum (Zweifel et al., 2016). The previous maximum could occur at any timeframe e.g. from minutes to months prior to the current stem radius reading. Factors influencing GRO include species traits,

environmental conditions, and water availability (Zweifel et al., 2016). Tree water deficit is calculated as the previous maximum minus the current stem radius reading when the current reading is lower, reflecting the balance between water loss through transpiration and water uptake (Zweifel et al., 2016). High TWD indicates cumulative depletion of stem water reserves, as trees draw on stored water to maintain transpiration when soil moisture is insufficient (Anderegg et al., 2020; Hu et al., 2018; Zhang et al., 2024a). Tree water deficit can also be used as an indicator of drought stress or cumulative water stress (Drew et al., 2011; Zweifel et al., 2005). Consistent with this, GRO typically decreases during drought because trees limit stomatal opening to preserve hydraulic integrity, reducing carbon assimilation and growth (Buckley, 2019; Prats et al., 2019; Zhang et al., 2025). Both GRO and TWD are expressed in μm (Zweifel et al., 2016). Maximum daily shrinkage is the difference between daily maximum and minimum stem diameter and reflects a tree's short-term response to current air and soil conditions, with high MDS indicating high tissue hydration, favourable conditions for photosynthesis, and reliance on elastic short-term water storage (Drew & Downes, 2009; Güney et al., 2020). Low MDS values may indicate either reduced transpiration due to closed stomata or reduced evaporation, or low tissue saturation resulting from a mismatch between water supply and demand (Güney et al., 2020).

The aim of this research was to measure and compare growth and shrinkage of five indigenous (*Fuscospora fusca*, *F. solandri*, *Lophozonia menziesii*, *Prumnopitys taxifolia*, and *Podocarpus totara*) and three exotic tree species (*Eucalyptus fastigata*, *P. radiata*, and *S. sempervirens*) at our study site, Rewanui Forest Park. We hypothesised that the exotic species would demonstrate higher GRO and MDS but lower TWD due to larger stem sizes, higher capacitance, and reportedly faster growth rates, compared to the indigenous species. We also hypothesised that the conifer species would have a longer growing season than the angiosperm species regardless of climatic conditions, due to higher drought tolerance and less restrictive stomatal control. Warm spring temperatures and dry summer conditions were expected to advance growth initiation and lead to earlier growth cessation, respectively, with stronger effects observed for the angiosperm species. Soil volumetric water content was hypothesised to have the highest strength of evidence for being included in the generalised additive models

(GAM; F statistic) for both GRO and TWD in both study years. For GRO, this was expected as GRO is reliant on sufficient turgor pressure. For TWD, this was expected as soil moisture availability directly constrains stem water status and determines the extent to which trees can replenish internal water stores. Potential evapotranspiration was hypothesised to have the highest strength of evidence for being included in the GAM for MDS in both study years, due to the link between MDS and transpiration and the strong link between transpiration and atmospheric demand.

2.2 Methods

2.2.1 Site and species

Rewanui Forest Park, a forestry trial site, was set up by the Montfort Trimble Foundation in the Wairarapa region of New Zealand approximately 23 km east of Masterton (Figure 2.1). An indigenous trial was established in 2006 including fifteen indigenous tree species. The site was selected to be part of the Forest Flows programme, a 5-year programme utilising a combination of terrestrial and remote-sensing technologies to gain a better understanding of hydrological fluxes in planted forests (Meason et al., 2020).

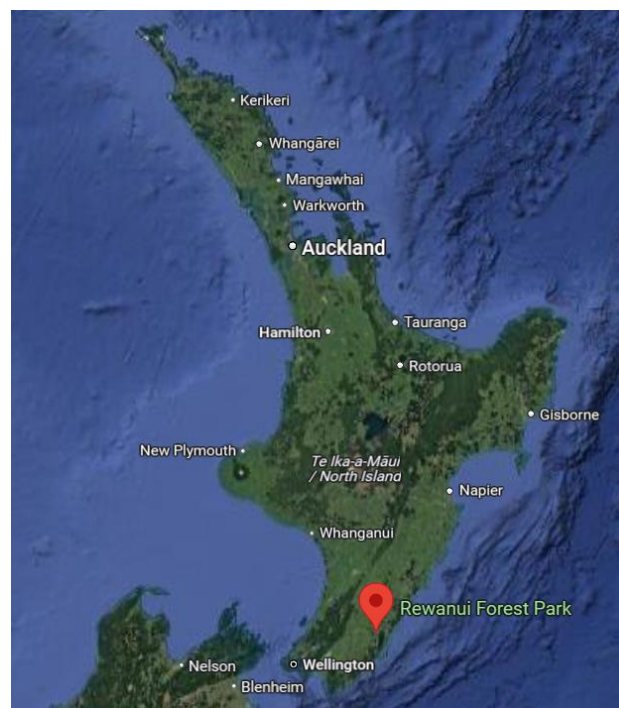


Figure 2.1: Location of Rewanui Forest Park.

Eight species, five indigenous and three exotic species, from a range of families were selected for this study (Table 2.1). All eight species were evergreen. Twenty plots were established between January and May of 2022: two plots for each of the indigenous species, as well as one mixed indigenous plot, and three plots for each of the exotic species (Figure 2.2). Data were collected over a two-year period and separated into two study years. Year 1 was between 21/06/2022 and 21/06/2023 and Year 2 was between 22/06/2023 and 21/06/2024. Within each plot, all electronic point dendrometers and soil moisture sensors were connected to a battery-powered data logger (node; Figure 2.3b; FlowLab, inFact Ltd, Christchurch). Data from each node was transferred to a central, solar-powered FlowLab gateway via a mesh radio system. The gateway sent the data and error messages at 5-minute intervals via a cell phone network to an online interface.

Table 2.1: Study species including taxonomic groupings and status, leaf habit, the number of plots and dendrometers established for each species, and stem diameter measured at the height of the dendrometers at the start of the study period (21/06/2022).

Group	Species	Family	Status	Stem diameter
Angiosperm species	<i>Fuscospora fusca</i> (Hook.f.) Heenan et Smissen	Nothofagaceae	Indigenous	14.76 ± 1.86
	<i>Fuscospora solandri</i> (Hook.f.) Heenan et Smissen	Nothofagaceae	Indigenous	15.06 ± 1.39
	<i>Lophozonia menziesii</i> (Hook.f.) Heenan et Smissen	Nothofagaceae	Indigenous	10.67 ± 0.58
	<i>Eucalyptus fastigata</i> H.Deane & Maiden	Myrtaceae	Exotic	35.43 ± 1.64
Conifer species	<i>Podocarpus totara</i> G.Benn. ex D.Don var. <i>totara</i>	Podocarpaceae	Indigenous	13.56 ± 1.11
	<i>Prumnopitys taxifolia</i> (D.Don) de Laub.	Podocarpaceae	Indigenous	15.01 ± 3.75
	<i>Pinus radiata</i> D.Don	Pinaceae	Exotic	36.16 ± 1.76
	<i>Sequoia sempervirens</i> (D.Don) Endl.	Cupressaceae	Exotic	22.13 ± 1.92

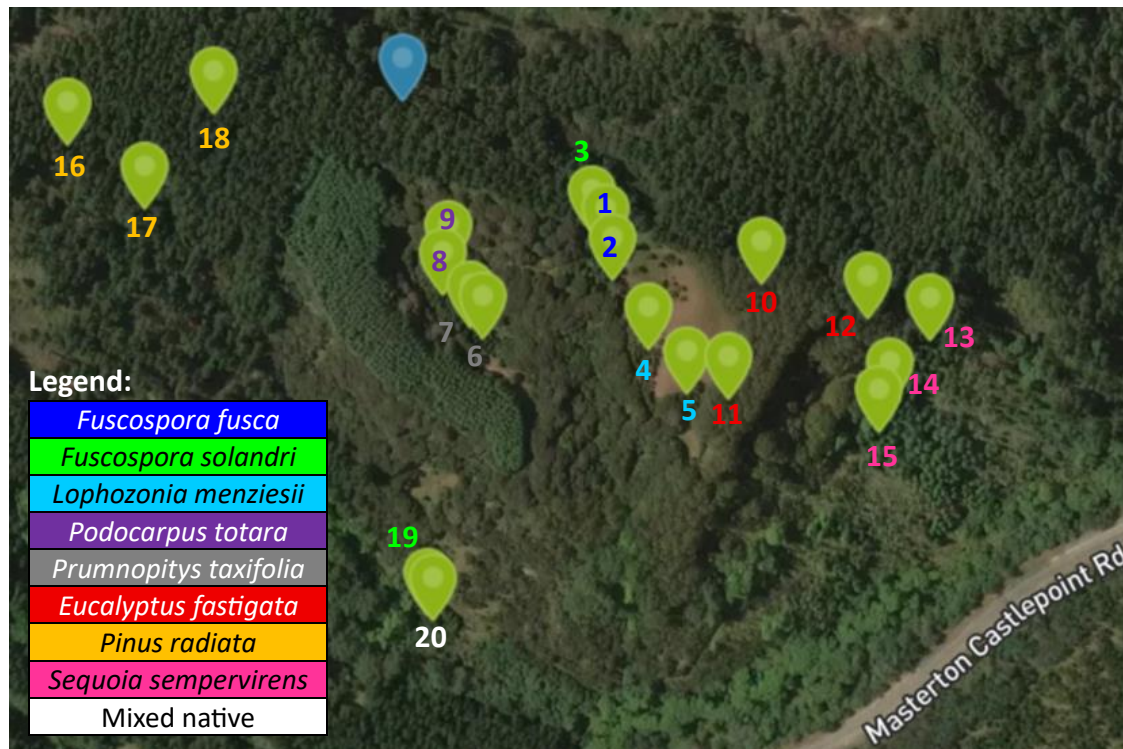


Figure 2.2: Map of study plots at Rewanui Forest Park. Green points indicate the location of a plot, and the blue point indicates the location of the central gateway.

Soil moisture sensors (TEROS 11; Meter Group, Pullman USA), with a probe length of 5.5 cm, were used to measure soil volumetric water content (soil VWC). The sensors were installed horizontally at the centre of each plot using a hand bucket auger and an installation tool to install the probes at set depths. Soil moisture sensors were placed at four different depths where possible (Table 2.2). The shallowest sensors were installed at a depth of 10 cm, followed by sensors at 30 cm. The third sensors were installed between 45 and 65 cm depending on the plot-specific soil depth. The deepest sensors were installed between 90 and 100 cm. Soil water potential sensors (TEROS 21; Meter Group, Pullman USA) were installed at one depth in three plots (Table 2.2) to obtain the relationship between soil VWC and soil water potential for soils at the site. The raw data suggested that the TEROS 21 sensors in the *S. sempervirens* and *E. fastigata* plots were either malfunctioning or not making adequate contact with the soil during the summer dry periods. Therefore, results from the *F. solandri* plot were selected to represent the relationship between soil VWC and soil water potential.

Table 2.2: Installation depths (cm) for the soil moisture probes in each of the study plots.

Species	Plot	Depth 1 (cm)	Depth 2 (cm)	Depth 3 (cm)	Depth 4 (cm)	TEROS 21 depth (cm)
<i>F. fusca</i>	1	10	30	50	-	-
	2	10	30	45	-	-
<i>F. solandri</i>	3	10	30	45	-	30
	19	10	30	60	100	-
<i>L. menziesii</i>	4	10	30	60	90	-
	5	10	30	60	100	-
<i>P. totara</i>	8	10	30	60	100	-
	9	10	30	60	90	-
<i>P. taxifolia</i>	6	10	30	60	95	-
	7	10	30	45	-	-
<i>E. fastigata</i>	10	10	30	60	95	-
	11	10	30	60	-	30
	12	10	30	60	-	-
<i>P. radiata</i>	16	10	30	60	100	-
	17	10	30	60	100	-
	18	10	30	60	100	-
<i>S. sempervirens</i>	13	10	30	60	100	-
	14	10	30	60	-	30
	15	10	30	60	100	-
Mixed native	20	10	30	60	99	-

Electronic point dendrometers (Figure 2.3a), designed for the Forest Flows programme (Cassales et al., 2025), were installed to measure stem radius changes. In each of the twenty plots, four trees were selected at random for dendrometer installation. The native species each had a total of 8 dendrometers installed, and the exotic species each had a total of 12 dendrometers installed. Dead outer bark was removed, leaving behind the inner living bark, particularly for the three exotic species that had thicker outer bark. Steel buttons were used to separate the dendrometer plunger and bark to spread the pressure of the plunger across a larger area. The dendrometer plates were adjusted to allow the plunger space to move, either when the plunger reached maximum travel (10 mm) or every six months.



Figure 2.3: An electronic point dendrometer in one of the *Pinus radiata* plots (a), showing the steel button and scraped bark. A data logger (node) in one of the *Lophozonia menziesii* plots (b) to which the soil moisture sensors and dendrometers were connected.

2.2.2 Growth and shrinkage

Raw data from the electronic point dendrometers were cleaned in Microsoft Excel by removing reset “steps” and unexplained spikes of more than 0.50 mm. Diameter at sensor height was used alongside the cleaned data to calculate daily stem radial increment. Three of the twenty plots, one each for *F. fusca* and *L. menziesii*, and the mixed indigenous species plot, were excluded from analysis due to instrument errors. Three growth variables, TWD, GRO, and MDS, were calculated from the cleaned dendrometer data. A modified version of the Zweifel et al. (2016) method was used to calculate TWD and GRO:

$$TWD = \begin{cases} \max[SR(< t)] - SR(t), & SR(t) < \max[SR(< t)] \\ 0, & SR(t) \geq \max[SR(< t)] \end{cases} \quad (1)$$

$$GRO = \begin{cases} SR(t) - \max[SR(< t)], & SR(t) \geq \max[SR(< t)] \\ 0, & SR(t) < \max[SR(< t)] \end{cases} \quad (2)$$

$$MDS = \max[SR(t)] - \min[SR(t)] \quad (3)$$

where $SR(t)$ refers to the current day’s average stem radius, and $\max[SR(< t)]$ refers to the previous day’s maximum stem radius. The units used were mm for all three growth variables. Unexplained spikes of 0.50 mm or more, likely caused by mechanical

interference, were removed from the three growth variables. GRO, TWD, and MDS were expressed in mm. A modified version of the Zweifel et al. (2016) method was used to give a single value per day for each of the three growth and shrinkage variables, for easier comparison.

Relative growth rate (RGR) was calculated to quantify tree-level growth relative to size. For each tree, GRO was converted to cm and added cumulatively to the initial stem radius. The initial stem radius was measured with diameter tapes at the start of the study period. Relative growth rate was calculated for each study tree on a daily timescale:

$$r_t = r_{\text{start}} + \sum GRO \quad (4)$$

where r_{start} is the initial radius (cm) and $\sum GRO$ is the cumulative radial increment. Basal area at each measurement was then calculated as:

$$BA_t = \pi r_t^2 \quad (5)$$

where r_t is the current tree radius (cm). Relative growth rate was then calculated as:

$$RGR_t = \frac{\ln(BA_t) - \ln(BA_{t-1})}{t - t_{-1}} \quad (6)$$

where BA_t and BA_{t-1} are the basal areas at the current and previous measurements, respectively, and $t - t_{-1}$ is the number of days between measurements. For the first measurement of each study year, no RGR was calculated. Daily RGR values were averaged per month to reduce noise. These values were then averaged per plot and then per species to give monthly average RGR for each study species.

2.2.3 Weather

Weather variables were obtained from a meteorological station on the Rewanui property (40.930215°S, 175.908731°E), operated by Greater Wellington Regional Council for the duration of the study period (21/06/2022-21/06/2024). The weather variables included rainfall, air temperature at 1.2 m, maximum wind gust, relative humidity, solar radiation, wind direction, and wind speed. Rainfall data was obtained at a daily resolution, while all other variables were recorded at 10-minute intervals.

The Priestley-Taylor equation (Priestley & Taylor, 1972) was used to calculate potential evapotranspiration (PET) from the meteorological station air temperature and solar radiation measurements, obtained from the Rewanui property station:

$$ET = \alpha \cdot \frac{\Delta}{\Delta + \gamma} \cdot \frac{R_n - G}{\lambda} \quad (7)$$

Where ET = evapotranspiration (mm day⁻¹), α = Priestley–Taylor coefficient (1.26), Δ = slope of the saturation vapour pressure curve (kPa °C⁻¹), γ = psychrometric constant (kPa °C⁻¹), R_n = net radiation (MJ m⁻² day⁻¹), G = soil heat flux density (MJ m⁻² day⁻¹), and λ = latent heat of vapourization (2.37 MJ kg⁻¹).

Thirty-year average (1991-2021) rainfall and air temperature data (climate normal) were downloaded from the NIWA Datahub (National Institute of Water and Atmospheric Research) as the on-site dataset was not long enough. Total rainfall normal data was obtained from the Blairlogie weather station, located approximately 1.5 km east from Rewanui Forest Park and air temperature climate normal data was obtained from the Te Ore Ore weather station, located approximately 15 km west from Rewanui Forest Park, as neither station had a complete dataset for the two variables.

2.2.4 Statistical analysis and modelling

Statistical analysis was undertaken in RStudio version 2024.12.1+563 (Posit Software, 2024) using R Version 4.4.1 (R Core Team, 2024). The Gompertz model is commonly used to model sigmoidal growth and was used to determine species-specific growth periods (Tjørve & Tjørve, 2017; Wang et al., 2024b). First, cumulative growth (cGRO) was calculated from GRO for each plot and study year (Year 1 = 21/06/2022-21/06/2023, Year 2 = 22/06/2023-21/06/2024), by re-zeroing each study year so that cGRO = 0 on the first day of the study year and computing a running total. The Gompertz model was fit as a user-defined function in RStudio for each plot, species, and study year:

$$G(t) = A \exp(-\exp(B - Ct)) \quad (8)$$

where $G(t)$ is cumulative growth at time t (days since growth onset), A is the upper asymptote maximum cumulative growth, B controls the displacement along the time

axis, and C is the growth rate coefficient. C represents how fast the curve took to reach the asymptote or A .

To determine the timing of active growth, the first derivative of the Gompertz function was calculated, representing instantaneous growth rate:

$$(G'(t) = AC \exp^{(B-Ct)} \exp(-\exp(B - Ct))) \quad (9)$$

Fitting was performed per plot, species, and study year using nonlinear least squares via 'minpack.lm::nlsLM()', which uses the Levenberg–Marquardt algorithm and allows parameter bounds. Starting values were set to:

- A initial = observed maximum cGRO in the series,
- B initial = 2,
- C initial = 0.05.

Parameter bounds were used to aid convergence: lower = c(0, 0, 0.001) and upper = c(2 * max(cGRO), 10, 1). Fits that did not converge, or groups with fewer than five data points or no nonzero growth, were omitted from fitting. Daily fitted values and derivatives were predicted across the full date range 'seq.Date()' using the fitted parameter values and the Gompertz functions implemented in RStudio. We identified the active growth period by locating days when the derivative exceeded 5 % of the peak derivative for that fitted series. Model coefficients and their 95 % confidence intervals were extracted with 'coef()' and 'confint()'.

Generalised additive models were used to examine non-linear relationships between weather variables and tree physiological responses, while accounting for species-level differences. Generalised additive models were chosen to allow for flexible, non-linear responses of physiological variables to weather drivers without imposing a priori assumptions about functional form. Weather variables were selected using a correlation matrix (Appendix A); weather variables with low correlation and high expected influence on the dendrometer variables were selected, including PET, rainfall, and soil VWC. Generalised additive models were fitted using the 'mgcv' package (Wood, 2017). Response variables, growth rate (GRO), tree water deficit (TWD), and maximum daily shrinkage (MDS), were standardised (mean = 0, SD = 1) to facilitate

comparison of effect sizes across models. Weather predictors, soil VWC, rainfall, and PET, were also standardised. Standardisation was performed using the base R 'scale()' function (R Core Team, 2024). Species and plot identifiers were treated as categorical variables. *Pinus radiata* was specified as the reference species for all models to allow species effects to be interpreted as deviations from this baseline.

Separate GAMs were fitted for each response variable (GRO, TWD, and MDS) and for each growing year. Models took the general form:

$$Y \sim s(\text{soil VWC}) + s(\text{Rainfall}) + s(\text{PET}) + \text{Species}$$

where Y represents the standardised response variable. Weather predictors were included as smooth terms using thin-plate regression splines 's()', while species was included as a parametric factor. The basis dimension (k) was specified a priori ($k = 5$ for soil VWC; $k = 10$ for rainfall and PET) to allow sufficient flexibility while avoiding overfitting. Smoothness parameters were estimated using restricted maximum likelihood (REML), which provides stable smoothing parameter estimation and improved inference for GAM. Model fitting was performed using the 'gam()' function in 'mgcv', and model summaries were inspected to evaluate effective degrees of freedom (edf), F-statistics, and approximate p-values for each smooth term.

Model adequacy was assessed using the 'gam.check()' function (mgcv), which evaluates convergence, residual behaviour, and the appropriateness of the chosen basis dimensions. The k-index diagnostic was used to assess whether the specified basis dimension was sufficient to capture the underlying structure in the data. In cases where k-index values were low and effective degrees of freedom approached the maximum allowed, basis dimensions were increased and models refitted.

To assess differences among species after accounting for weather effects, estimated marginal means (EMMs) were computed using the 'emmeans' package (Lenth, 2024). Pairwise species comparisons were conducted with Tukey-adjusted contrasts to control for multiple testing. These comparisons were based on model-adjusted means, providing inference on species differences conditional on the fitted smooth weather effects.

Partial effects of weather variables were visualised using the 'draw()' function from the gratia package (Simpson, 2024), which provides representations of GAM smooths. Smooth plots display the estimated partial effect of each weather variable on the response, centred on zero, with shaded 95 % confidence intervals. Rugs along the x-axis indicate the distribution of observed data.

2.3 Results

2.3.1 Weather

There were clear differences and similarities in weather between Year 1 and Year 2, partially driven by Cyclones Hale and Gabrielle in Year 1. Average air temperature and PET were similar between study years, and average air temperature was similar to climate normal levels (Figure 2.4).

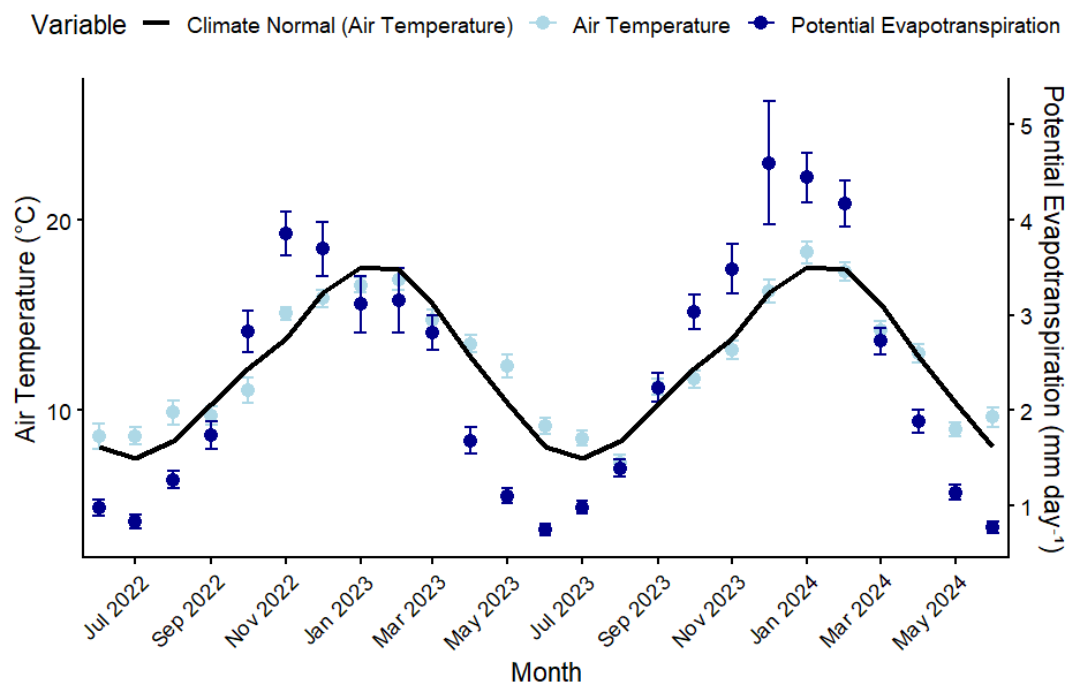


Figure 2.4: Average air temperature (light blue) and potential evapotranspiration from the Priestley-Taylor equation (dark blue) across the study period (21/06/2022-21/06/2024). The black line represents climate normal (1991-2021) average air temperature.

Total rainfall was generally higher in Year 1 compared to both Year 2 and climate normal levels. Rainfall was lower than normal in Year 2, particularly in February 2024 (total rainfall = 16 mm). Soil volumetric water content was near field capacity for the

duration of Year 1, while a clear seasonal pattern was observed in Year 2 (Figure 2.5). Soil VWC differed between species, lowest for *F. solandri* and *E. fastigata* and highest for *P. radiata* and *S. sempervirens*. The wettest soil was observed in the *P. radiata* plots in Year 1 (Average soil VWC = $0.35 \text{ m}^3 \text{ m}^{-3}$) and the driest soil was observed in the *E. fastigata* plots in Year 2 (Average soil VWC = $0.19 \text{ m}^3 \text{ m}^{-3}$). Soil water potential results reflected the seasonal patterns of soil VWC. The most negative soil water potential values were observed in February when soil VWC was lowest for *F. solandri* (Figure 2.5).

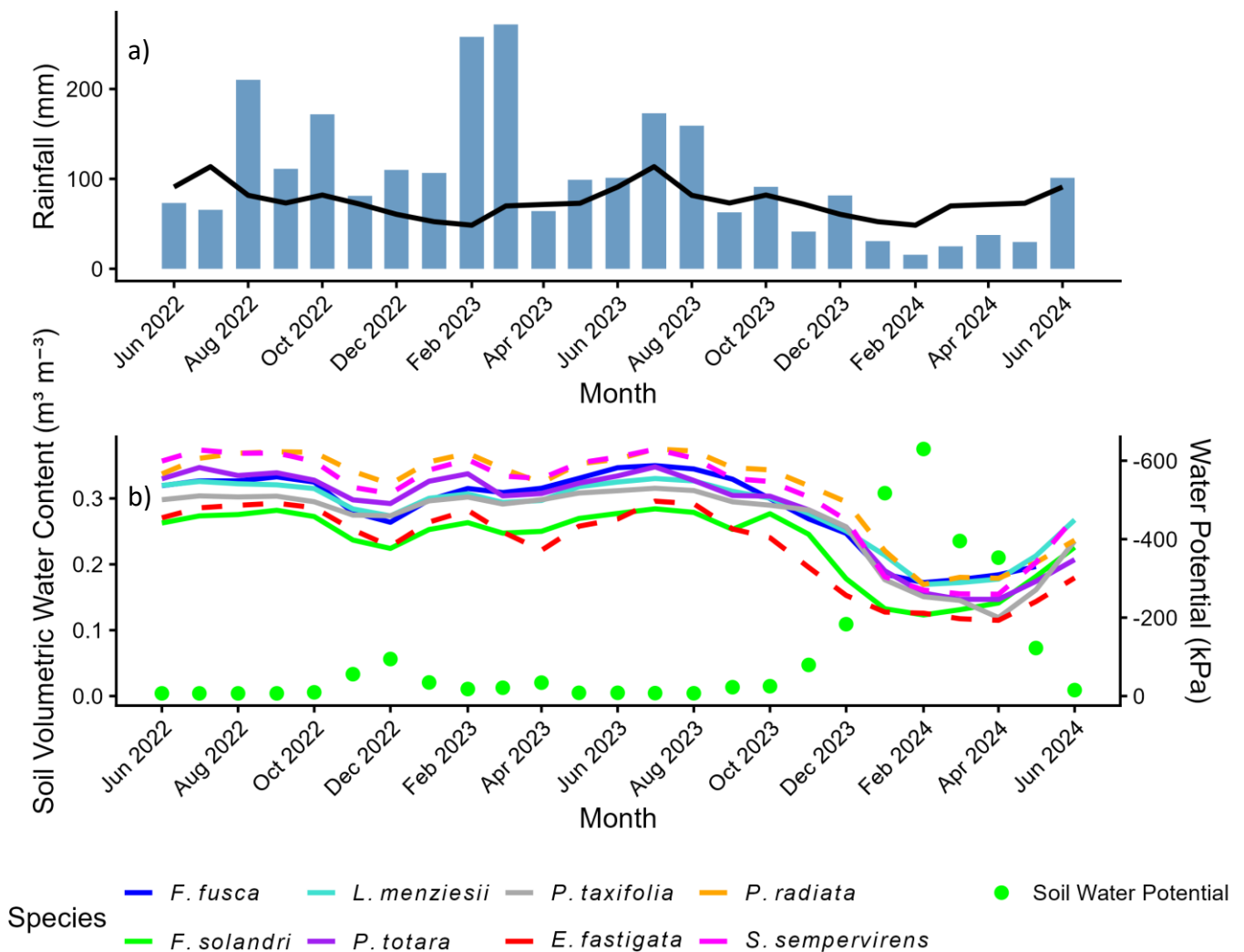


Figure 2.5: Total monthly rainfall (blue bars; a), climate normal (1991-2021 average) total monthly rainfall (black line; a), average soil volumetric water content (soil VWC; coloured lines; b), and soil water potential (coloured dots; b) across the study period for each species. Exotic species indicated with dashed lines. Soil VWC was averaged across soil depths and plots to give an average for each species; *F. fusca* n = 6, *F. solandri* n = 7, *L. menziesii* n = 8, *P. totara* n = 8, *P. taxifolia* n = 7, *E. fastigata* n = 10, *P. radiata* n = 12, *S. sempervirens* n = 11.

2.3.2 Growth and shrinkage

The exotic species had larger starting stem diameters compared to the indigenous species (Table 2.3) despite being planted at the same time. *Pinus radiata* had the largest average diameter and *L. menziesii* the smallest, across the study period. Mean increment was variable across the study species. The exotic conifer species demonstrated a larger mean increment than the exotic angiosperm species. Two of the native angiosperm species exhibited a larger mean increment than the native conifer species. One of the exotic conifer species, *S. sempervirens*, had the largest mean increment. One of the native angiosperm species, *F. fusca*, had the smallest mean increment.

Table 2.3: Species-level average diameter at breast height (DBH) at the start (21/06/2022) and end (21/06/2024) of the study period, and mean DBH increment. Values are expressed as mean $\pm$ standard error.

Species (sample size)	Starting Diameter (cm)	End Diameter (cm)	Mean Increment (cm)
<i>F. fusca</i> (4)	14.76 $\pm$ 1.86	15.88 $\pm$ 1.88	1.12 $\pm$ 1.87
<i>F. solandri</i> (8)	15.06 $\pm$ 1.39	17.14 $\pm$ 1.56	2.08 $\pm$ 1.78
<i>L. menziesii</i> (4)	10.67 $\pm$ 0.58	12.77 $\pm$ 0.48	2.10 $\pm$ 0.53
<i>P. totara</i> (8)	13.56 $\pm$ 1.11	15.01 $\pm$ 1.07	1.45 $\pm$ 1.09
<i>P. taxifolia</i> (8)	15.01 $\pm$ 3.75	16.56 $\pm$ 3.85	1.55 $\pm$ 3.80
<i>E. fastigata</i> (12)	35.43 $\pm$ 1.64	37.09 $\pm$ 1.80	1.66 $\pm$ 1.72
<i>P. radiata</i> (12)	36.16 $\pm$ 1.76	38.64 $\pm$ 1.99	2.48 $\pm$ 1.88
<i>S. sempervirens</i> (12)	22.13 $\pm$ 1.92	26.07 $\pm$ 2.07	3.94 $\pm$ 2.00

Distinct patterns were observed in GRO (Figure 2.6 & 2.9), RGR (Figure 2.9a), TWD (Figure 2.7 & 2.10a), and MDS (Figure 2.8 & 2.10b) between the study species. All study species demonstrated a similar GRO and RGR pattern, increasing in the warmer months and decreasing in the colder months. Of the exotic study species, only *S. sempervirens* had larger summer GRO and RGR peaks than the indigenous species. These large peaks were followed by those for *F. fusca* (indigenous angiosperm). The exotic species generally appeared to initiate growth earlier than the indigenous species. Expressing growth relatively (RGR) resulted in similar growth rates between the indigenous and exotic species.

All study species exhibited a TWD peak in Year 2; this peak was higher for the exotic species and indigenous conifer species than the indigenous angiosperm species. Only

E. fastigata showed a TWD in Year 1. Across the study period, TWD was generally highest for *E. fastigata*, except for *P. radiata* in winter 2023, and lowest for *F. solandri*. Similar to GRO and RGR, MDS followed a general trend of increasing in the spring and summer months and decreasing in the winter months for all study species. A larger MDS peak was observed in Year 2 for all species. Peaks in MDS were highest for *S. sempervirens* and lowest for *F. solandri*. The conifer species generally peaked later than the angiosperm species in Year 2.

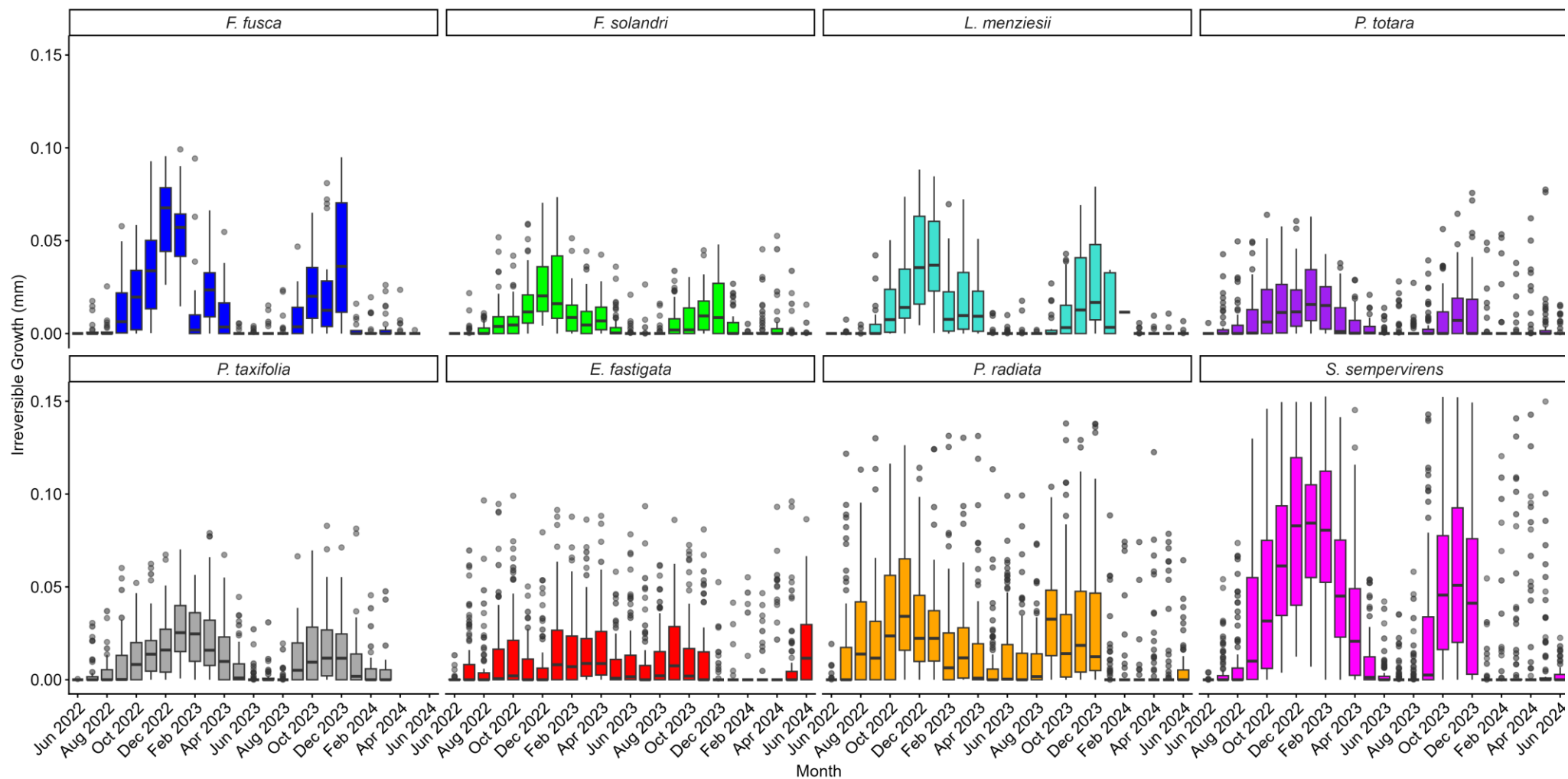


Figure 2.6: Monthly box plots of irreversible growth (GRO) across the study period (21/06/2022-21/06/2024). Exotic species indicated in red (*E. fastigata*), yellow (*P. radiata*), and pink (*S. sempervirens*).

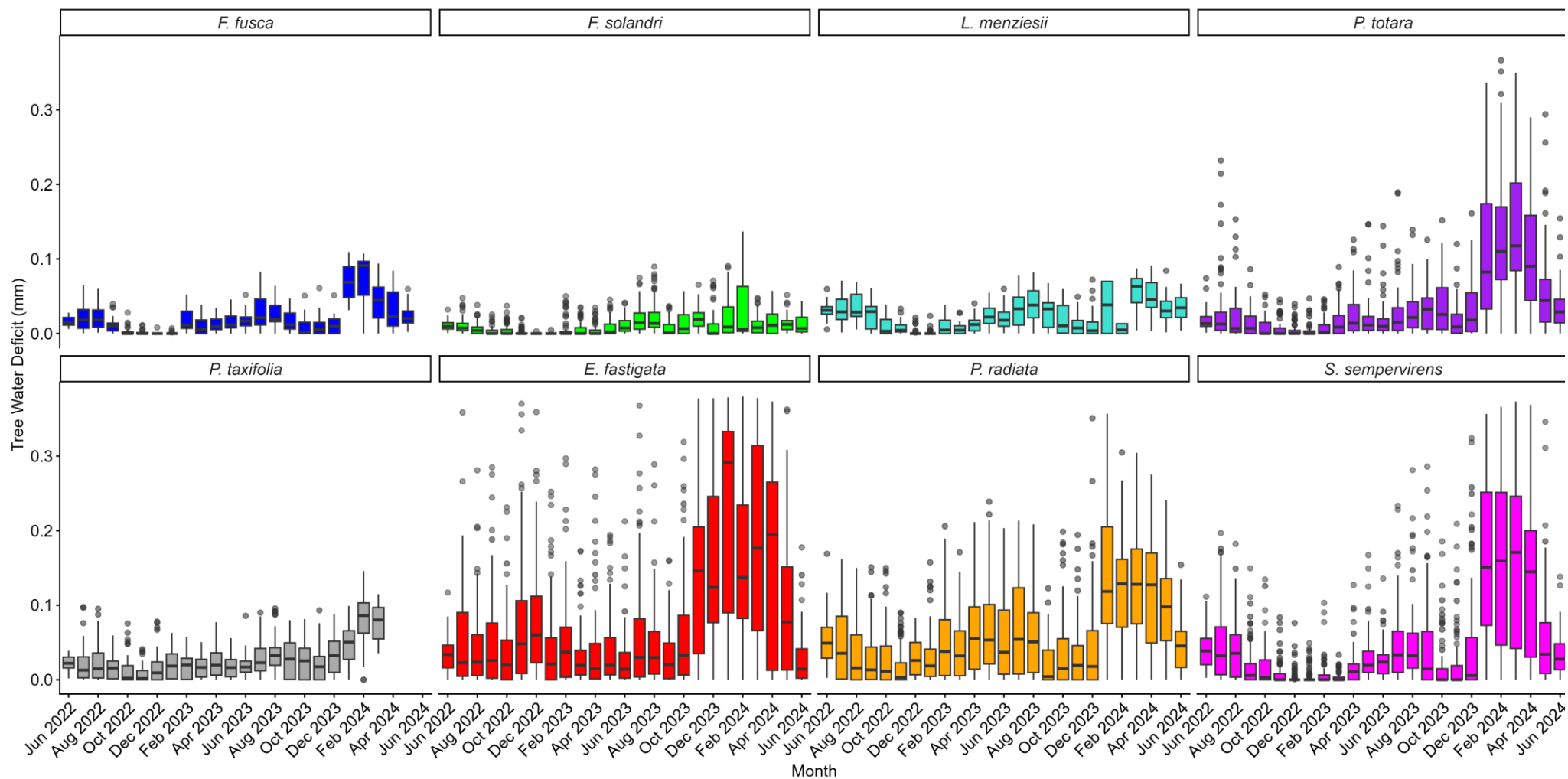


Figure 2.7: Monthly box plots of tree water deficit (TWD) across the study period (21/06/2022-21/06/2024). Exotic species indicated in red (*E. fastigata*), yellow (*P. radiata*), and pink (*S. sempervirens*).

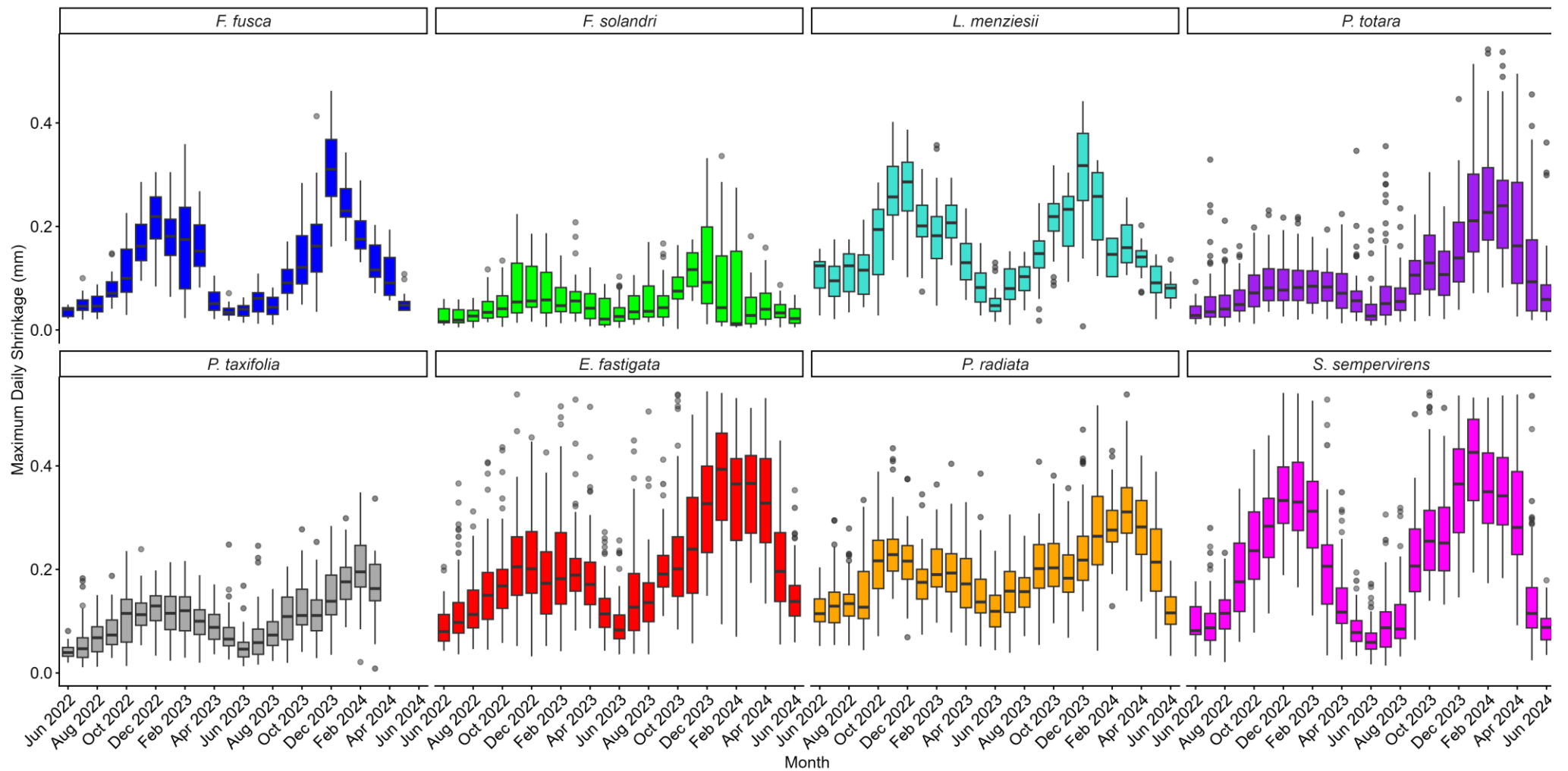


Figure 2.8: Monthly box plots of maximum daily shrinkage (MDS) across the study period (21/06/2022-21/06/2024). Exotic species indicated in red (*E. fastigata*), yellow (*P. radiata*), and pink (*S. sempervirens*).

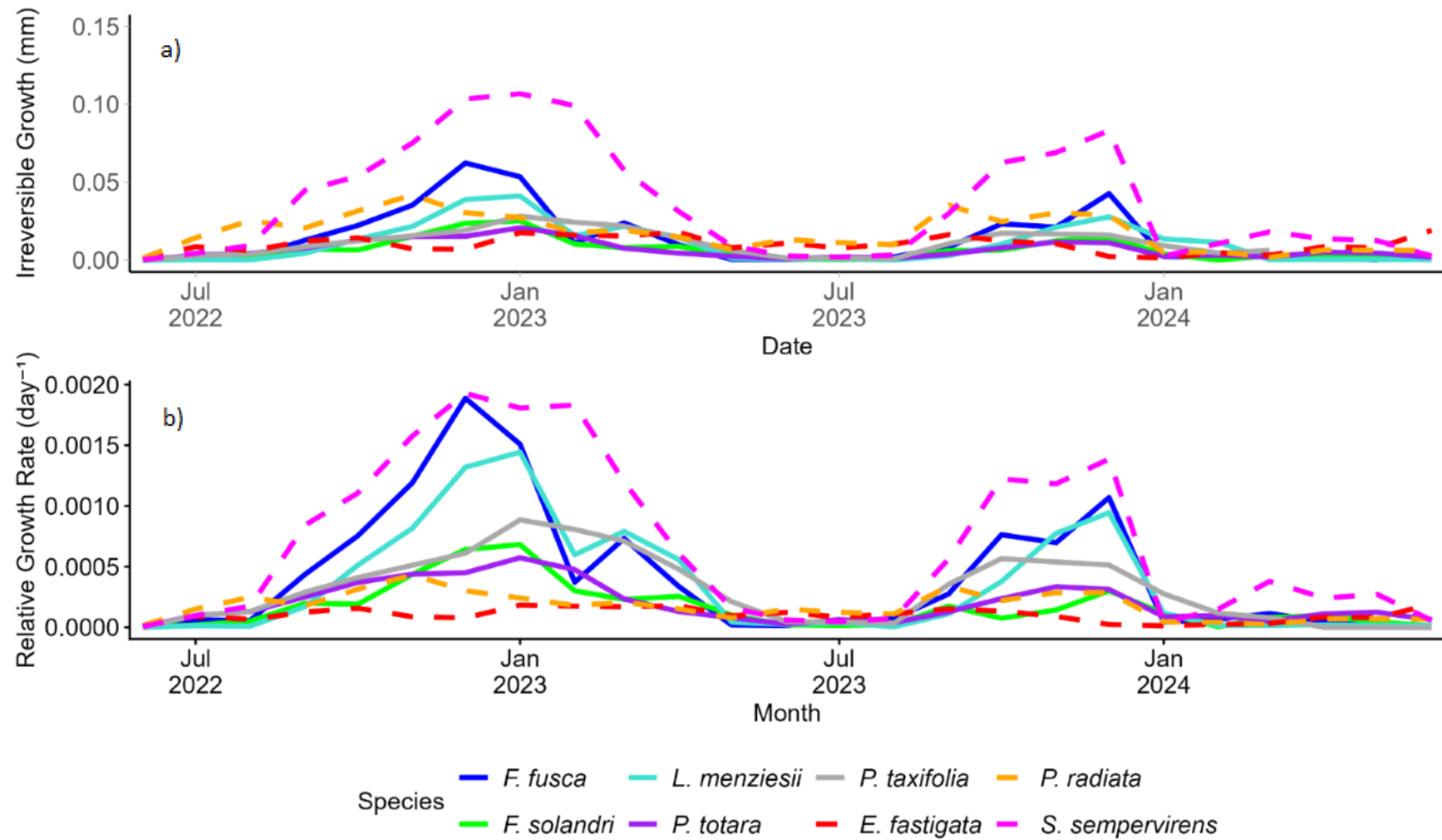


Figure 2.9: Monthly average irreversible growth (GRO, a) and relative growth rate (RGR, b). Exotic species indicated by dashed lines, indigenous species indicated by solid lines.

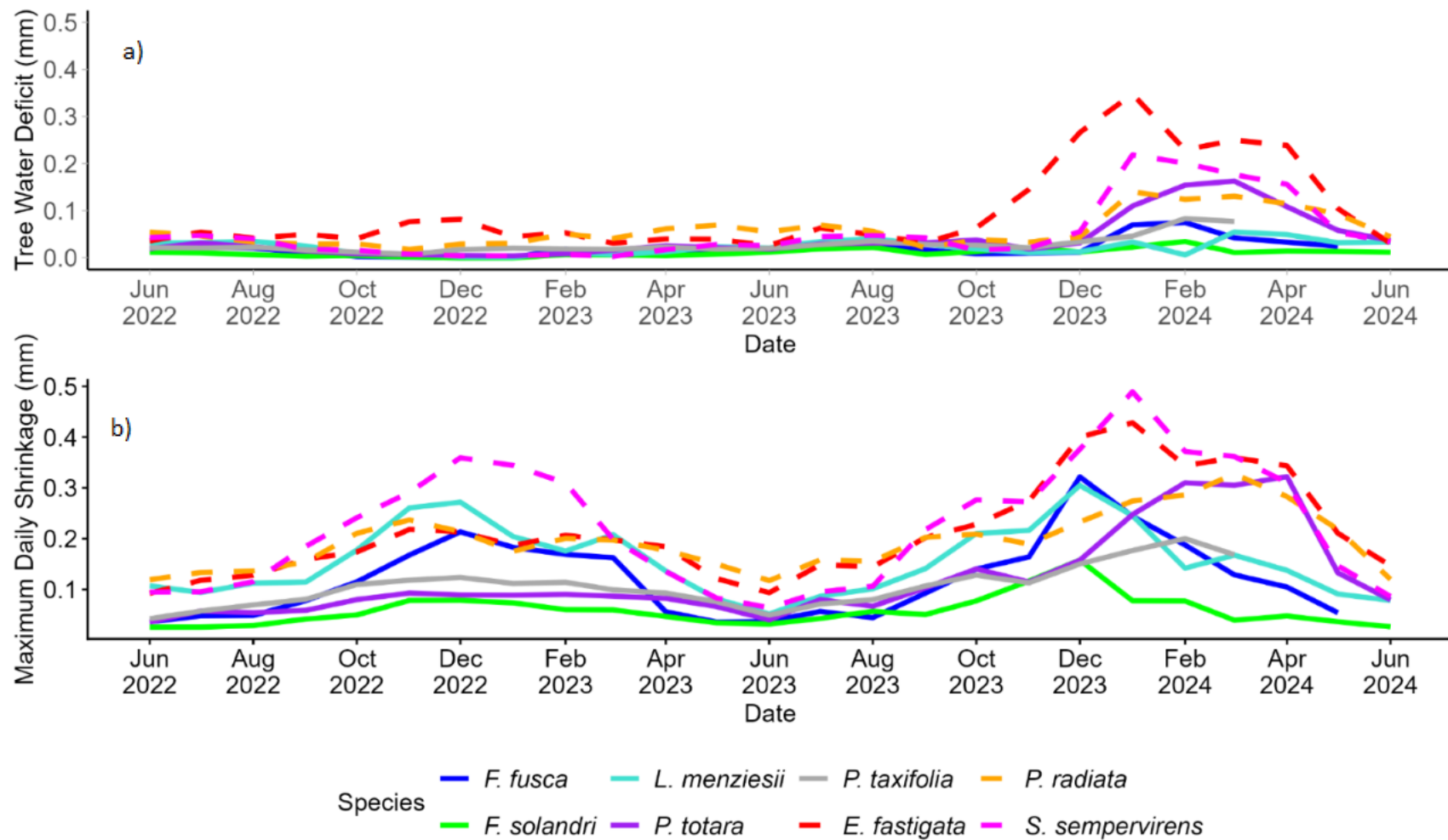


Figure 2.10: Monthly average tree water deficit (TWD) and maximum daily shrinkage (MDS). Exotic species indicated by dashed lines, indigenous species indicated by solid lines.

2.3.3 Growing season duration

There were clear differences in cumulative growth between the study species (Figure 2.11). In both study years, *S. sempervirens* had the highest measured (Figure 2.11a & b) and modelled (Figure 2.11c & d) cGRO of the study species. The other two exotic species had comparable cGRO to the indigenous species in Year 1 (Figure 2.11a & c); *P. radiata* exhibited higher cGRO than the indigenous species in Year 2 (Figure 2.11b & d). *Podocarpus totara* and *F. solandri* had the lowest measured and modelled cGRO in Year 1 and Year 2, respectively. Start dates for growth were variable across species, ranging from June to September (Table 2.4). In Year 1, *E. fastigata* and *P. radiata* initiated growth earlier and *L. menziesii* initiated growth later than the other study species. All species were modelled to cease growth beyond the end of Year 1, whereas in Year 2 cessation ranged from early March to early June. In Year 2, *E. fastigata* had the longest growing season (346 days; 22/06/2022-22/06/2024) and *L. menziesii* had the shortest growing season in Year 2 (158 days; 27/09/2023-3/03/2024). Asymptotic maximum cumulative growth (*A*) varied substantially among species in Year 1, from 3.6 mm in *P. totara* to 19.6 mm in *S. sempervirens*. Growth rate coefficient (*C*) ranged from 0.006 mm day⁻¹ in *E. fastigata* to 0.020 mm day⁻¹ in *F. fusca*. Compared to Year 1, Year 2 *A* values were markedly lower for all species, ranging from 1.33 mm for *F. solandri* to 8.27 mm for *S. sempervirens*. However, *C* rates were higher in Year 2, particularly for *L. menziesii* (0.036 mm day⁻¹) and *F. fusca* (0.029 mm day⁻¹). Confidence intervals for *A*, *B*, and *C* were narrow for most fits, indicating stable parameter estimation and well-defined growth trajectories.

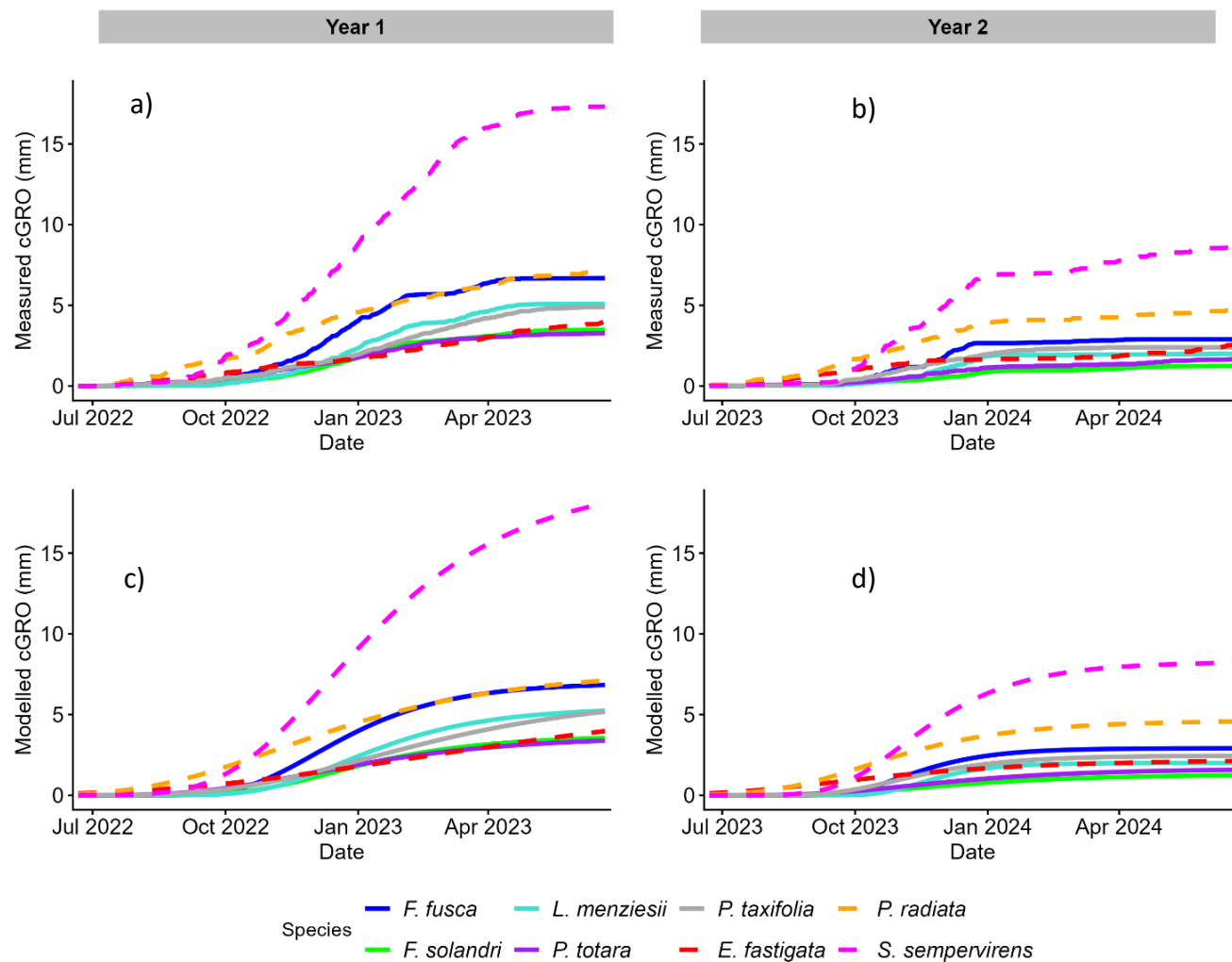


Figure 2.11: Measured and fitted cumulative GRO. a) measured Year 1, b) measured Year 2, c) modelled Year 1, d) modelled Year 2. Exotic species are indicated in dashed lines, indigenous species are indicated in solid lines.

Table 2.4: Species-specific Gompertz model parameters and growth timing. For each species and study year, the table shows the modelled start date and end date of growth, the asymptotic maximum cumulative growth (A, mm), the displacement along the x-axis (B, days), and the growth rate coefficient (C, mm day⁻¹), and 95 % confidence intervals for A, B, and C. Start and end dates correspond to the period when daily growth rate exceeded 5 % of the species' maximum modelled growth rate.

Year	Species	Start Date	End Date	Duration	A (95 % CI lower-upper)	B (95 % CI lower-upper)	C (95 % CI lower-upper)
1	<i>F. fusca</i>	4/09/2022	21/06/2023	290	6.97 (6.92-7.01)	3.20 (3.13-3.28)	0.020 (0.019-0.020)
	<i>F. solandri</i>	25/08/2022	21/06/2023	300	3.74 (3.70-3.77)	2.88 (2.80-2.96)	0.016 (0.016-0.017)
	<i>L. menziesii</i>	15/09/2022	21/06/2023	279	5.43 (2.40-5.46)	3.30 (3.25-3.35)	0.018 (0.018-0.018)
	<i>P. totara</i>	16/07/2022	21/06/2023	340	3.64 (3.60-3.69)	2.07 (2.02-2.12)	0.013 (0.013-0.013)
	<i>P. taxifolia</i>	24/07/2022	21/06/2023	332	6.18 (6.08-3.29)	2.09 (2.05-2.13)	0.011 (0.010-0.011)
	<i>E. fastigata</i>	21/06/2022	21/06/2023	365	6.44 (5.89-6.35)	1.41 (1.43-1.47)	0.006 (0.006-0.007)
	<i>P. radiata</i>	21/06/2022	21/06/2023	365	7.70 (7.63-7.77)	1.52 (1.50-1.55)	0.011 (0.011-0.011)
	<i>S. sempervirens</i>	5/08/2022	21/06/2023	320	19.62 (19.42-19.82)	2.38 (2.34-2.43)	0.014 (0.013-0.014)
2	<i>F. fusca</i>	2/09/2023	17/03/2024	197	2.91(2.89-2.93)	3.81 (3.66-3.96)	0.029 (0.028-0.030)
	<i>F. solandri</i>	15/07/2023	16/06/2024	337	1.33 (1.30-1.36)	2.16 (2.07-2.25)	0.014 (0.013-0.015)
	<i>L. menziesii</i>	27/09/2023	3/03/2024	158	2.00 (1.99-2.01)	5.24 (3.25-3.35)	0.036 (0.035-0.038)
	<i>P. totara</i>	20/07/2023	3/06/2024	319	1.65 (1.62-1.68)	2.24 (2.17-2.32)	0.016 (0.016-0.017)
	<i>P. taxifolia</i>	13/08/2023	25/04/2024	256	2.46 (2.45-2.47)	2.94 (2.88-2.99)	0.023 (0.022-0.023)
	<i>E. fastigata</i>	22/06/2023	2/06/2024	346	2.22 (2.22-2.36)	1.14 (1.05-1.18)	0.013 (0.010-0.012)
	<i>P. radiata</i>	30/06/2023	29/05/2024	334	4.64 (4.61-4.67)	1.65 (1.61-1.69)	0.016 (0.016-0.016)
	<i>S. sempervirens</i>	12/08/2023	4/05/2024	266	8.27 (8.18-8.35)	2.89 (2.77-3.02)	0.022 (0.021-0.023)

2.3.4 Weather effects on growth and shrinkage

The GAMs showed clear differences between species and weather effects on the dendrometer-obtained growth and shrinkage variables (Table 2.5). The GAMs and EMMs (Appendix B-Appendix G) showed clear differences in mean GRO, TWD, and MDS between study species in both study years. *Sequoia sempervirens* had the highest mean GRO and MDS in both study years. *Eucalyptus fastigata* had the highest mean TWD in both study years. In many cases the exotic species had higher GRO, TWD, and MDS compared to the indigenous species with a few exceptions. *Eucalyptus fastigata* had a similar mean to one or more indigenous species for GRO in both Year 1 (Appendix B) and Year 2 (Appendix C) and MDS in Year 1 (Appendix F). *Sequoia sempervirens* had a similar mean TWD to the indigenous species in Year 1 (Appendix D).

For GRO, more deviance was explained in the Year 1 GAM ($R^2 = 0.32$) compared to Year 2 GAM ($R^2 = 0.17$). Rainfall was the strongest predictor of GRO in Year 1 and Year 2, followed by PET in both study years. In Year 1, high soil VWC was associated with low GRO, and high rainfall and PET were associated with high GRO (Figure 2.12). In Year 2, moderate soil VWC and rainfall were associated with high GRO, and low PET was associated with high GRO (Figure 2.13).

For TWD, more deviance was explained in the Year 2 GAM ($R^2 = 0.33$) than the Year 1 GAM ($R^2 = 0.21$). Rainfall was the strongest predictor of TWD followed by PET, in Year 1. Soil VWC was the strongest predictor followed by PET in Year 2. In Year 1, low soil VWC, rainfall, and PET, as well as high PET were associated with high TWD (Figure 2.14). In Year 2, low soil VWC and rainfall and moderate to high PET were associated with high TWD (Figure 2.15).

For MDS, marginally higher deviance was explained by the Year 1 GAM ($R^2 = 0.55$) than the Year 2 GAM ($R^2 = 0.51$). Potential evapotranspiration was the strongest predictor of MDS in both study years, followed by rainfall in Year 1 and soil VWC in Year 2. In Year 1, low soil VWC and high rainfall and PET were associated with high MDS (Figure 2.16). In Year 2, low soil VWC and moderate rainfall and PET were associated with high MDS (Figure 2.17).

Table 2.5: Summary of generalised additive model (GAM) smooth-term results for dendrometer variables across two study years. Models were fitted separately for GRO, TWD, and MDS and each study year, with *Pinus radiata* as the reference species. Each weather variable (soil volumetric water content, rainfall, and potential evapotranspiration) was modelled using thin-plate regression splines (k = 5 for soil VWC; k = 10 for rainfall and PET). Reported values include the effective degrees of freedom (edf), F-statistics, and associated p-values for each smooth term.

Dendrometer variable	Study Year	Weather variable	edf	F	p
GRO	1	Soil VWC	3.44	83.63	<0.01
		Rainfall	8.62	402.89	<0.01
		PET	8.73	237.23	<0.01
GRO	2	Soil VWC	3.86	94.86	<0.01
		Rainfall	8.85	155.84	<0.01
		PET	8.41	104.56	<0.01
TWD	1	Soil VWC	3.75	17.21	<0.01
		Rainfall	8.01	121.02	<0.01
		PET	8.26	41.19	<0.01
TWD	2	Soil VWC	3.73	431.27	<0.01
		Rainfall	7.46	25.89	<0.01
		PET	8.87	117.77	<0.01
MDS	1	Soil VWC	3.89	111.80	<0.01
		Rainfall	7.38	143.30	<0.01
		PET	8.47	1078.70	<0.01
MDS	2	Soil VWC	3.80	554.63	<0.01
		Rainfall	4.34	52.63	<0.01
		PET	4.34	638.13	<0.01

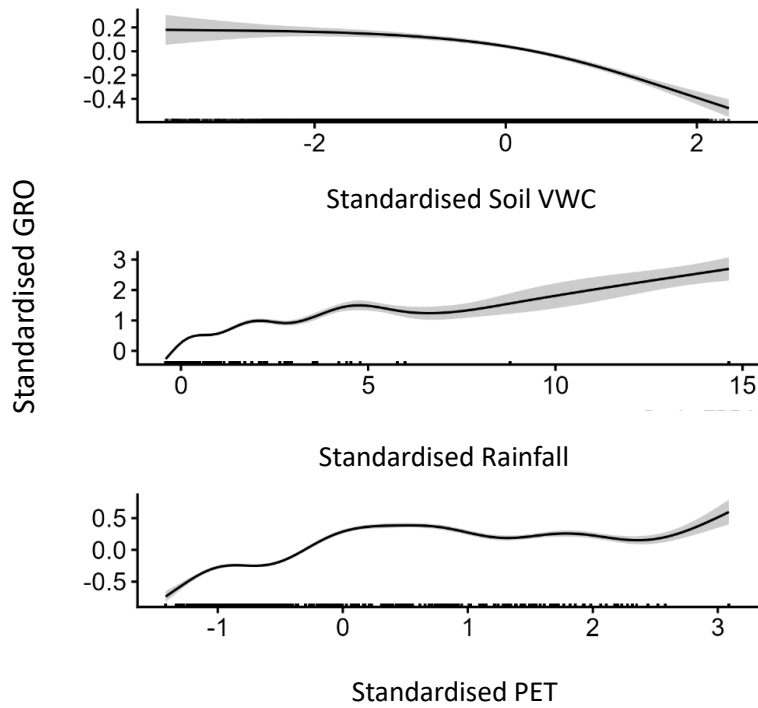


Figure 2.12: Smooth partial-effect plots for GRO in Year 1, showing nonlinear responses to (a) soil volumetric water content (VWC), (b) rainfall, and (c) potential evapotranspiration (PET). Shaded bands indicate 95 % confidence intervals, and rug marks along the x-axis show the distribution of observations. All predictors were standardised (mean = 0, standard deviation = 1).

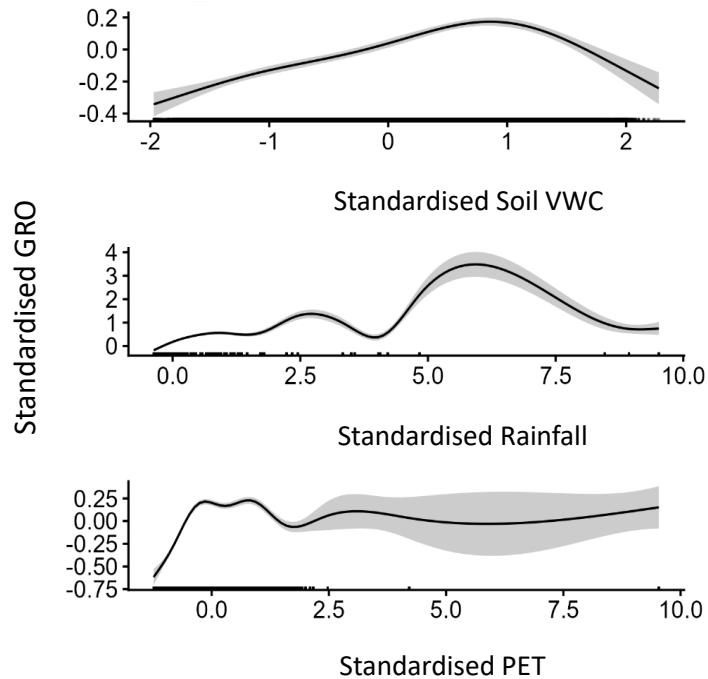


Figure 2.13: Smooth partial-effect plots for GRO in Year 2, showing nonlinear responses to (a) soil volumetric water content (VWC), (b) rainfall, and (c) potential evapotranspiration (PET). Shaded bands indicate 95 % confidence intervals, and rug marks along the x-axis show the distribution of observations. All predictors were standardised (mean = 0, standard deviation = 1).

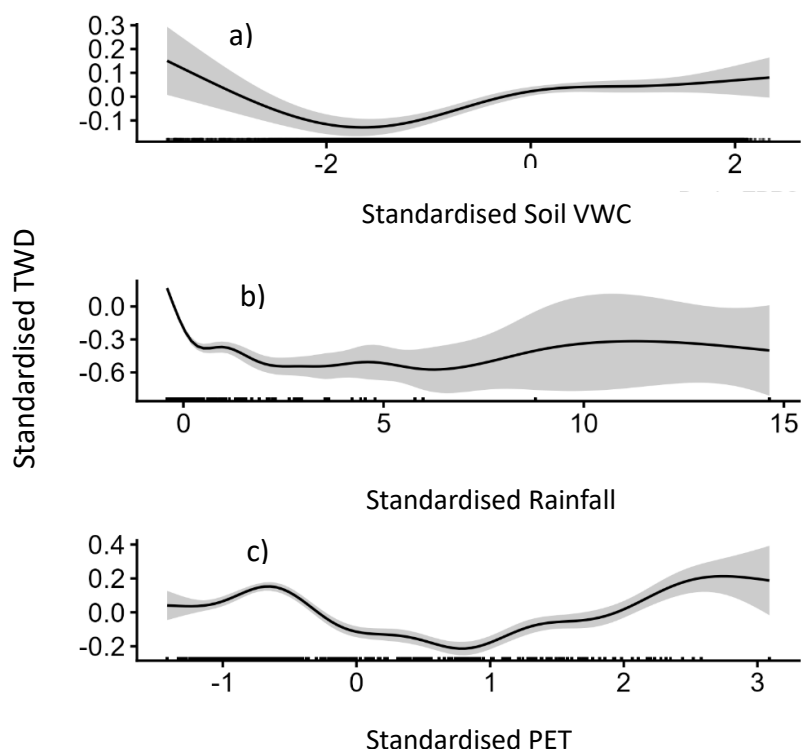


Figure 2.14: Smooth partial-effect plots for TWD in Year 1, showing nonlinear responses to (a) soil volumetric water content (VWC), (b) rainfall, and (c) potential evapotranspiration (PET). Shaded bands indicate 95 % confidence intervals, and rug marks along the x-axis show the distribution of observations. All predictors were standardised (mean = 0, standard deviation = 1).

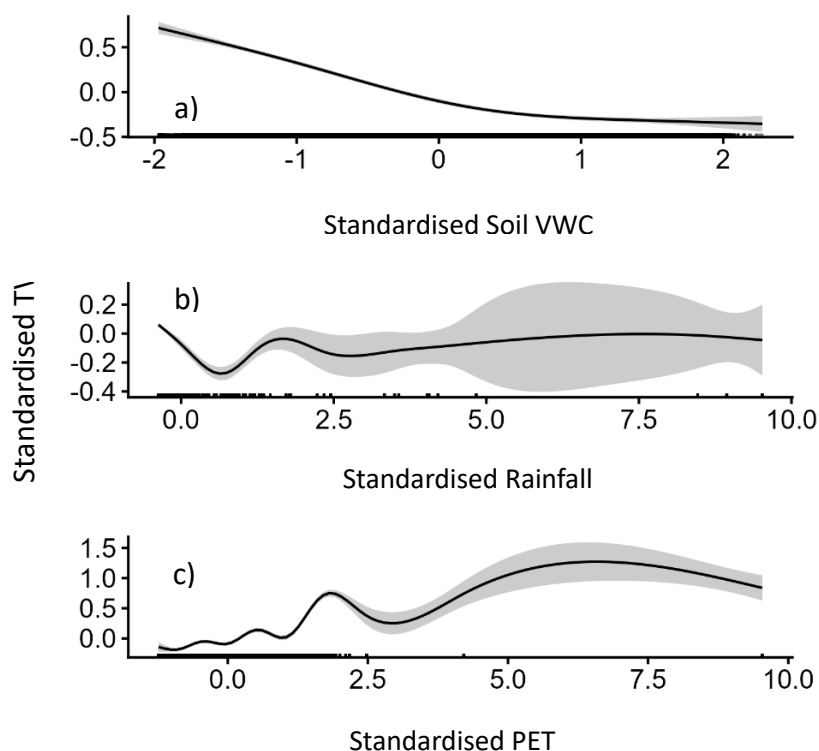


Figure 2.15: Smooth partial-effect plots for TWD in Year 2, showing nonlinear responses to (a) soil volumetric water content (VWC), (b) rainfall, and (c) potential evapotranspiration (PET). Shaded bands indicate 95 % confidence intervals, and rug marks along the x-axis show the distribution of observations. All predictors were standardised (mean = 0, standard deviation = 1).

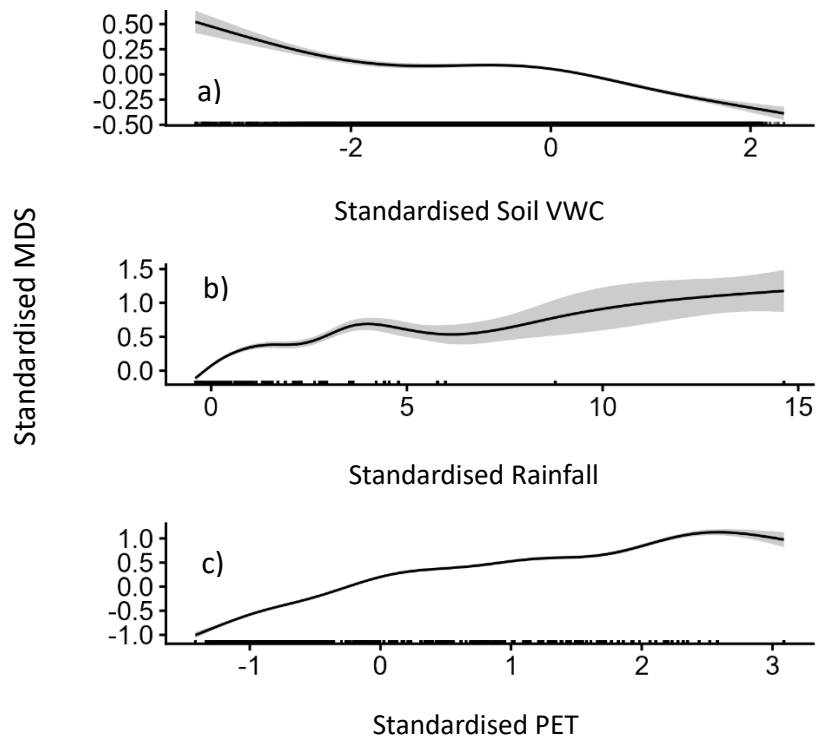


Figure 2.16: Smooth partial-effect plots for MDS in Year 1, showing nonlinear responses to (a) soil volumetric water content (VWC), (b) rainfall, and (c) potential evapotranspiration (PET). Shaded bands indicate 95 % confidence intervals, and rug marks along the x-axis show the distribution of observations. All predictors were standardised (mean = 0, standard deviation = 1).

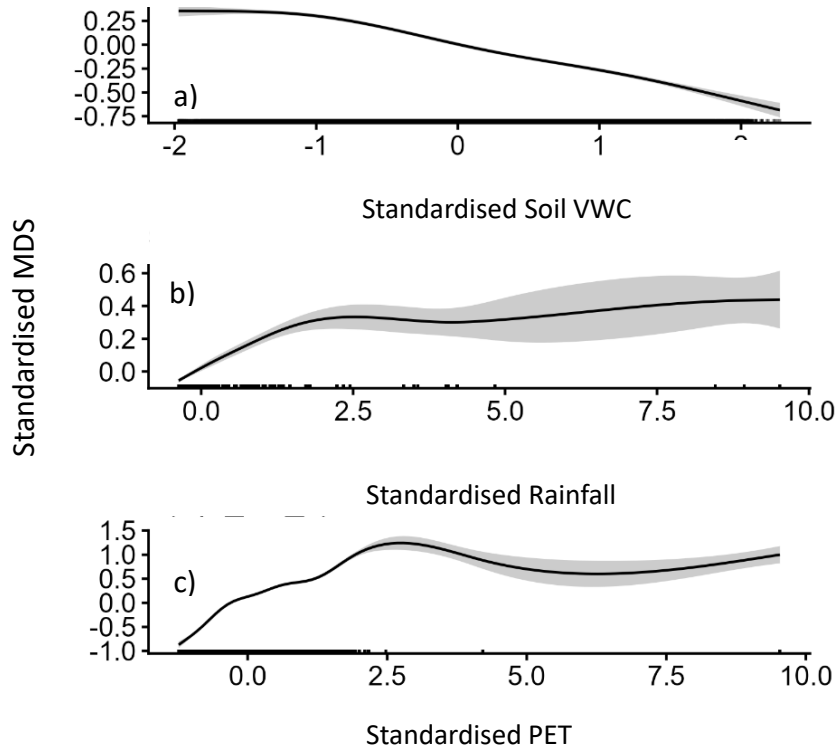


Figure 2.17: Smooth partial-effect plots for MDS in Year 2, showing nonlinear responses to (a) soil volumetric water content (VWC), (b) rainfall, and (c) potential evapotranspiration (PET). Shaded bands indicate 95 % confidence intervals, and rug marks along the x-axis show the distribution of observations. All predictors were standardised (mean = 0, standard deviation = 1).

2.4 Discussion

There were clear differences in weather conditions between the two study years. Both years had lower than normal rainfall, except for late summer and early autumn in Year 1 which were particularly wet partly due to Cyclones Hale and Gabrielle. Year 1 was generally wetter than Year 2 and the soil in all plots was near field capacity for the duration of the year. Both years had air temperatures similar to normal. These differences in conditions resulted in differences in growth and species response between years. All species exhibited reduced GRO and increased TWD and MDS in response to the reduced rainfall and volumetric water content during the growing season in Year 2.

Weather timing affected the relationship between the weather variables and dendrometer variables. In Year 1, soil VWC was high for the majority of the year, rainfall was highest in February and March, and PET was highest from November through February. This timing resulted in higher GRO and MDS in December through March. In Year 2, soil VWC and rainfall were low between January and April, and PET was highest from December through February. This timing caused GRO to decline at the start of January, and both TWD and MDS to peak in January.

Deviance explained by the GAMs was variable between the two study years for all three of the dendrometer variables. More deviance was explained in the Year 1 GAM for GRO, due to the limitation of GRO under the drier conditions of Year 2. More deviance was explained by the Year 2 GAM for TWD, due to the high soil VWC in Year 1 inhibiting TWD. Marginally higher deviance was explained by the Year 1 GAM for MDS, likely due to stomatal closure under the drier conditions of Year 2.

Rainfall had the highest F statistic for GRO in both study years, a result similar to the findings of a study in a boreal climate where precipitation and relative humidity were the key drivers of GRO (Oogathoo et al., 2024). Our results suggest that when rainfall is plentiful and VPD is low, like in Year 1, GRO is promoted by ongoing water replenishment and is not limited by stomatal responses to high VPD. Under drier conditions, like in Year 2, GRO is constrained by soil water reserves and stomatal responses to increased VPD, but promoted by periodic inputs of water from rainfall.

Soil VWC had the highest F statistic for TWD in Year 2 but not Year 1. This result was due to the high soil VWC across Year 1 inhibiting TWD. Previous studies have shown a wide range of key drivers of TWD (Güney et al., 2020; Oogathoo et al., 2024; Zweifel et al., 2016). Zweifel et al. (2016) found that in a temperate region, VPD and soil water potentials are key predictors of TWD. Güney et al. (2020) found that in a Mediterranean climate, air temperature is a key driver of TWD. Oogathoo et al. (2024) found that in a boreal climate, solar radiation, precipitation, and VPD are key drivers of TWD. In the present study, rainfall had a higher F statistic than soil VWC, likely driven by the soils being near field capacity for the majority of Year 1. The Year 2 result supports the expectation that soil water is important for stem water replenishment. The Year 2 result also supports the expectation that the drying of soils in the summer months of Year 2 results in increased TWD.

Potential evapotranspiration had the highest F statistic for MDS in both study years, supporting the links between MDS, transpiration, and atmospheric drivers. Previous studies have found that key drivers of MDS include air temperature in a Mediterranean climate (Güney et al., 2020), air temperature and VPD in a temperate climate (Paltineanu et al., 2020), and a combination of air temperature, VPD, and soil moisture in a temperate to semi-arid climate (Dong et al., 2019). In the present study, PET had an overall positive relationship with MDS until high PET in Year 1 and positive at low-moderate PET in Year 2. These results support previous findings that atmospheric drivers result in increased MDS, especially when soil moisture is limiting (Dong et al., 2019) like in Year 2 of the present study. The lack of a positive relationship after low-moderate PET in Year 2 potentially represents stomatal closure under water limiting conditions, driven by species-specific stomatal behaviour.

The strong link between MDS and atmospheric demand, in contrast to the strong link between TWD and rainfall and soil VWC, highlights the difference between the two variables. The relationship between MDS and atmospheric demand highlights the link between MDS and transpiration (Zweifel & Häsler, 2000) and the role that MDS plays in indicating short-term water stress and current climatic conditions (Güney et al., 2020). Comparatively, the relationship between TWD and rainfall and soil VWC highlights the link between TWD and cumulative water loss (Zweifel et al., 2016), as well as the role of TWD as a longer-term drought stress indicator (Drew et al., 2011; Zweifel et al.,

2005). These links suggest that TWD is an indicator of water-driven growth limitation and MDS is an indicator of potential growth.

2.4.1 Species comparison

Although the exotic species generally demonstrated higher TWD and MDS than the indigenous species, only *P. radiata* and *S. sempervirens* exhibited higher average GRO. *Sequoia sempervirens* exhibited the highest monthly average GRO, overall average GRO, and highest RGR in both study years, suggesting that this species is still in a rapid growth phase at the study site. This observation is congruent with recent findings that *S. sempervirens* can outperform *P. radiata* at sites with optimal conditions for *S. sempervirens* such as warm and wet sites with moderate to high fertility (Watt, 2022).

All species exhibited larger TWD in Year 2 compared to Year 1. In Year 1, *E. fastigata* and *P. radiata* exhibited higher monthly and overall average TWD than the indigenous species. In Year 2, all three of the exotic species exhibited higher monthly and overall average TWD than the indigenous species, although *P. totara* had a TWD summer peak higher than *P. radiata* in Year 2. Interestingly, *P. totara* exhibited a large peak in TWD in Year 2, despite moderate soil VWC compared to the other species, and high drought tolerance metrics (Laughlin et al., 2020). These results suggest that high stand density may have contributed to water stress in this species.

On a monthly scale, two of the indigenous angiosperm species, *F. fusca* and *L. menziesii*, exhibited larger summer GRO peaks than *P. radiata*, and large MDS peaks in early summer, particularly in Year 1. These two indigenous angiosperm species also exhibited the fastest Gompertz modelled growth rates and the shortest growing seasons. These results suggest that these two species have rapid growth rates over short periods of time. Low drought tolerance has been reported for *F. fusca* and *L. menziesii* (Laughlin et al., 2020) suggesting that these species grow rapidly early in the growing season, avoiding late-season drought stress.

The exotic species had larger starting diameters than the indigenous species for this study, despite being planted at a similar time. Both *P. radiata* and *S. sempervirens* exhibited higher rates of GRO than the indigenous species. However, *E. fastigata* did not have a higher rate of GRO than the indigenous species during the study period, indicating a slowdown in growth rate which may be due to canopy closure. Both *E.*

fastigata and *P. radiata* displayed lower RGR in Year 1 than the indigenous species, giving further evidence of a slowdown in growth rate. In the case of *P. radiata*, it is likely that the wet microsite conditions are preventing this species from reaching its growth potential at our study site. *Pinus radiata* also reached canopy closure prior to the study period. This is congruent with previous findings of an asymptotic growth pattern observed in *E. fastigata* and *P. radiata* compared to a linear growth pattern over a long period of time observed for *S. sempervirens* and *P. totara* (Salekin et al., 2024). In Year 2, RGR was higher for *E. fastigata* and *P. radiata* than the indigenous species, suggesting that the exotic species were less limited by the dry summer conditions than the indigenous species.

2.4.2 Growing season duration

Average air temperature in spring was similar between Year 1 and Year 2 and to climate normal levels. These similar air temperatures resulted in similar growth initiation between Year 1 and Year 2 for most study species. However, lower rainfall and soil volumetric water content during the following summer resulted in earlier cessation and lower cumulative growth for all species, particularly *F. fusca* and *L. menziesii*. These results are partially consistent with previous findings that warm spring temperatures followed by dry summer conditions result in earlier growth initiation but reduced annual growth (Bose et al., 2025). In Year 2, *F. solandri*, *P. totara*, and *E. fastigata* growth ceased later than the other species, indicating a tolerance for drier conditions. This is a surprising result as low drought tolerance has been reported for *F. solandri* (Laughlin et al., 2020), along with moderate drought tolerance for species closely related to *E. fastigata* (Pan et al., 2026). The longer growing season and low rates of GRO, TWD, and MDS for *F. solandri* suggest a slow but consistent approach to growth. Previous studies have suggested that species with lower growth rates and a longer growing season duration may perform better under drought conditions (Güney et al., 2020). While *F. solandri* is not a drought-tolerant species, it may be able to grow more in a year than the other indigenous angiosperm species included in this study, due to the longer growing season.

In contrast with our hypothesis, the conifer species did not demonstrate a longer growing season duration than the angiosperm species. For example, of the exotic study

species, one of the conifer species, *S. sempervirens*, consistently had a shorter growing season duration compared to the exotic angiosperm species *E. fastigata*. Another example includes *F. solandri* demonstrating a longer growing season duration under the drier weather conditions of Year 2 than both indigenous conifer species, *P. totara* and *P. taxifolia*. Together these results highlight the role of both species traits and microsite effects in predicting growing season duration.

For all of the study species the modelled growth cessation date in Year 1 was the final date of the study year, likely indicating that all species continued to grow within the model parameters through winter into Year 2. In contrast, all species had a more well-defined growing season in Year 2. Despite inter-annual differences in growing season as a result of differing climatic conditions, previous studies have found defined growing seasons for northern hemisphere species (Debel et al., 2024). This suggests that the Gompertz model parameters are limited in defining growth cessation for our study species under the wet temperate conditions of our study site.

2.4.3 Future afforestation projects

Results from the present study highlight the different physiology and water use strategies of our study species and the potential implications for future afforestation projects. Two of the exotic species, *E. fastigata* and *P. radiata*, demonstrated larger starting diameters and low RGR relative to the other study species. This indicates that of our study species, these two species may be the most appropriate for afforestation projects with shorter-term goals, for example less than 25 years. Wet microsite conditions may be limiting the growth potential of *P. radiata* at our study site, indicating that careful site selection may be required if optimal performance is a project requirement. Dry microsite conditions and high TWD for *E. fastigata*, as well as canopy closure, are contributing to the reduced growth rates for this species. Of the remaining exotic species, *S. sempervirens* had the highest GRO, RGR, and MDS as well as a larger starting diameter than the indigenous species. This species may be appropriate for projects with medium (e.g. 25-75 years) to longer-term (e.g. > 75 years) goals.

The lower GRO and starting diameters of the indigenous species suggest that they may be candidates for projects with longer-term goals. Two of the indigenous angiosperm

species, *F. fusca* and *L. menziesii*, had rapid seasonal growth concentrated within a relatively short growing period, and peaks in TWD and MDS in early summer, suggesting tight stomatal control, drought avoidance, and higher climate sensitivity. These results also indicate that careful site selection may be required for these two species as they may be less resilient to climate fluctuations. Of the remaining indigenous angiosperm species, *F. solandri* exhibited slower growth rates, a longer growing season, and the lowest TWD and MDS of the study species, suggesting that this species may be more resilient than the other indigenous angiosperm study species and potentially increasing the range of suitable planting locations for *F. solandri* relative to *F. fusca* and *L. menziesii*. The two indigenous conifer species, *P. totara* and *P. taxifolia*, demonstrated low to moderate GRO, RGR, TWD, and MDS, a long growing season duration, and shrinkage peaks that occurred later in the season than the angiosperm species. These results suggest that these two species may be appropriate for projects with long-term goals and that they may be more resilient to climate fluctuations, increasing the range of sites where they may be planted. Stand density should also be considered for *P. totara* as this species showed higher shrinkage than predicted based on soil volumetric water content, in contrast with its reported high drought tolerance (Laughlin et al., 2020).

2.4.4 Conclusions

Two of the exotic species, *S. sempervirens* and *P. radiata*, demonstrated higher growth rates than the indigenous species. However, *P. radiata* displayed low RGR compared to the other study species. These results suggest that the growth rates for *P. radiata* were faster prior to the study period than during, likely due to wet microclimate conditions limiting growth during the study. *Eucalyptus fastigata* also exhibited low RGR but large starting diameter, suggesting faster growth rates prior to the study period. This result is likely due to canopy closure being reached by *E. fastigata*. Unlike the other exotic species, *S. sempervirens* showed no signs of a slowdown in growth. Two of the indigenous species, *F. fusca* and *L. menziesii*, had rapid seasonal growth concentrated within a relatively short growing period, indicating a drought avoidance growth strategy. *Fuscospora solandri* displayed a slow growth rate over a longer period of time in both study years, suggesting that this species may be more tolerant of drier

conditions than the other indigenous angiosperm species. Water stress in *P. totara* was likely due to high stand density, which has important implications for stand management. Together, our results highlight the interactions among species-specific physiology and water use strategies, stand growth stage, and the effects of weather and climate on growth rates. Our results also highlight the species-specific role that growing season duration plays in determining annual growth increment.

Our results demonstrate the utility of using electronic point dendrometers to understand growth responses and tree responses to water availability across species and years. Future research could include longer-term installation, more sites and study species, measurements of stomatal behaviour and water use efficiency, and interventions to ensure equal soil water content at the time of measuring start and end diameters. Longer-term installation would capture more extreme climate events and possible lags in species response to climate events. More sites, including both planted and natural forests, and more study species, would help in gaining a better understanding of species performance and guide future afforestation projects. Relative stomatal behaviour and water use efficiency would help gain further understanding of carbon and water dynamics across the study species. Intervening to ensure equal soil water at the time of measuring start and end diameters would help disentangle moisture shrinking from growth.

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Chapter 3: Comparison of sap flow between exotic and indigenous planted trees

3.1 Introduction

Water availability is increasingly becoming an issue in New Zealand due to increased rural and urban demand, climate change, and intensification of the primary sector (Meason et al., 2019). There are concerns about the effects of forests, both existing and newly planted, on local hydrology and water supply (Meason et al., 2025; Meason et al., 2019). New Zealand studies have shown that planting *Pinus radiata* D.Don. forest on pasture or tussock land reduces the annual water yield by 20 to 50 %, depending on the catchment (Davie & Fahey, 2005). The majority of forest hydrology research in New Zealand has focused on *P. radiata*, reflecting its dominance in plantation forestry, whereas comparatively little is known about the water use and hydrological effects of indigenous tree species. Research on the water use of New Zealand indigenous trees has focused on a select number of species including *Agathis australis* (D.Don) Lindl. ex Loudon. (e.g. Cranston, 2022; Kaplick et al., 2018; Zhao et al., 2020), *Dacrydium cupressinum* Sol. ex Lamb. (Barbour et al., 2005; Bowman et al., 2005) and *Podocarpus totara* G.Benn. ex D.Don var. totara (Bown et al., 2024; Kaplick et al., 2018). Occasional work has been done on other species including *Fuscospora fusca* (Hook.f.) Heenan et Smissen and *Lophozonia menziesii* (Hook.f.) Heenan et Smissen (Kostner et al., 1992). These studies often focus on measuring the dominant tree species within old growth forests (Barbour et al., 2005; Bowman et al., 2005; Cranston, 2022; Kostner et al., 1992; Zhao et al., 2020). These studies have opened the door for new research on a wider range of species, sites, and climatic conditions.

Part of the forest hydrological cycle includes evapotranspiration (ET). Forest ET is made up of evaporation from the understory and canopy as well as interception and transpiration (Amatya et al., 2016). Transpiration accounts for approximately 61 % of global ET (Amatya et al., 2016) and is the loss of water through stomata (Jarvis & McNaughton, 1986). Estimates of transpiration can be measured with sap flow meters. Raw sap flow data can be converted into sap flux density and total volumetric sap flow rate (flow rate). Sap flux density is the rate of sap flow per unit area of sapwood. Flow

rate gives an indication of total flow regardless of sapwood area. These estimates of transpiration vary across species, seasons, and climates.

Tree water use and transpiration are affected by climatic conditions. Under climate change, increasing drought frequency and intensity are expected to affect both tree mortality and productivity (Aldea et al., 2024). Rising temperature and evaporative demand (vapour pressure deficit, VPD) trigger stomatal closure to limit water loss, but at the cost of carbon assimilation (Jarvis & McNaughton, 1986; Monteith, 1995). Elevated VPD has been shown to increase transpiration, depleting soil moisture and inducing drought stress earlier in the growing season (Will et al., 2013). Sap flow varies across individuals and species as well as across seasons and years (Bhusal et al., 2024). Higher rates of sap flow are often recorded early in the growing season, which decline later in the season, likely reflecting increasing drought stress (Bhusal et al., 2024). Reduced rainfall and prolonged drought consistently lower transpiration across species and sites (Luo et al., 2016; Zavadilová et al., 2023; Zhang et al., 2025). However, recovery and resilience differ among species. For example, some evergreen species maintain higher resilience than deciduous species (Zhang et al., 2025), and angiosperm species generally exhibit higher maximum water use while having greater sensitivity to VPD compared to gymnosperm species (Flo et al., 2021). Differences in water use and transpiration between conifer species and angiosperm species are driven by differences in their ecophysiological traits, including hydraulic architecture and leaf area. Tracheids are the water conductive elements found in conifer xylem, while vessels are those found in angiosperm xylem (Hacke & Sperry, 2001). The angiosperm vessels have higher maximum conductivity, largely due to larger vessel diameter (Sperry et al., 2006). Angiosperm species also tend to have greater leaf area than conifer species, which can contribute to higher rates of sap flow.

Sap flow is influenced by ecophysiological traits. Leaf area, including specific leaf area and leaf area index, determines the transpiring surface, while xylem anatomy, rooting depth, and xylem vulnerability set the capacity and reliability of water transport (Flo et al., 2021; Tyree & Zimmermann, 2002). Species with higher photosynthetic capacity, higher stomatal conductance, and weaker stomatal control typically exhibit greater sap flow (Meinzer et al., 2009). Sapwood area is a key predictor of whole-tree

transpiration, with larger trees and more conductive angiosperm species generally showing higher transpiration rates than conifer species (McCulloh et al., 2010).

Comparisons of the water use of two commonly planted genera, *Pinus* (coniferous) and *Eucalyptus* (angiosperm) have returned differing results (e.g. Benyon et al., 2006; Scott & Lesch, 1997). Scott and Lesch (1997) found that afforestation with *E. grandis* W. Hill. ex Maiden resulted in faster reductions of streamflow than afforestation with *P. patula* Scheide ex Schltdl. & Cham in South Africa. In contrast, Benyon et al. (2006) found that regardless of access to shallow fresh groundwater, annual ET of *E. globulus* Labill. and *P. radiata* plantations in southeastern Australia were not significantly different. A recent global meta-analysis found that under the same potential evapotranspiration (PET) and rainfall conditions, the ET of *Pinus* and *Eucalyptus* plantations is comparable (White et al., 2022). However, the annual level did not capture the stronger seasonality of *Eucalyptus* ET as expected by the ecophysiological traits and as reported elsewhere (e.g. White et al., 1999). Another recent study in Chile also found that there was no difference in the ET of *P. radiata* and *E. globulus* plantations (White et al., 2021). Recent studies in Chile have compared ET and transpiration of *P. radiata*, *E. globulus*, and indigenous *Nothofagus* species (White et al., 2021; White et al., 2020). White et al. (2021) found that both *P. radiata* and *E. globulus* plantations used approximately 100 mm more water per year (here meaning ET) compared to indigenous *N. obliqua* (Mirb.) Oerst. forest, regardless of low or moderate rainfall. The differences in ET between exotic plantations and indigenous forests were driven by the larger sapwood area of *P. radiata* and the much higher sap flux density of *E. globulus* in spring and summer (White et al., 2021). Another study in Chile measuring transpiration in indigenous *N. glauca* forest with wilding *P. radiata* found that *P. radiata* contributed 60 % of the total stand transpiration despite only contributing 34 % of the stand sapwood area (White et al., 2020). This disproportionate transpiration contribution was attributed to significantly higher sap flux density between May and October in *P. radiata* (White et al., 2020).

Measuring estimates of transpiration, including sap flux density and flow rate, is most commonly done using thermal methods. These thermal methods include energy balance, heat dissipation, and heat ratio methods (Wullschlegel et al., 1998). The heat ratio method employs a heater inserted into woody tissue with upstream and

downstream probes positioned equidistantly (Burgess et al., 2001). Thermocouples on the probes record temperature changes following a heat pulse; the ratio of temperature increases indicates sap flow direction and velocity, after correcting for wood properties and probe wounding. While effective, this technique is costly, invasive, and requires numerous probes to capture spatial variation in sap velocity within and among trees.

The aim of this research was to measure and compare sap flux density of five indigenous (*Fuscospora fusca*, *Fuscospora solandri*, *Lophozonia menziesii*, *Prumnopitys taxifolia*, and *Podocarpus totara*) and three exotic tree species (*Eucalyptus fastigata*, *Pinus radiata*, and *Sequoia sempervirens*) at our study site, Rewanui Forest Park. We hypothesised that the exotic species would exhibit higher flow rates, cumulative water transpired, and sap flux density than the indigenous species due to their larger stem sizes, higher sapwood area, and greater leaf area. The exotic angiosperm species was expected to exhibit higher daily mean sap flux density than the exotic conifer species due to differences in their hydraulic architecture. The indigenous angiosperm species were expected to exhibit higher daily mean sap flux density than the indigenous conifer species also due to differences in their hydraulic architecture. We also hypothesised that the climate variables would explain more sap flux density variation under wetter conditions, as physiology and drought tolerance would limit the explanatory power of climate variables under drier conditions. Potential evapotranspiration was hypothesised to be a significant predictor for all species regardless of weather conditions, as atmospheric demand is consistently a key driver of transpiration. Rainfall and soil volumetric water content were hypothesised to be significant predictors of sap flux density for all species under drier conditions but not under wetter conditions, as rainfall events and subsequent soil water replenishment would temporarily relieve water stress under drier conditions, temporarily increasing sap flux density.

3.2 Methods

3.2.1 Site and Species

The same site, Rewanui Forest Park (Figure 2.1), species (Table 2.1), and site setup from Chapter 2 were used in this study. The same soil volumetric water content (soil VWC;

Table 2.2) and climate variable datasets from Chapter 2 were also included in this study. Data were collected over the same two-year period as Chapter 2. The two years were separated into Year 1 and Year 2. Year 1 was between 21/06/2022 and 21/06/2023 and Year 2 was between 22/06/2023 and 21/06/2024.

One plot for each species (eight plots total) was selected for sap flow meter installation. Sap flow meters were powered by 12 V solar panels, one solar panel per plot. Three trees within each plot were selected for sap flow meter installation. ICT International SFM1 heat ratio sap flow sensors (ICT International, Armidale, NSW, Australia) were installed between January and May of 2022. The ICT International method (Burgess & Downey, 2020) was used to install three SFM1s per species; one each on an existing dendrometer tree. Excess bark was chiselled away, particularly on the exotic species. A guide was used to determine drilling points for the probes. A Dremel drill was used to drill the probe holes. Bark spacers were included on the thinner-barked species, primarily the indigenous species. The probes were installed carefully with lubricant, with the upstream probe at the bottom and the heater in the centre. Sensors were reinstalled as required, due to sensor failure or growth beyond the external part of the probes. Measurements were taken every 15 minutes, and the data were downloaded from the internal SD cards approximately four times per year. Sensors were reinstalled when the stems started to grow around the probes or when sensor malfunctions were detected.

Increment cores were used to measure sapwood depth for each species to provide estimates of sapwood area for sap flow measurements. Four to six trees were selected at random for coring. The cores were dyed with pH indicator dyes. The angiosperm species were dyed with methyl orange, and the conifer species were dyed with bromocresol green (White et al., 2021). Most of the study species showed a clear colour change between the sapwood and heartwood, although the *Lophozonia menziesii*, *Podocarpus totara*, and *Prumnopitys taxifolia* cores were almost entirely sapwood. Stem diameter was measured with diameter tapes; bark thickness and sapwood thickness were measured with a ruler. Sapwood area was calculated by calculating radius under-bark, then the cross-sectional and heartwood areas, and finally by subtracting the heartwood area from the cross-sectional area. The percentage of sapwood was calculated by dividing the sapwood area by the cross-

sectional area. The percentage of sapwood was used to calculate sapwood area for each of the sap flow meter trees (Table 3.1) by multiplying the diameter by the percentage of sapwood.

Table 3.1: Average sapwood depth and percentage of sapwood for each of the study species, as well as standard error. Average sapwood depth was calculated for the three sap flow meter trees per species. Average percentage sapwood was calculated for the four to six random trees for each species.

Species	Sapwood Depth (cm)	Number of sap flow trees	Percentage Sapwood (%)	Number of cored trees
<i>Fuscospora fusca</i>	11.55 ($\pm$ 0.94)	3	0.87 ($\pm$ 0.03)	6
<i>Fuscospora solandri</i>	12.84 ($\pm$ 1.97)	3	0.94 ($\pm$ 0.06)	4
<i>Lophozonia menziesii</i>	11.17 ($\pm$ 0.22)	3	1.00 ($\pm$ 0.00)	4
<i>Podocarpus totara</i>	12.83 ($\pm$ 0.84)	3	1.00 ($\pm$ 0.00)	4
<i>Prumnopitys taxifolia</i>	11.47 ($\pm$ 0.94)	3	1.00 ($\pm$ 0.00)	5
<i>Eucalyptus fastigata</i>	12.57 ($\pm$ 1.41)	3	0.47 ($\pm$ 0.05)	5
<i>Pinus radiata</i>	24.50 ($\pm$ 0.51)	3	0.70 ($\pm$ <0.01)	5
<i>Sequoia sempervirens</i>	21.90 ($\pm$ 4.88)	3	0.80 ($\pm$ 0.09)	5

3.2.2 Sap flow

Raw sap flow data were processed using the ICT Sap Flow Tool (v1.5.1. ICT International, Armidale, NSW, Australia), following the procedures described by Merlin et al. (2020). The linear transform tool was used to realign any data steps and ensure that the bulk of the data was above zero in instances when large segments of the data were below zero. Unexplained data spikes of more than 3 cm h⁻¹ or less than -1 cm h⁻¹ were removed. Stem diameter, sapwood depth, and bark thickness for each species, as well as default heat ratio method sensor properties were entered into the Sap Flow Tool. Diurnal patterns of sap flow were visually assessed before calculating daily values to reduce noise and assess longer time periods. The Sap Flow Tool was used to calculate daily volumetric flow rate (Q_{daily} , cm³ day⁻¹). Daily flow rate was then divided by 24 to give hourly flow rate (Q , cm³ h⁻¹) and was converted to sap flux density (J_s , cm³ cm⁻² h⁻¹) by normalising flow by sapwood area:

$$J_s = \frac{Q}{A_s} \quad (1)$$

where Q is the hourly flow rate and A_s is the cross-sectional area of sapwood through which water transport occurs. This conversion standardised sap flow measurements across stems of different sizes, providing a comparable measure of water transport efficiency per unit of conducting tissue. Flow rate and sap flux density were both averaged per species.

Daily flow rate was used to calculate cumulative and total water transpired per species for each study year (Year 1 = 21/06/2022-21/06/2023, Year 2 = 22/06/2023-21/06/2024) and the two dry periods (Dry Period 1 = 01/01/2023-31/03/2023, Dry Period 2 = 01/01/2024-31/03/2024). Daily flow rate was first divided by 1000 to give daily water transpired (L). The cumulative sum of daily water transpired was calculated from the first day of a given study year or dry period to the last to give cumulative water transpired (L). The sum of daily water transpired across a given study year or dry period was calculated to give total water transpired (L). Total water transpired was also calculated for each month across the study period.

3.2.3 Statistical analysis

Statistical analysis was undertaken in RStudio version 2024.12.1+563 (Posit Software, 2024) using R Version 4.4.1 (R Core Team, 2024). As the variance of the residuals was not homogeneous, non-parametric Kruskal-Wallis tests were used to determine if there were statistically significant differences in the cumulative water transpired between our study species. Kruskal-Wallis tests were also used to determine if there were statistically significant differences in daily mean sap flux density between our study species as the variance of the residuals was not homogeneous. Kruskal-Wallis tests were run for each of Year 1, Year 2, Dry Period 1, and Dry Period 2. The 'kruskal.test' function (R Core Team, 2024) was used. Where the Kruskal-Wallis tests showed significant differences, post-hoc Dunn tests were used to determine which species had significantly different cumulative water transpired. The 'dunnTest' function from the 'FSA' package (Ogle, 2023) and the Bonferroni correction were used.

To assess the effects of the climate variables on sap flux density for each species in Year 1 and Year 2, generalised additive models (GAMs) were used. GAMs were selected as the relationships between the climate variables and sap flux density were non-linear. GAMs were fitted using the ‘mgcv’ package (Wood, 2017). Predictor variable selection was undertaken using a correlation matrix (Appendix A). Variables with low correlation that were biologically meaningful were selected for the models. These variables included rainfall, PET, and soil VWC. Predictor variables were standardised (mean = 0, SD = 1) to facilitate comparison of effect sizes within each model. Separate GAMs were fitted for each species and each study year. Models took the general form:

$$\text{Sap flux density} \sim s(\text{Rainfall}, k=10) + s(\text{PET}, k=10) + s(\text{soil VWC}, k=5) \quad (2)$$

Where s denotes a penalised regression spline and k defines the basis dimension or maximum flexibility. The Gaussian family was used as the residuals were approximately normally distributed (Appendix H, I, J, & K). The restricted maximum likelihood estimation method (‘REML’) was used to give a stable smoothing parameter estimation. Smooth graphs were generated to visualise the relationship between each climate variable and sap flux density for each species and study year. Predictions were obtained from the fitted GAM using the ‘predict’ function from base R (R Core Team, 2024), and the estimated smooth relationship was plotted as a line. Shaded ribbons represent ± 2 standard errors around the fitted smooth, approximating 95 % confidence intervals.

3.3 Results

3.3.1 Weather and climate

As outlined in Chapter 2, there were clear differences in weather between Year 1 and Year 2. Air temperatures were similar between Year 1 and Year 2, and to climate normal levels. Mean air temperature was 13 °C in both study years, 16 °C in Dry Period 1, and 17 °C in Dry Period 2. Potential evapotranspiration was similar between study years until the summer months; the average was 2 mm day⁻¹ in Year 1, 3 mm day⁻¹ in Year 2, 3 mm day⁻¹ in Dry Period 1, and 4 mm day⁻¹ in Dry Period 2. Aside from late summer into early autumn in Year 1, total monthly rainfall was below climate normal levels in both study years. Total annual rainfall was 1543 mm in Year 1 and 829 mm in Year 2.

During the dry periods, total rainfall was higher than normal in Dry Period 1, particularly in March (total rainfall = 272 mm). Rainfall was lower than normal in Dry Period 2, particularly in February (total rainfall = 16 mm). Soil volumetric water content appeared to be near field capacity for the duration of Year 1, while a clear seasonal pattern was observed in Year 2. Of all the species, *F. solandri* and *E. fastigata* experienced the lowest soil volumetric water content in both years. *Pinus radiata* and *S. sempervirens* experienced the highest soil volumetric water content in both years, alongside *F. fusca* in Year 2. The wettest soil was observed in the *P. radiata* plots in Year 1 (Average soil VWC = $0.35 \text{ m}^3 \text{ m}^{-3}$) and the driest soil was observed in the *E. fastigata* plots in Year 2 (Average soil VWC = $0.19 \text{ m}^3 \text{ m}^{-3}$). Weather differences between Year 1 and Year 2 were partially driven by Cyclones Hale and Gabrielle, which hit New Zealand in January and February 2023 respectively.

3.3.2 Seasonality and importance of tree size

All the study species followed a general trend of increased flow rate (Figure 3.1 & 3.3b) and sap flux density (Figure 3.2 & 3.3a) in the spring and summer months, and decreased rates in the winter months. *Eucalyptus fastigata* demonstrated the highest sap flux density in Year 1 and in Year 2, and *P. taxifolia* demonstrated the lowest in Year 1 and in Year 2. The remaining species demonstrated moderate sap flux density. However, the species rankings shifted for flow rate; all three exotic species demonstrated higher flow rates than the indigenous species. The two exotic conifer species, *P. radiata* and *S. sempervirens*, exhibited high total water use but moderate water use per unit sapwood area. *Eucalyptus fastigata* demonstrated high total water use and high demand for water relative to size. *Prumnopitys taxifolia* demonstrated low total water use and low demand for water relative to size.

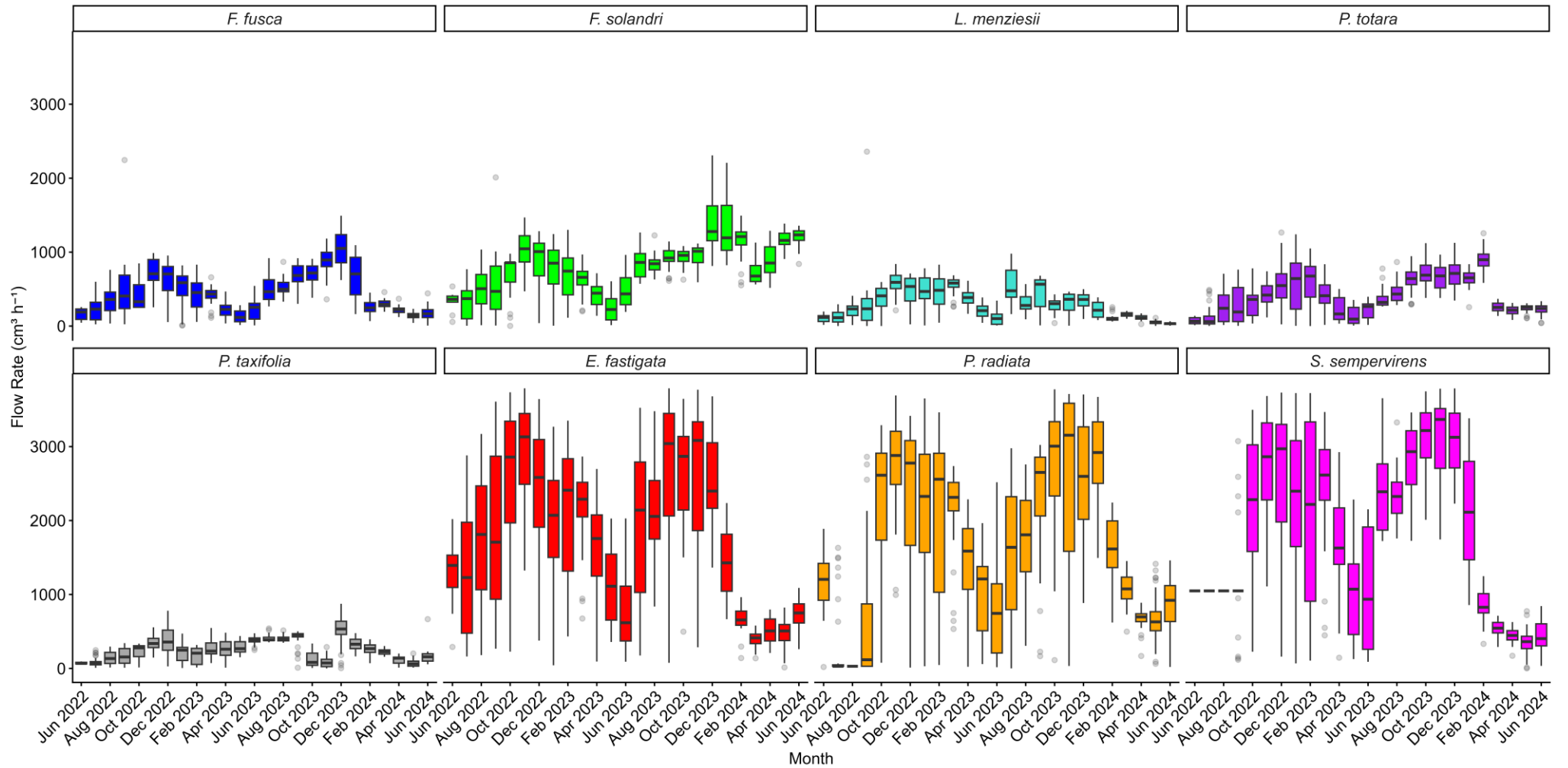


Figure 3.1: Monthly box plots of flow rate across the study period (21/06/2022-21/06/2024). Sample size was 3 for all species. The three sensors were averaged to give the species average. Exotic species indicated in red, yellow, and pink.

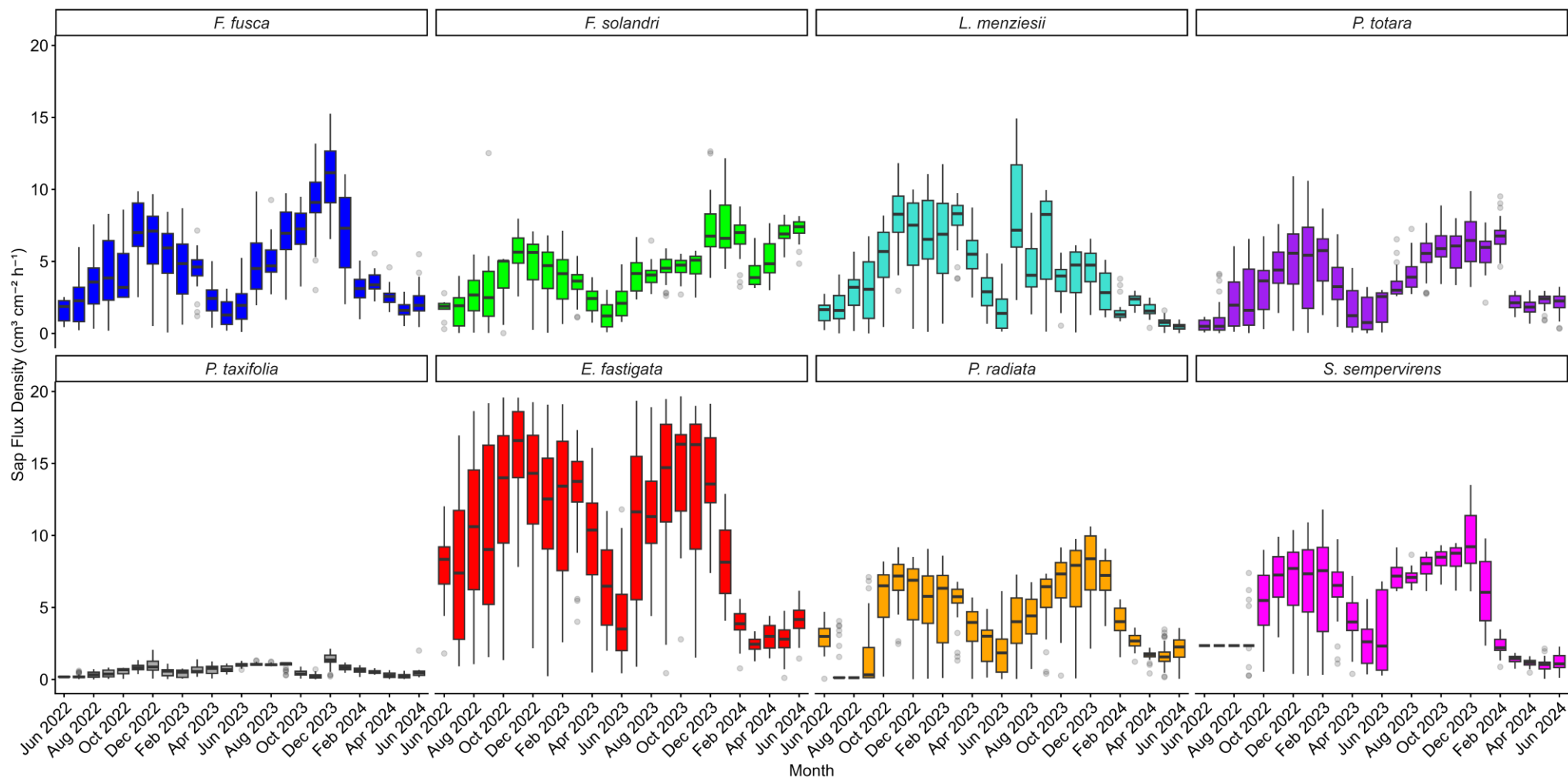


Figure 3.2: Monthly box plots of sap flux density across the study period (21/06/2022-21/06/2024). Sample size was 3 for all species. The three sensors were averaged to give the species average. Exotic species indicated in red, yellow, and pink.

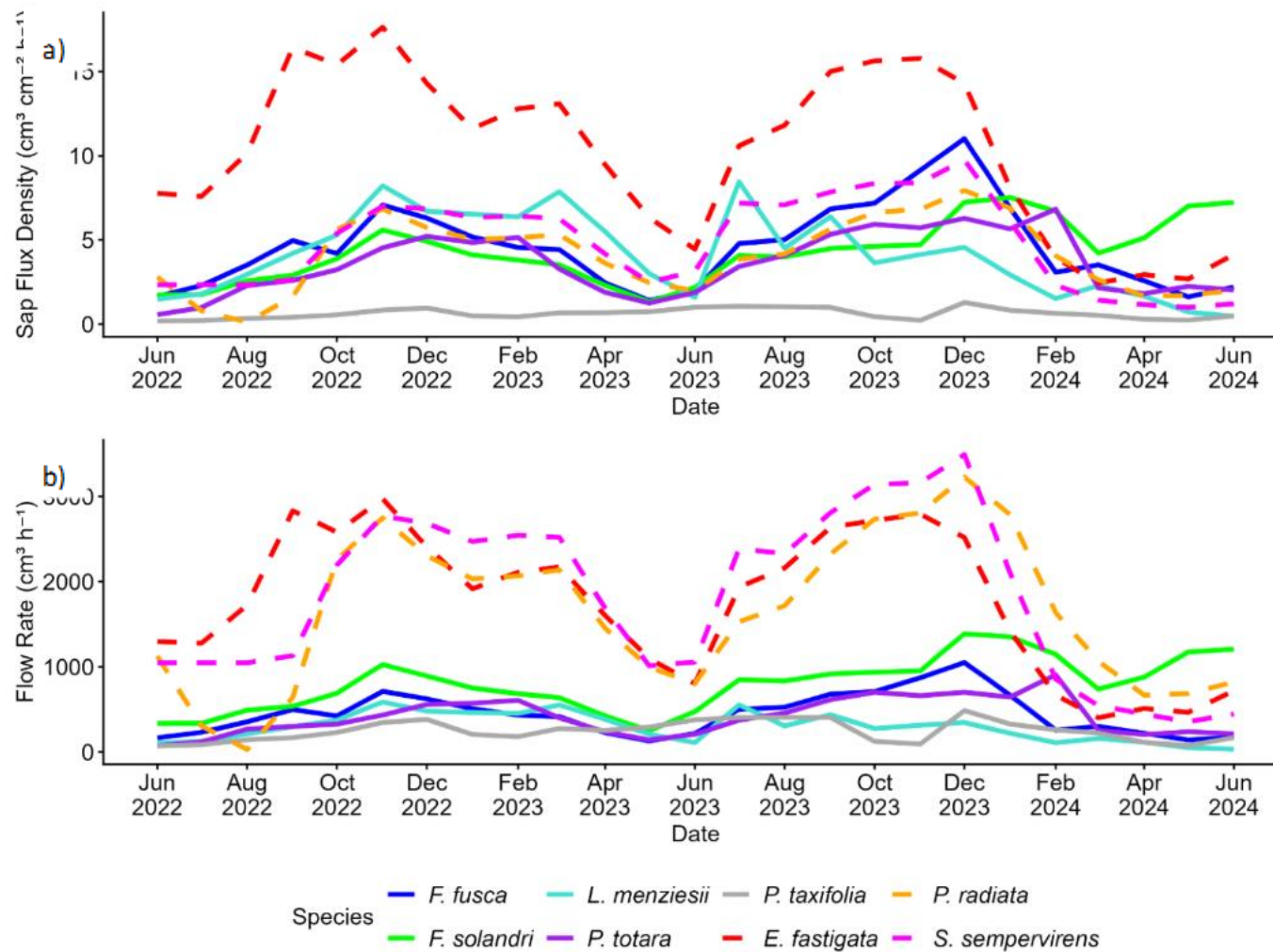


Figure 3.3: Monthly average sap flux density (a) and flow rate (b) across the study period. Sample size was 3 for all species. The three sensors were averaged to give the species average. Exotic species indicated with dashed lines.

3.3.3 Cumulative water transpired

The exotic species generally exhibited higher total water transpired than the indigenous species in both study years (Figure 3.4) and both dry periods (Figure 3.5). Most species increased total water transpired in Year 2, except for *E. fastigata*, *L. menziesii*, and *P. taxifolia*. Most species decreased their total water transpired in Dry Period 2, except for *F. solandri*, *P. totara*, and *P. taxifolia*. Results from the Kruskal-Wallis tests showed that cumulative water transpired was significantly different between species within years and dry periods (Table 3.2). Results from post-hoc Dunn tests showed that cumulative water transpired was lowest for *P. taxifolia* in both years (Appendix L) and dry periods (Appendix M; $p < 0.01$; Year 1 total = 2069.45 L, Year 2 total = 2040.41 L, Dry Period 1 total = 481.42 L, Dry Period 2 total = 571.71 L) alongside *L. menziesii* in Year 1 (total = 3038.23 L), Year 2 (total = 2158.43 L), and Dry Period 2 ($p = 1$; total = 357.66 L). The exotic species demonstrated higher cumulative water transpired than the indigenous species ($p < 0.01$) except for *E. fastigata* in Dry Period 2 (total = 1820.73 L) when it was statistically similar to *F. solandri* ($p = 1$; total = 2353.58 L). Compared to the other four indigenous study species, *F. solandri* statistically had the highest cumulative water transpired in both study years and both dry periods ($p < 0.01$; Year 1 total = 5134.25 L, Year 2 total = 8926.42 L, Dry Period 1 total = 1477.09 L). The remaining four indigenous species demonstrated moderate cumulative water transpired, with values statistically similar to one another.

Table 3.2: Kruskal-Wallis test results assessing differences in cumulative water transpired between each species, in each of Year 1, Year 2, Dry Period 1, and Dry Period 2.

Year/Dry Period	H	df	p
Year 1	1051.40	7	<0.01
Year 2	1324.80	7	<0.01
Dry Period 1	336.91	7	<0.01
Dry Period 2	444.84	7	<0.01

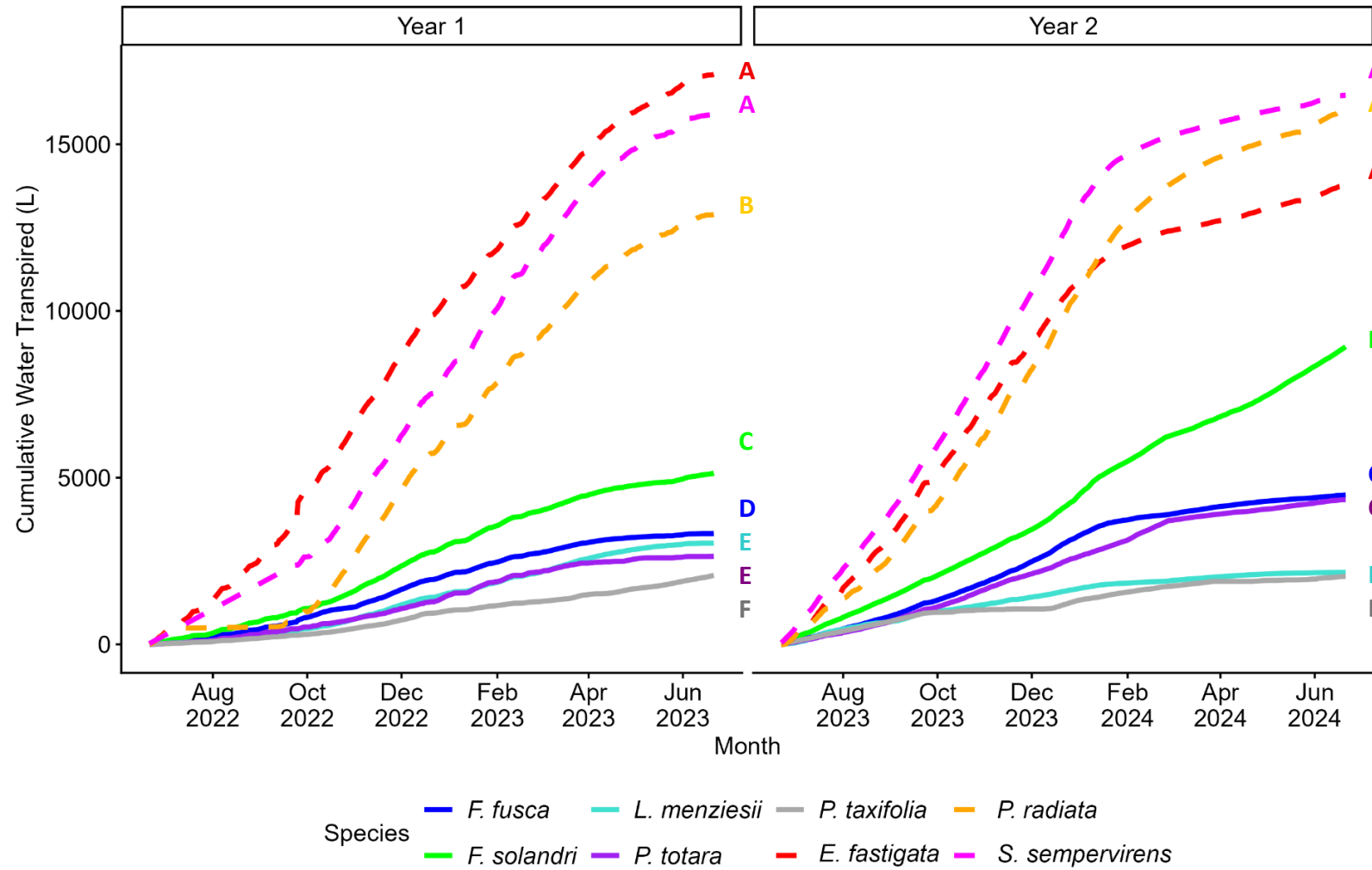


Figure 3.4: Cumulative water transpired (L) in Year 1 (21/06/2022-21/06/2023) and Year 2 (22/06/2023-21/06/2024) for each species. Exotic species indicated with dashed lines. Dunn test groupings of species with similar means indicated with letters.

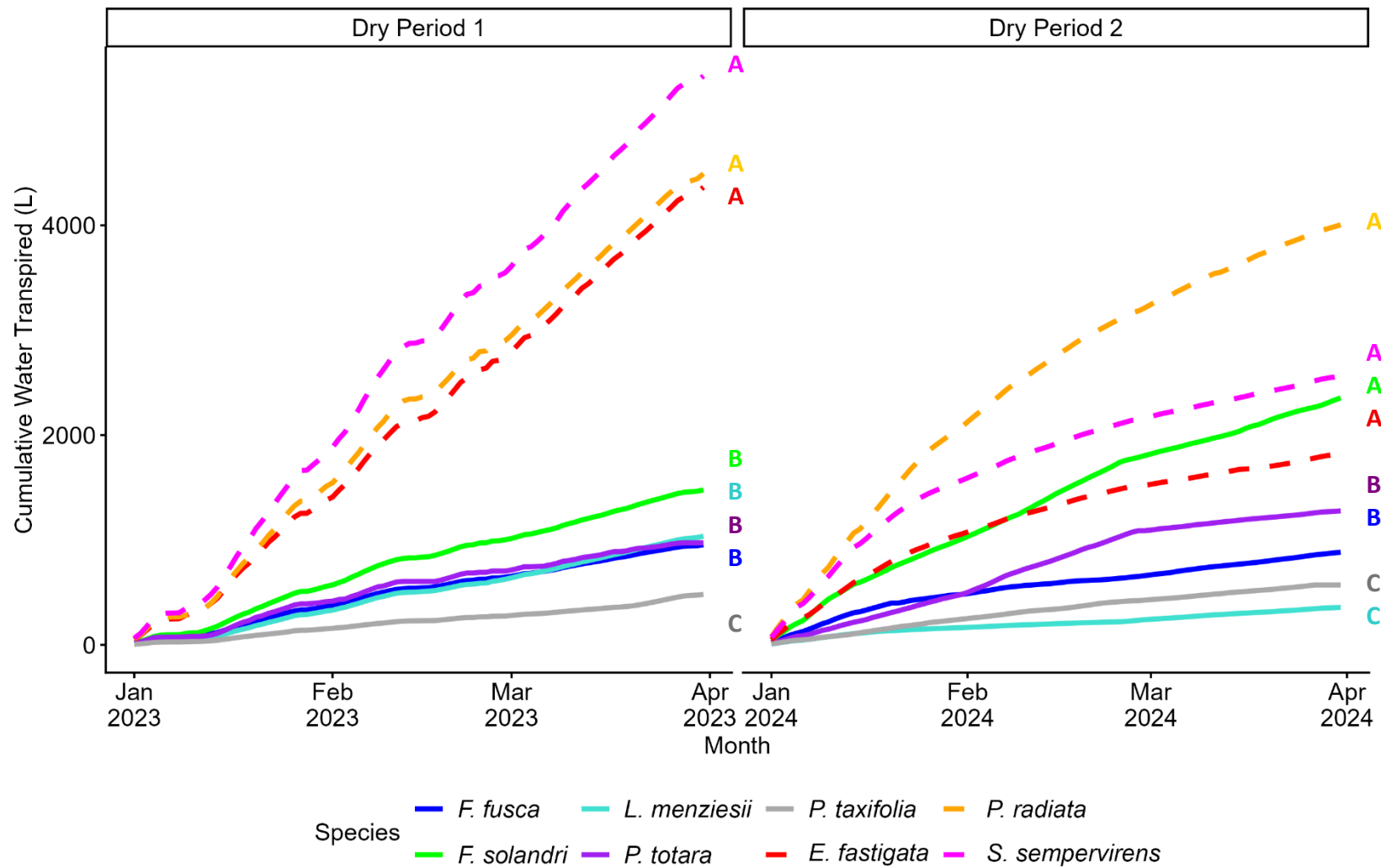


Figure 3.5: Cumulative water transpired (L) in Dry Period 1 (01/01/2023-31/03/2023) and Dry Period 2 (01/01/2024-31/03/2024) for each species. Exotic species indicated with dashed lines. Dunn test groupings of species with similar means indicated with letters.

3.3.4 Year level sap flux density comparison

In Year 1, a Kruskal–Wallis test indicated significant differences in mean daily sap flux density among species (Table 3.3). Post hoc Dunn tests showed that *E. fastigata* had the highest sap flux density, significantly higher than most other species (adj. $p < 0.01$), though the difference compared with *F. solandri* was weaker (adj. $p = 0.03$; Figure 3.6 & Appendix N). In contrast, *P. taxifolia* had the lowest sap flux density, significantly lower than most species (adj. $p < 0.01$). Several species did not differ significantly from one another, including *F. fusca* and *L. menziesii* (adj. $p = 0.20$), *F. fusca* and *P. radiata* (adj. $p = 0.09$), and *F. fusca* and *S. sempervirens* (adj. $p = 1.00$). Other non-significant comparisons included *F. solandri* with *P. totara*, *P. radiata* with *P. totara*, and *L. menziesii* with *S. sempervirens* (all adj. $p = 1.00$).

In Year 2, a Kruskal–Wallis test indicated significant differences in daily mean sap flux density among species (Table 3.3). Post hoc Dunn tests showed that the exotic angiosperm, *E. fastigata*, had the highest sap flux density, significantly greater than all other species (adj. $p < 0.01$), although the difference compared with *F. solandri* was weaker (adj. $p = 0.03$; Figure 3.7 & Appendix N). In contrast, *P. taxifolia* had the lowest sap flux density (mean = $0.71 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$), significantly lower than all other species (adj. $p < 0.01$). Most other species had broadly similar sap flux densities. For example, the indigenous angiosperm *F. fusca* did not differ significantly from *F. solandri* (adj. $p = 0.51$), *P. radiata* (adj. $p = 0.35$), or *P. totara* (adj. $p = 0.06$), and was statistically indistinguishable from *S. sempervirens* (adj. $p = 1.00$). Similarly, *P. radiata* showed no significant differences from *P. totara* or *S. sempervirens* (both adj. $p = 1.00$), and *P. totara* and *S. sempervirens* were also not significantly different from one another (adj. $p = 0.21$). *Lophozonia menziesii* demonstrated statistically different mean sap flux density to the other species (adj. $p = <0.01$).

Table 3.3: Kruskal-Wallis test results assessing differences in sap flux density between each species, in each of Year 1 and Year 2.

Year	H	df	p
1	1042.10	7	<0.01
2	955.88	7	<0.01

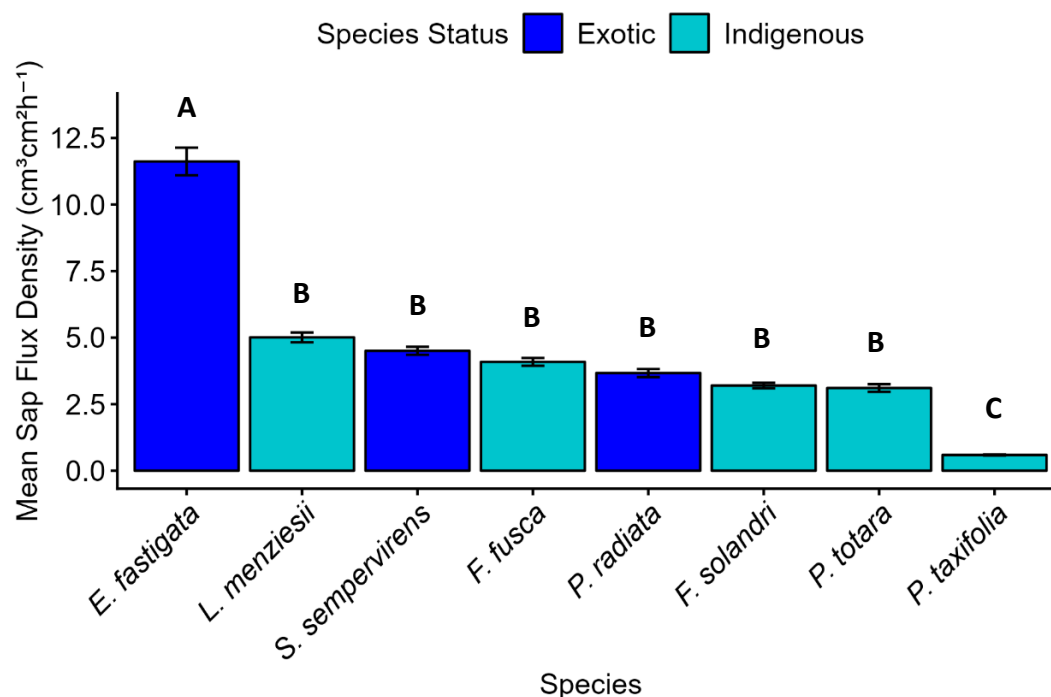


Figure 3.6: Species mean daily sap flux density ($\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$) in Year 1 (21/06/2022–21/06/2023), calculated at the species level. Exotic species are shown with dark blue bars and indigenous species shown with light blue bars. Error bars represent standard error.

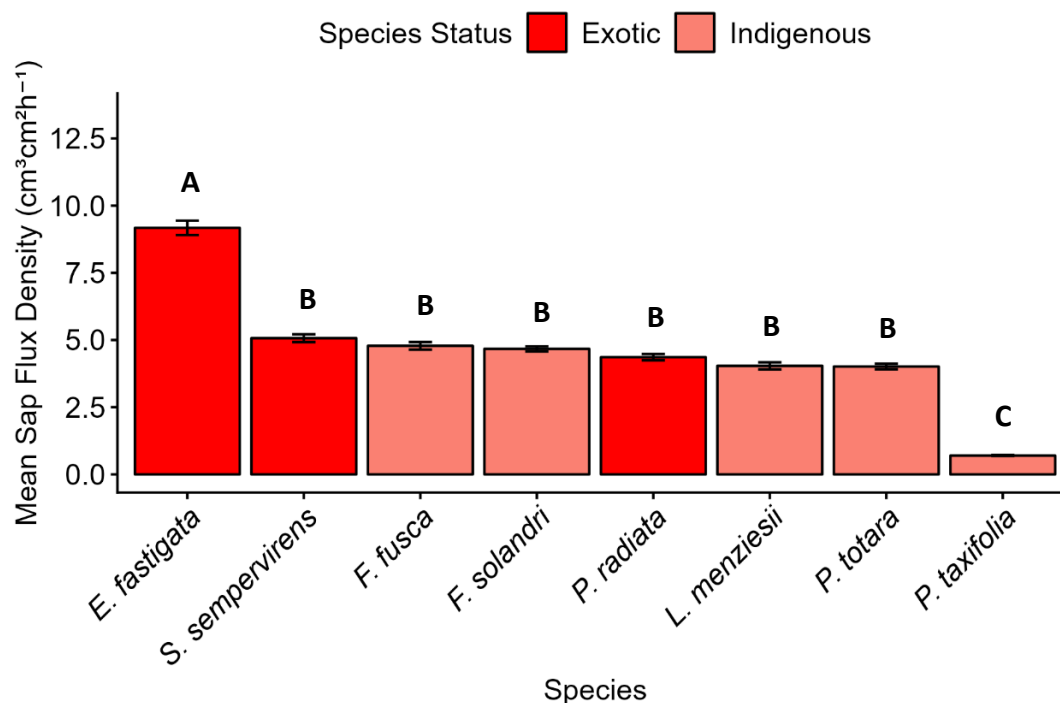


Figure 3.7: Species mean daily sap flux density ($\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$) in Year 2 (22/06/2023–21/06/2024), calculated at the species level. Exotic species are shown with red bars and indigenous species shown with salmon bars. Error bars represent standard error.

3.3.5 Dry period level sap flux density comparison

In Dry Period 1, the Kruskal-Wallis test showed that the study species had statistically distinct mean sap flux density (Table 3.4). Results from the Dunn test showed that, in Dry Period 1, *E. fastigata* had the highest mean sap flux density of the study species and *P. taxifolia* the lowest (Figure 3.8 & Appendix O). *Lophozonia menziesii* demonstrated the highest mean sap flux density of the indigenous species, higher than that of *P. radiata* ($p = 0.02$), but statistically similar to that of *S. sempervirens* ($p = 1$).

In Dry Period 2, results from the Kruskal-Wallis test showed that the study species had statistically distinct mean sap flux density (Table 3.4). Results from the post-hoc Dunn test showed that *F. solandri* had the highest mean sap flux density and *P. taxifolia* the lowest (Figure 3.9 & Appendix O). The remaining species had statistically similar mean sap flux density in Dry Period 2 ($p = > 0.05$). There was no clear pattern among indigenous and exotic species.

Table 3.4: Kruskal-Wallis test results assessing differences in sap flux density between each species, in each of Dry Period 1 and Dry Period 2.

Dry Period	H	df	p
1	356.05	7	<0.01
2	360.32	7	<0.01

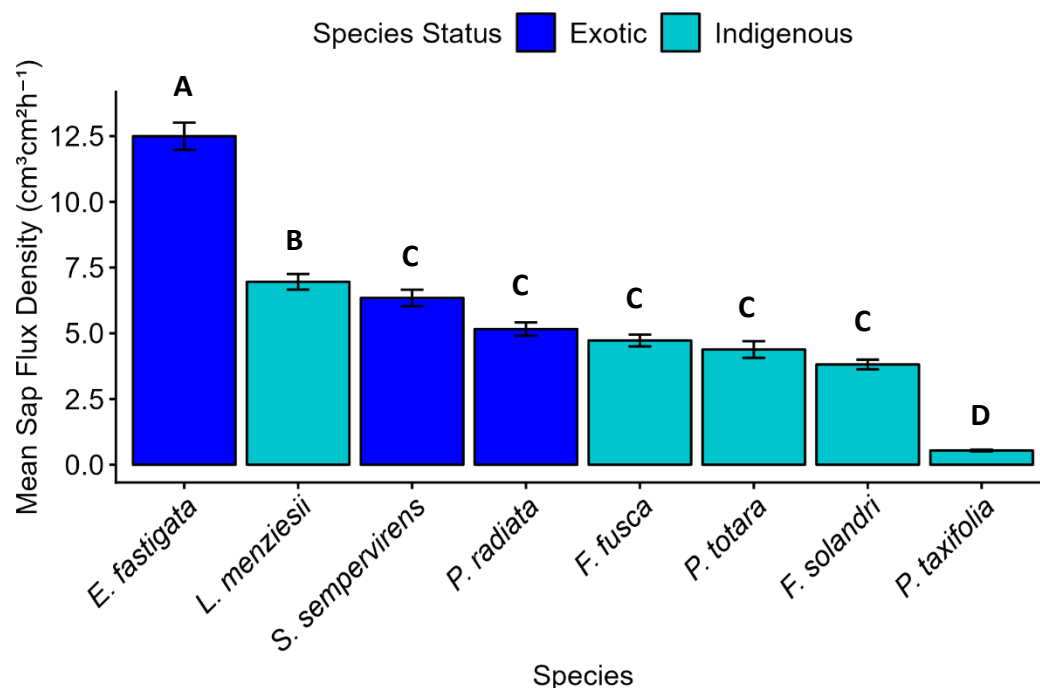


Figure 3.8: Species mean daily sap flux density ($\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$) in Dry Period 1 (01/01/2023-31/03/2023), calculated at the species level. Exotic species are shown with dark blue bars and indigenous species shown with light blue bars. Error bars represent standard error.

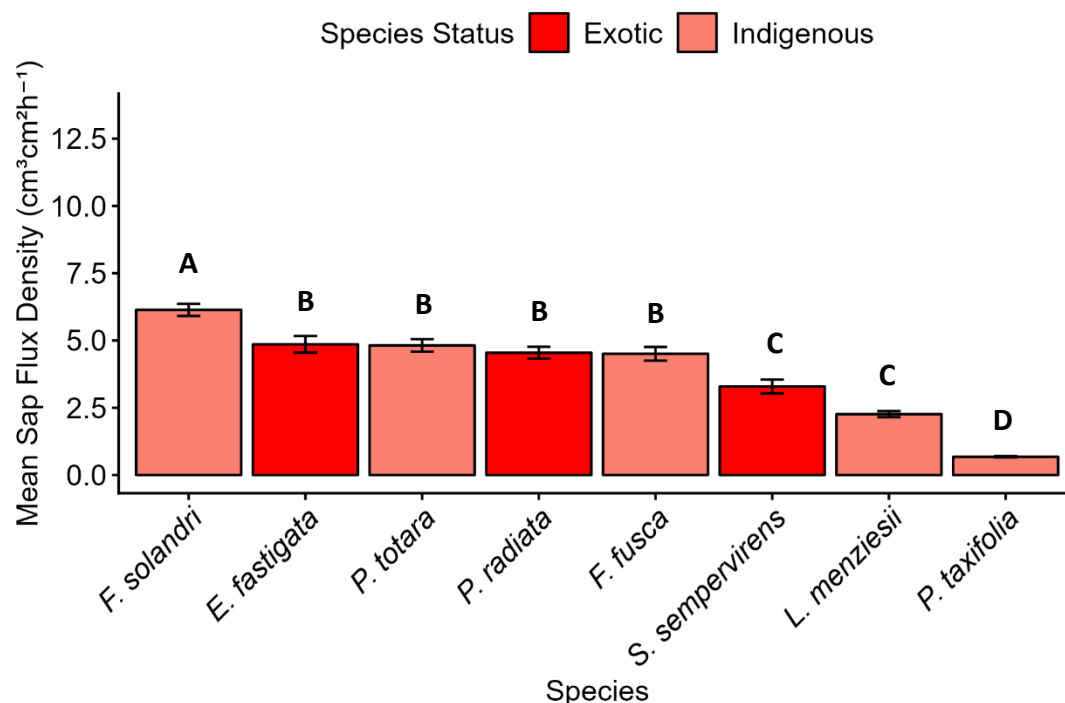


Figure 3.9: Species mean daily sap flux density ($\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$) in Dry Period 2 (01/01/2024-31/03/2024), calculated at the species level. Exotic species are shown with red bars and indigenous species shown with salmon bars. Error bars represent standard error.

3.3.6 Weather effects on sap flow at the species level

Results from the GAMs showed varying responses to weather across species and study years (Table 3.5 & 3.6). PET was a significant predictor for all species in both study years. Soil VWC was not a significant predictor for *P. totara* in Year 1 but was a significant predictor in Year 2 and for the other study species in both study years. Rainfall was not a significant predictor for *L. menziesii* or *P. totara* in either study year, *P. radiata* in Year 1, or *S. sempervirens* in Year 2.

Results from the smooth graphs showed that the relationships between the climate variables and sap flux density were generally non-linear (Figure 3.10-3.15 & Appendix P-T). For some species, PET had an overall positive relationship with sap flux density in Year 1, including *F. fusca* (Figure 3.12) and *L. menziesii* (Figure 3.14), as well as *E. fastigata* in both study years (Figure 3.10 & 3.11). For some species, rainfall had an overall negative relationship with sap flux density in Year 1, including *E. fastigata*, *F. fusca*, and in both study years, including *L. menziesii* (Figure 3.14 & 3.15). Only one species had an overall negative relationship with soil VWC in one of the study years, *L. menziesii* in Year 1.

There was variation across species as to which study year had a higher R^2 . Species with higher R^2 in Year 1 were indigenous angiosperm species, *L. menziesii* (Year 1 R^2 = 0.63, Year 2 R^2 = 0.38) and *F. solandri* (Year 1 R^2 = 0.69, Year 2 R^2 = 0.47). Species with higher R^2 in Year 2 were *E. fastigata* (Year 1 R^2 = 0.27, Year 2 R^2 = 0.74), *F. fusca* (Year 1 R^2 = 0.51, Year 2 R^2 = 0.77), and *P. radiata* (Year 1 R^2 = 0.78, Year 2 R^2 = 0.81). Species with similar R^2 in both study years were *P. totara* (Year 1 R^2 = 0.67; Year 2 R^2 = 0.68) and *S. sempervirens* (Year 1 R^2 = 0.82, Year 2 R^2 = 0.82). The two exotic conifer species, *P. radiata* and *S. sempervirens*, had the highest R^2 in both study years. In Year 1, *E. fastigata* had the lowest R^2 . In Year 2, *P. taxifolia* had the lowest R^2 of 0.32.

Table 3.5: Summary of Gaussian generalised additive model (GAM) smooth-term results for the native study species across two study years. Models were fitted separately for each study species each study year. Each climate variable (soil volumetric water content, rainfall, and potential evapotranspiration) was modelled using thin-plate regression splines (k = 5 for soil VWC; k = 10 for rainfall and PET). Reported values include the effective degrees of freedom (edf), F-statistics, and associated p-values for each smooth term.

Species	Year	Climate variable	edf	F	p
<i>F. fusca</i>	1	Rainfall	1.00	6.23	0.01
		PET	2.11	63.72	<0.01
		Soil VWC	3.24	5.14	<0.01
	2	Rainfall	1.49	4.88	0.01
		PET	3.43	48.52	<0.01
		Soil VWC	3.92	175.43	<0.01
<i>F. solandri</i>	1	Rainfall	2.85	9.41	<0.01
		PET	2.10	101.32	<0.01
		Soil VWC	1.00	30.64	<0.01
	2	Rainfall	2.07	7.75	<0.01
		PET	5.10	12.38	<0.01
		Soil VWC	3.65	33.97	<0.01
<i>L. menziesii</i>	1	Rainfall	1.89	2.66	0.08
		PET	2.28	61.96	<0.01
		Soil VWC	3.14	10.97	<0.01
	2	Rainfall	1.75	0.78	0.47
		PET	2.53	18.32	<0.01
		Soil VWC	2.48	56.00	<0.01
<i>P. totara</i>	1	Rainfall	3.02	1.95	0.09
		PET	2.62	113.56	<0.01
		Soil VWC	2.27	2.15	0.08
	2	Rainfall	2.06	1.69	0.20
		PET	4.04	75.07	<0.01
		Soil VWC	3.21	55.65	<0.01
<i>P. taxifolia</i>	1	Rainfall	2.61	19.90	<0.01
		PET	2.45	10.36	<0.01
		Soil VWC	3.80	20.06	<0.01
	2	Rainfall	2.81	4.13	<0.01
		PET	1.20	18.80	<0.01
		Soil VWC	3.83	34.51	<0.01

Table 3.6: Summary of Gaussian generalised additive model (GAM) smooth-term results for the exotic study species across two study years. Models were fitted separately for each study species each study year. Each climate variable (soil volumetric water content, rainfall, and potential evapotranspiration) was modelled using thin-plate regression splines (k = 5 for soil VWC; k = 10 for rainfall and PET). Reported values include the effective degrees of freedom (edf), F-statistics, and associated p-values for each smooth term.

Species	Year	Climate variable	edf	F	p
<i>E. fastigata</i>	1	Rainfall	1.77	8.67	<0.01
		PET	2.02	30.38	<0.01
		Soil VWC	2.95	4.04	<0.01
	2	Rainfall	2.34	8.44	<0.01
		PET	4.40	69.14	<0.01
		Soil VWC	4.65	162.64	<0.01
<i>P. radiata</i>	1	Rainfall	2.29	2.60	0.07
		PET	4.51	147.57	<0.01
		Soil VWC	3.29	13.30	<0.01
	2	Rainfall	2.94	14.90	<0.01
		PET	4.22	121.20	<0.01
		Soil VWC	3.26	154.70	<0.01
<i>S. sempervirens</i>	1	Rainfall	2.44	4.25	0.01
		PET	4.87	124.26	<0.01
		Soil VWC	3.61	22.17	<0.01
	2	Rainfall	1.00	0.90	0.34
		PET	5.91	68.46	<0.01
		Soil VWC	3.94	341.16	<0.01

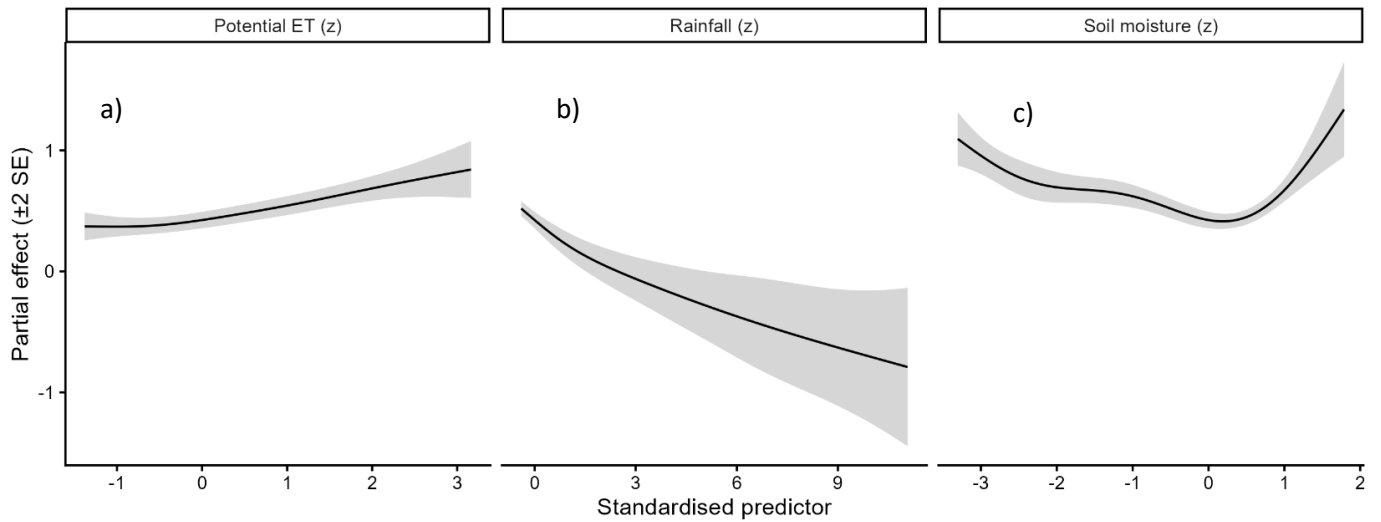


Figure 3.10: Partial-effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *E. fastigata* in Year 1. Each panel shows the estimated nonlinear relationship between sap flux density and Potential ET (PET; a), rainfall (b), and soil moisture (soil VWC; c), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.

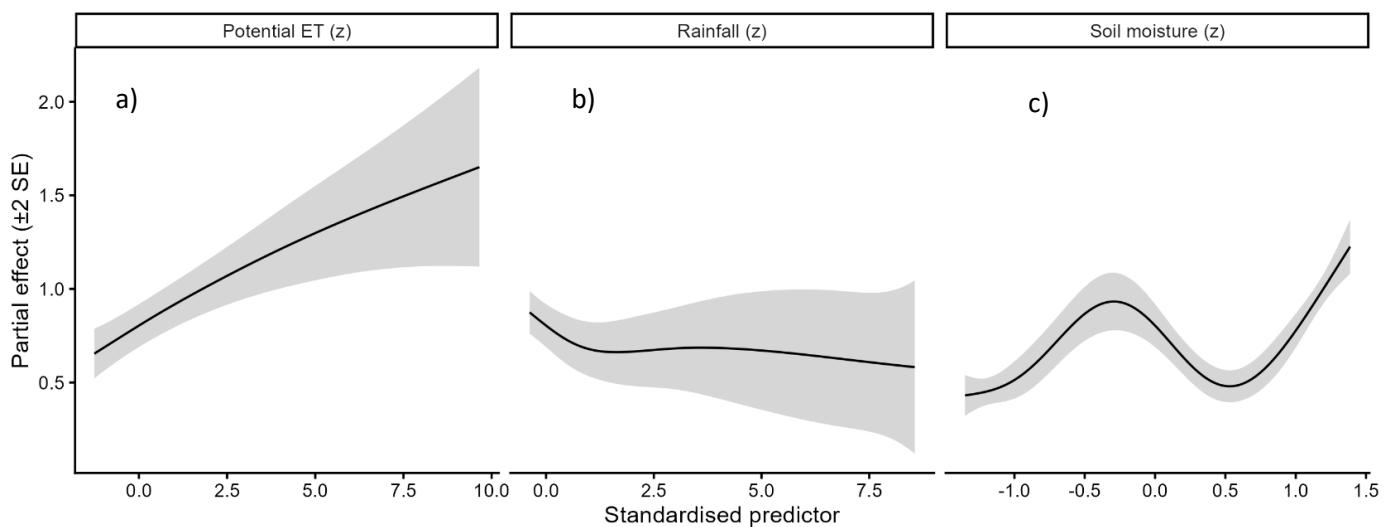


Figure 3.11: Partial-effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *E. fastigata* in Year 2. Each panel shows the estimated nonlinear relationship between sap flux density and Potential ET (PET; a), rainfall (b), and soil moisture (soil VWC; c), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.

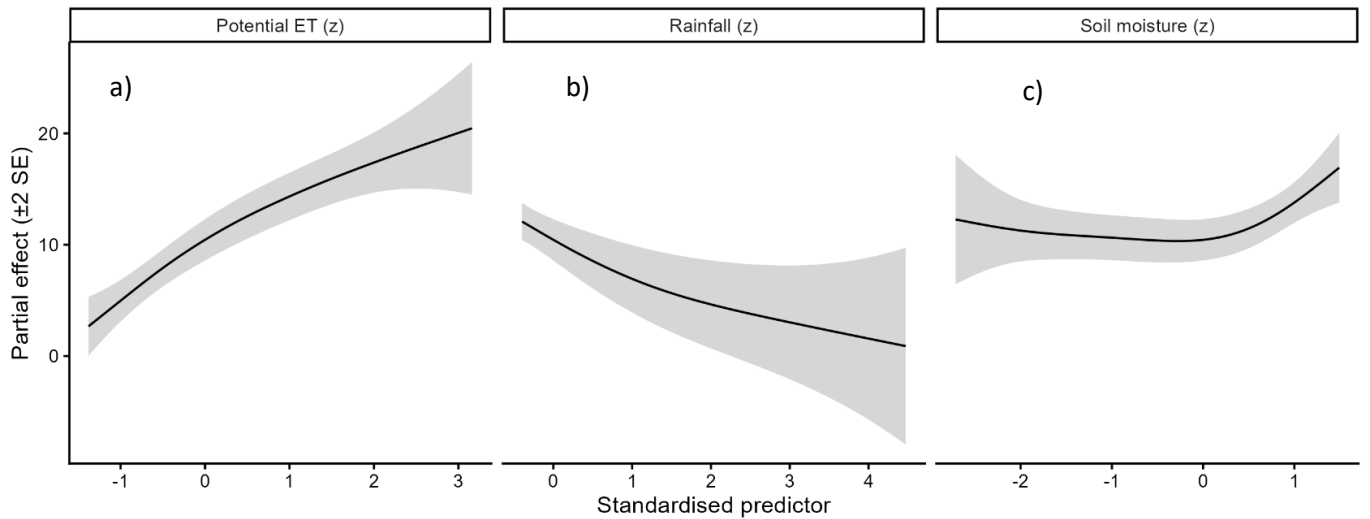


Figure 3.12: Partial-effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *F. fusca* in Year 1. Each panel shows the estimated nonlinear relationship between sap flux density and Potential ET (PET; a), rainfall (b), and soil moisture (soil VWC; c), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.

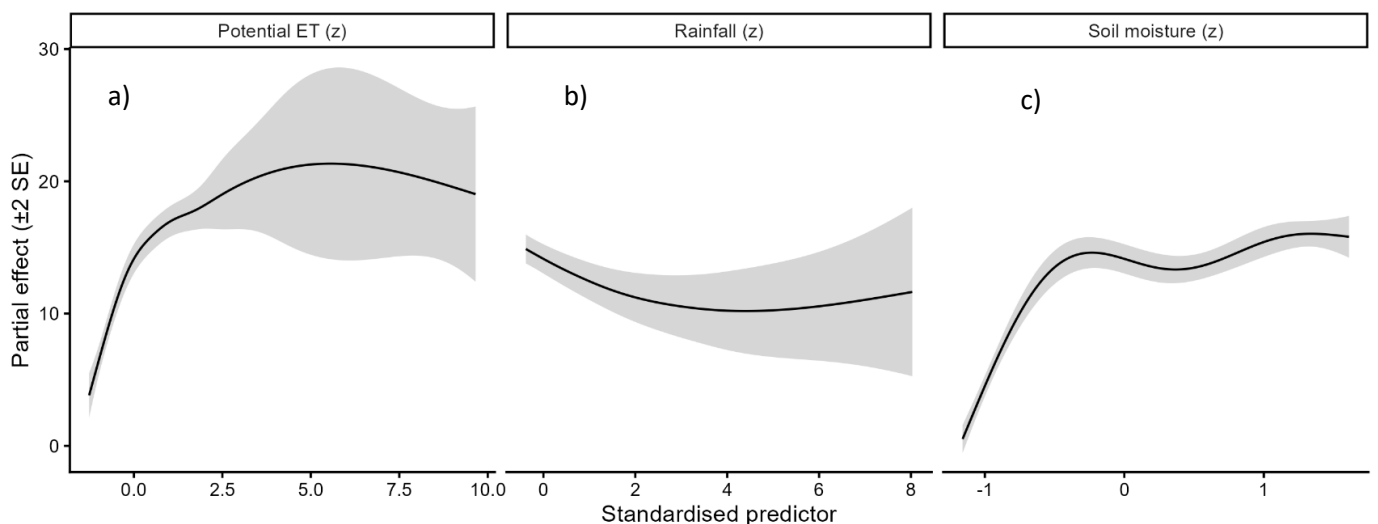


Figure 3.13: Partial-effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *F. fusca* in Year 2. Each panel shows the estimated nonlinear relationship between sap flux density and Potential ET (PET; a), rainfall (b), and soil moisture (soil VWC; c), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.

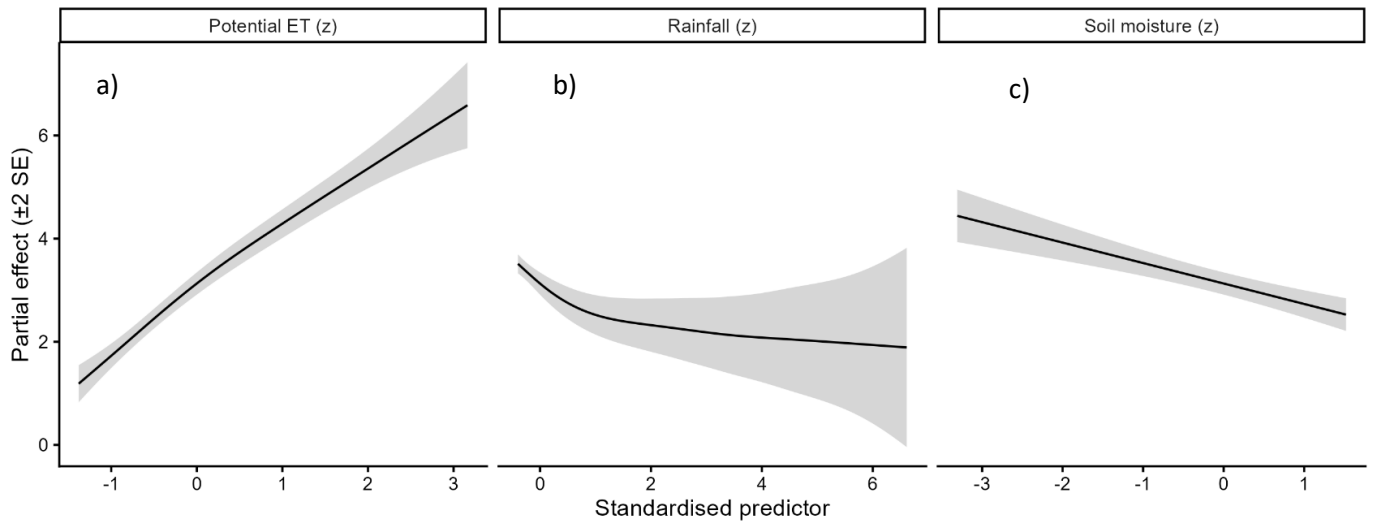


Figure 3.14: Partial-effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *L. menziesii* in Year 1. Each panel shows the estimated nonlinear relationship between sap flux density and Potential ET (PET; a), rainfall (b), and soil moisture (soil VWC; c), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.

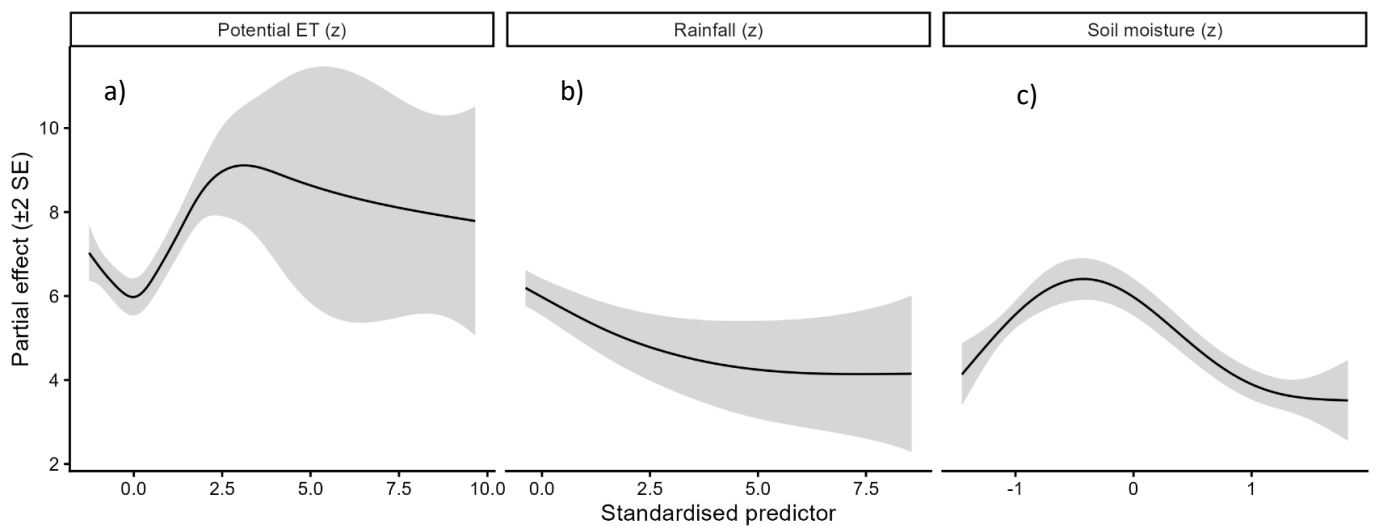


Figure 3.15: Partial-effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *L. menziesii* in Year 2. Each panel shows the estimated nonlinear relationship between sap flux density and Potential ET (PET; a), rainfall (b), and soil moisture (soil VWC; c), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.

3.4 Discussion

In partial support of our hypothesis, all three of the exotic study species demonstrated higher flow rates than the indigenous study species. This result likely reflects their larger stem size and supports previous findings that more sapwood area results in more water use (Butz et al., 2018; Kaptein et al., 2023). Generally, the exotic species

exhibited higher cumulative water transpired than the indigenous species. However, only *E. fastigata* demonstrated higher sap flux density than the indigenous study species. Together, these results indicate that stem size explains differences in total water use, whereas species-level hydraulic traits such as xylem anatomy, stomatal behaviour, and leaf area regulate per-area flux (Loritz et al., 2024). In support of our hypothesis, among the exotic and indigenous species groups there generally were clear patterns of angiosperm species exhibiting higher daily mean sap flux density than the conifer species, with exceptions. One of the indigenous conifer species, *P. totara*, often exhibited statistically similar daily mean sap flux density to the indigenous angiosperm species, generally supporting previous findings that angiosperm species exhibit higher maximum sap flux density compared to gymnosperm species (Hu et al., 2024).

3.4.1 Weather effects on sap flux density

There were clear differences in weather conditions across the four time periods. The rainfall and soil VWC conditions were contrasting among the four time periods. Rainfall and soil VWC were high in Year 1 and Dry Period 1, with soils near field capacity for the majority of Year 1. In contrast, rainfall and soil VWC were low in Year 2 and Dry Period 2, with a clear seasonal pattern of soil drying. Total rainfall was generally higher in Year 1 than Year 2, and to climate normal levels, especially in February and March of 2023, coinciding with Cyclone Gabrielle. Average air temperatures and potential evapotranspiration were similar between Year 1 and Year 2, and to climate normal levels. These weather differences across time periods were reflected in our results.

Only three species, *L. menziesii*, *F. solandri*, and *P. taxifolia*, showed results consistent with our hypothesis of more sap flux density explained under wetter weather conditions such as those in Year 1. This result suggests that for these three species, under drier weather conditions like those in Year 2, physiological traits better explain sap flux density variation than rainfall, potential evapotranspiration, and soil volumetric water content for most of our study species. These results support recent findings that sap flow sensitivity to climate variables can increase under wetter conditions, particularly for nighttime flows (Fang et al., 2024; Su et al., 2022). For the remaining species, it is likely that microsite conditions played a role in more sap flux density variation being explained in the drier weather conditions of Year 2, or similar variation

explained between study years. The microsite conditions include higher planting density for *P. totara*, which creates increased competition for soil water, for example. Consistent with our hypothesis and previous findings (e.g. Sun et al., 2022), PET was a significant predictor of sap flux density for all of our study species in both study years. In partial support of our hypothesis, soil VWC was a significant predictor of sap flux density under the drier weather conditions in Year 2 for all study species. However, only one species, *P. totara*, followed the hypothesised trend of soil VWC being a non-significant predictor under the wetter weather conditions of Year 1, indicating that even under wetter weather conditions, soil VWC was an important predictor of sap flux density for the other study species. Previous studies have found soil water content to have a strong effect on transpiration in a wetter year (Fang et al., 2024). Only *P. radiata* showed results consistent with our hypothesis that rainfall would be a significant predictor of sap flux density in the drier weather conditions of Year 2 but not in the wetter weather conditions of Year 1. This result likely reflects the particularly wet microsite conditions for this species. Species differences are explored in the following sections.

3.4.2 *Eucalyptus fastigata*

One of the exotic species, *E. fastigata*, did not exhibit higher cumulative water transpired in Dry Period 2 than all the indigenous species. Previous studies on closely related *E. regnans* (F. Muell.) have also found reduced water use under drying conditions (Pfautsch & Adams, 2013). Our result likely suggests that cumulative water transpired was suppressed by early stomatal closure due to the low soil VWC recorded for *E. fastigata* (Grossiord et al., 2017). In partial support of our hypothesis, only *E. fastigata* demonstrated higher daily mean sap flux density than the indigenous species in all time periods, likely reflecting the observed large leaf area for this species. Leaf area measurements have previously been shown to have a positive relationship with sap flux density (Hu et al., 2024). These results suggest that, despite dry microsite conditions and canopy closure limiting growth (Chapter 2), high leaf area is driving high daily mean sap flux density for *E. fastigata*. Interestingly, previous work on closely related *E. regnans* at a site with similar climate to the present study site measured an average sap flux density of $4.79 \text{ cm}^3 \text{ cm}^{-2} \text{ hr}^{-1}$ (Pfautsch et al., 2010). This result was

similar only to the measurements in Dry Period 2, the drier of the two dry periods, in the present study. Further research is needed to test if this contrast is simply a species difference. Pfautsch et al. (2010) found a logistic relationship between sapwood area and water use. As *E. fastigata* has reached canopy closure at Rewanui Forest Park, it could be assumed that water use would not continue to increase for this species.

3.4.3 *Pinus radiata*

Previous studies have found *P. radiata* to have higher sap flux density than indigenous species (White et al., 2021; White et al., 2020). A Chilean study found that wilding *P. radiata* contributed approximately 60 % of the total transpiration in an indigenous *N. glauca* forest due to higher sap flux density in winter and spring. This result was largely driven by the lack of leaves in the deciduous *N. glauca* during those months (White et al., 2020). In the present study, *P. radiata* did exhibit higher flow rates and cumulative water transpired compared to the indigenous study species. However, *P. radiata* did not exhibit higher sap flux density than the indigenous study species. This result is congruent with the findings of White et al. (2021). White et al. (2021) found that larger sapwood area of *P. radiata* compensated for lower sap flux density, resulting in higher transpiration than the Chilean indigenous *N. obliqua* (Mirb.) Oerst. and *N. glauca*, further highlighting the role of stem size in total water use.

3.4.4 *Sequoia sempervirens*

Sequoia sempervirens did not demonstrate higher sap flux density than the indigenous study species, particularly in Dry Period 2. In the particularly dry conditions of Dry Period 2, it is likely that the relatively low mean sap flux density measured for *S. sempervirens* was due to the drier conditions and smaller stem size than the other exotic study species. Summer fog has been shown to buffer the effects of increased VPD and subsequent increased transpiration, alleviating water stress in the natural range of *S. sempervirens* (Burgess & Dawson, 2004). Although we did not measure fog, summer fog is not common in the region of our study site. There is a possibility that the lack of summer fog to buffer water stress in Dry Period 2 resulted in *S. sempervirens* not exhibiting higher sap flux density than the indigenous species. This theory would need to be tested in the future. The measured stem size of *S. sempervirens* was smaller than that of the other exotic study species, indicating that

the buffering capacity of *S. sempervirens* was lower than that of *E. fastigata* and *P. radiata*. Together, these results suggest increased water stress for *S. sempervirens* resulting in early stomatal closure in drier conditions of Dry Period 2.

3.4.5 Indigenous angiosperm species

Tree size has been previously shown to influence sap flux density of *F. fusca* and *L. menziesii*, with higher sap flux density measured in larger trees (Kostner et al., 1992). In the Kostner et al. (1992) study, rainfall was almost double that of the wettest study year in the present study, with an annual total of 2054 mm and a December to March total of 678 mm. As there were distinct climatic conditions in the four time periods of the present study, stem size appeared to explain cumulative water transpired but not daily mean sap flux density. Compared to the other indigenous study species, stem size was large for *F. solandri*, moderate for *F. fusca*, and small for *L. menziesii*, which was generally reflected in the rankings of cumulative water transpired compared to the other indigenous study species.

The rankings of daily mean sap flux density appeared to be affected by both climate and stem size, particularly for *F. solandri* and *L. menziesii*. *Lophozonia menziesii* ranked higher in daily sap flux density under wetter conditions (Year 1 and Dry Period 1) and low under drier conditions (Year 2 and Dry Period 2). Kostner et al. (1992) also found in their study that trees only used minimal amounts of stored water which, in combination with the small stem size, could explain the low sap flux density ranking under drier conditions for *L. menziesii*. *Fuscospora solandri* ranked low in daily mean sap flux density under wetter conditions (Year 1 and Dry Period 1) and high under drier conditions (Year 2 and Dry Period 2). It is possible that the large stem size compared to the other indigenous study species buffered sap flux density in Year 2 and Dry Period 2 for *F. solandri*, a pattern observed in other native species (Macinnis-Ng et al., 2016). It is also possible that the high cumulative water transpired and low sap flux density ranking in Year 1 and Dry Period 1 reflect the long growing season (Chapter 2) but low instantaneous sap flux density.

Fuscospora solandri was the only species for which soil VWC had a negative relationship with sap flux density under the drier conditions of Year 2 and Dry Period 2. Previous studies have found the water use of related *Nothofagus* species to be

governed by atmospheric demand more so than soil moisture (Rocha et al., 2025). It is possible that our results reflect low sap flux density on days with low VPD and PET, and high soil VWC.

3.4.6 Indigenous conifer species

Unlike the indigenous angiosperm species, stem size does not appear to explain cumulative water transpired and daily mean sap flux density for *P. taxifolia*. Despite a moderate to large stem size compared to the other indigenous study species, *P. taxifolia* consistently ranked low in cumulative water transpired and daily mean sap flux density relative to all the other study species. The GAMs also had little explanatory power (low R^2) for *P. taxifolia*, potentially suggesting that while transitioning from a divaricating life stage, neither stem size nor climate variables such as rainfall, PET, and soil VWC, are good predictors of water use and sap flux density for *P. taxifolia*.

The other indigenous conifer species, *P. totara*, exhibited statistically similar daily mean sap flux density to the three indigenous angiosperm species in at least one time period each. A potential theory is nitrogen and soil water availability. Previous studies have found that low nitrogen is a limiting factor for transpiration in New Zealand indigenous conifer forests (Barbour et al., 2005; Bown et al., 2024). Barbour et al. (2005) found that the combination of high rainfall, high leaf area index, and low nitrogen in old growth *Dacrydium cupressinum* (Lamb.) forest resulted in low transpiration. Bown et al. (2024) estimated transpiration in 20-year-old planted stands of indigenous conifer species, *P. totara*, and *Dacrycarpus dacrydioides* (A.Rich.) de Laub. Due to lower nitrogen availability and lower irradiance, *P. totara* exhibited lower transpiration than *D. dacrydioides* (Bown et al., 2024). However, the planting site of the forestry trial at Rewanui Forest Park was previously grazed pasture, likely resulting in a high nitrogen environment. *Podocarpus totara* is known to be tolerant of dry and poorly drained soils (Bergin, 2000). The microsite soil moisture conditions for *P. totara* at our study site were moderately wet compared to the other study species' microsites. It is possible that these microsite conditions aided the similar daily mean sap flux density measurements between *P. totara* and the indigenous angiosperm species. However, the results in Chapter 2 did suggest some water stress for *P. totara* due to high planting

density and high competition for water. As nitrogen was not measured in the present study, further research is needed to test this theory.

3.4.7 Future afforestation projects

Results from this study highlight the different water use strategies of our study species and the potential implications for future afforestation projects. The exotic study species exhibited higher total water use and generally higher cumulative water use, due to larger stem sizes, than the indigenous study species. This suggests that when planted at the same time, the exotic species will likely have higher total water use than the indigenous species at any given time. However, this result could change as the indigenous species reach a similar size to the exotic species, a topic for future research. Only *E. fastigata* exhibited higher sap flux density than the indigenous species, supported by high leaf area but limited by dry microsite conditions. Also limited by microsite conditions was *P. radiata*, which experienced high soil VWC, implying that wetter sites may not be suitable when maximum growth is the project goal for *P. radiata*. *Sequoia sempervirens* had a smaller average stem size than the other exotic species. Combined with the results in Chapter 2, it is possible that growth and water use could continue to increase for *S. sempervirens*, whereas both *E. fastigata* and *P. radiata* appear to have reached their maximum growth rate and possibly reached maximum water use at our study site.

The indigenous study species generally had lower total and cumulative water use compared to the exotic species, suggesting that when planted at the same time, the indigenous species may be better suited to planting projects where water use is of concern. Both *F. fusca* and *L. menziesii* appeared to have high instantaneous sap flux density over short periods of time. Sap flux density of *L. menziesii* in particular appeared to be sensitive to climatic conditions, suggesting that these species would do best in locations where water is non-limiting, particularly in winter and spring. Tight stomatal control and early stomatal closure may put these two species forward as contenders for sites with mild late summer drought, especially if water availability in late summer is a concern for landowners. The remaining indigenous angiosperm species, *F. solandri*, demonstrated low sap flux density over a longer period of time. This resulted in a higher cumulative water transpired compared to the other

indigenous species. This means that for projects where cumulative water use is a concern, *F. solandri* may be less suitable than the other indigenous angiosperm species. *Podocarpus totara* had statistically similar daily mean sap flux density to the indigenous angiosperm species. It is possible that *P. totara* will have higher water use at sites with high nitrogen, although this would need to be tested. The remaining indigenous species, *P. taxifolia*, exhibited low total water use and neither climate nor stem size was a good predictor of sap flux density for this species. Based on the ecology of *P. taxifolia* it can be assumed that this species would be suitable for planting at water-limited sites, although further research is required to fully understand *P. taxifolia* water use at differing life stages.

3.4.8 Conclusions

The exotic species, *E. fastigata*, *P. radiata*, and *S. sempervirens*, demonstrated higher flow rates than the indigenous species due to larger stem sizes and sapwood area. However, only *E. fastigata* demonstrated higher sap flux density for the majority of the study period than the indigenous species, likely reflecting larger leaf area. GAMs' results were variable across the species, including comparisons between Year 1 and Year 2 of R^2 and climate predictor significance. These results highlight the role that species traits and microsite conditions play in affecting the relationships between sap flux density and weather conditions. For example, *P. totara*, which generally ranked low in sap flux density, was the only species for which soil VWC was not a significant predictor of sap flux density in Year 1 and was one of two species for which rainfall was not a significant predictor in either study year. Despite ranking moderately for soil VWC, *P. totara* appeared to be limited by high competition for soil VWC due to high planting density. *Prumnopitys taxifolia* demonstrated the lowest sap flux density across the study period and little sap flux density variation was explained by the GAMs for this species, suggesting low transpiration and photosynthetic activity across the study period. Together our results highlight the complex interactions between microsite effects, weather conditions, and species-specific physiology. Future research could expand on our findings by sampling more study sites and exploring other factors influencing tree water use. Including a range of study sites would capture the different responses to a wider range of weather conditions and microsite effects and better

inform future afforestation projects. Other factors influencing tree water use could include stomatal behaviour, whole-tree hydraulic conductance, vessel and tracheid diameters, and wood density.

3.5 References

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Chapter 4: Can electronic point dendrometers be used as cost-effective alternatives to sap flow meters for estimating transpiration?

4.1 Introduction

Sap flow meters are the leading method for measuring transpiration of woody plants (Poyatos et al., 2016). However, these devices are costly, invasive, and not without issues (López-Bernal et al., 2017), including wounding effects, biased results, effects of variable wood properties, and improper installation (Flo et al., 2019). Other issues include high cost of devices and difficulties with installing and maintaining the devices and supporting infrastructure including solar panels and batteries. To address wounding effects and installation issues, wound corrections (e.g. Green et al., 2003; Swanson & Whitfield, 1981) and corrections for incomplete probe contact have been developed (Clearwater et al., 1999). Less invasive external methods have also been developed, such as the external heat pulse method developed by Clearwater et al. (2009). These less invasive methods are best suited to low flow rates and small stems and organs (Clearwater et al., 2009). The possibility of using dendrometers as a cost-effective alternative has been studied previously, particularly in the context of crop irrigation scheduling (e.g. Biel et al., 2012; Conejero et al., 2007). Few studies have considered whether dendrometers could provide an alternative to sap flow measurements in a forest setting (Donfack et al., 2024; Tian et al., 2019).

Plants lose approximately 90 % of the water taken up via transpiration (Kramer & Boyer, 1995). Water supplied for transpiration is transported via the xylem (Hacke & Sperry, 2001). There are differences in xylem anatomy between conifer and angiosperm species resulting in differences in xylem safety and transport efficiency. In general, angiosperm species have less safe xylem but higher transport efficiency (Hacke & Sperry, 2001). The widely accepted cohesion-tension theory, reliant on negative hydrostatic pressures, explains the passive process of water transport through the xylem (Dixon & Joly, 1894). The passive transport of water in the xylem contrasts with the active transport of photosynthesis products within the phloem (van Bel, 1999). In

most angiosperm species, phloem conduction relies on sieve-tube elements paired with companion cells, forming wide, efficient conduits for long-distance sugar transport (Evert, 2006). In contrast, conifers use narrower sieve cells accompanied by Strasburger cells rather than companion cells, which results in higher hydraulic resistance and slower phloem transport (Liesche et al., 2015). As angiosperm species differ from conifer species in their hydraulic architecture and phloem hydraulics, as well as stomatal behaviour and water-use strategy, it can be expected that the relationship between dendrometer variables and sap flow will also differ between these two lineages.

Sap flow meters measure the rate of water movement through the xylem (Poyatos et al., 2016). Variables extracted from sap flow meters include sap flow rate (e.g. $\text{cm}^3 \text{h}^{-1}$) and sap flow per unit sapwood area (sap flux density, e.g. $\text{cm}^3 \text{cm}^{-2} \text{h}^{-1}$). Sap flow rate gives an indication of the total amount of water moving through the xylem. Sap flux density is useful for comparing trees as this variable is less influenced by differences in size and sapwood area. Comparing sap flow rate and sap flux density gives an indication of how efficiently the xylem is moving water.

Dendrometers measure changes in stem radius over time (Drew & Downes, 2009). Electronic point dendrometers are one type of dendrometer that use a potentiometer connected to a plunger to measure changes in stem radius (Cassales et al., 2025). These devices take frequent measurements, for example every five minutes both day and night across a study period (Cassales et al., 2025). Variables commonly extracted from dendrometer data include the growth variable irreversible growth (GRO), and two shrinkage variables, tree water deficit (TWD) and maximum daily shrinkage (MDS; Zweifel et al., 2016).

GRO is calculated as the current stem radius reading minus the previous maximum when the current day's average exceeds that maximum (Zweifel et al., 2016). GRO reflects true cell growth, including cell division and cell elongation (Zweifel et al., 2016). GRO is a result of cambial growth processes. These processes are triggered by increases in air temperature in spring (Körner & Paulsen, 2004), require turgor (Lockhart, 1965), and are limited by carbon allocation to cambial activity.

TWD is calculated as the previous maximum minus the current stem radius reading when the current reading is lower (Zweifel et al., 2016). TWD reflects the balance between water loss through transpiration and water uptake, as well as soil water availability and atmospheric demand. In the absence of transpiration, TWD will decrease. TWD can be used as a drought stress indicator due to the cumulative nature of the variable (Zweifel et al., 2016).

MDS is calculated as the difference between the daily maximum and minimum stem diameter (Drew & Downes, 2009). MDS reflects a tree's short-term response to current air and soil conditions as well as daily water stress (Güney et al., 2020). A small MDS indicates either a day with closed stomata or low transpiration (Güney et al., 2020).

Dendrometers measure the combined effect of irreversible cell growth, reversible shrinkage and swelling of living (phloem, parenchyma, cambium) and dead (xylem conduits and fibres) cells, and thermal expansion and contraction of the stem (Steppe et al., 2015). Radial fluctuations of the living cells can be attributed to changes in cell turgor, and therefore fluctuations in water stored internally in the stem (Zweifel et al., 2016). Radial fluctuations of the dead conducting xylem cells can be attributed to changes in apoplastic tension, the negative pressures that are generated by transpiration and explained by the cohesion-tension theory (Steppe et al., 2015). The contribution of the living and dead cells to reversible growth measurements has been measured in previous studies (De Schepper et al., 2012; Lazzarin et al., 2018; Oberhuber et al., 2023; Sevanto et al., 2002; Zweifel et al., 2014; Zweifel & Häslér, 2000). De Schepper et al. (2012), using a combination of magnetic resonance imaging (MRI) and point dendrometers, found that in the angiosperm, *Quercus robur* (L.), stem diameter fluctuations were mainly driven by the elastic young conductive phloem and cambium. Oberhuber et al. (2023) measured xylem and inner bark radial fluctuations concurrently in *Pinus sylvestris* (L.) and found that the daily amplitude of the inner bark was 10 times higher than that of the xylem. The lower amplitude of xylem fluctuations can be explained by the lignified and less elastic xylem cell walls (Oberhuber et al., 2023). As sap flow meters measure axial flow in the sapwood, and dendrometers measure the cumulative radial variation of the elastic tissues and sapwood, differences in xylem and phloem anatomy and functioning between angiosperm species and

gymnosperm species are likely to drive differences in the relationship between sap flow and reversible changes in stem diameter.

Previous studies have found relationships between sap flow and either stem diameter or dendrometer variables, including diameter at breast height (DBH), MDS, and TWD. A previous study utilising sap flow meters has found linear correlations between sap flow and daily stem diameter variation on a daily scale for all six of the deciduous tree species measured, suggesting that stem diameter measurements could be used to estimate sap flow (Sevanto et al., 2008). The relationship between DBH and sap flow has been found to differ across species, stem sizes, tree ages, sites, and environmental conditions including atmospheric demand and soil moisture conditions (Tsuruta et al., 2023). Correlations between DBH and sap flow also have been found to be dependent on climatic conditions (Zhao et al., 2023). Only in wetter years was a positive correlation observed between DBH and sap flow for *Populus tomentosa* (Carr.) in a study in northeastern China (Zhao et al., 2023). Previous studies with point dendrometers have found MDS to be a better signal than sap flow for crop irrigation scheduling due to a stronger and earlier response to water stress (Biel et al., 2012; Conejero et al., 2007). Conejero et al. (2007) conducted their study in a plot of *Prunus persica* (L.) trees and Biel et al. (2012) conducted their study on *Prunus avium* (L.) trees in a greenhouse setting. The relationship between TWD and sap flow is affected by a range of variables including stem and leaf water potential, sapwood area, tree height, stem diameter, and canopy stomatal conductance (Donfack et al., 2024). A study in a mixed forest including *Fagus sylvatica* (L.), *Fraxinus excelsior* (L.), and *Acer pseudoplatanus* (L.), in Germany, found a non-linear relationship between TWD and sap flow and concluded that TWD and sap flow cannot be used as proxy variables for one another under drought conditions (Donfack et al., 2024). In contrast, a study in *Larix gmelinii* (Rupr.) forest in northeastern China found TWD to be the most correlated with sap flow, compared to other stem diameter variables including MDS (Tian et al., 2019). The strong correlation was observed under most climate conditions, except for days with low air temperatures and high cloud cover (Tian et al., 2019).

The aim of this research was to add to the limited body of knowledge regarding the relationship between dendrometer variables and sap flow measurements. We hypothesised that GRO would have the weakest relationship with sap flux density. This

hypothesis was based on differences in timing between GRO and sap flux density; turgor is required for GRO to occur, which occurs in spring and at night when water status is high, whereas sap flux density peaks after spring and occurs during the day. We hypothesised that the relationship between TWD and sap flux density would be poor under wetter weather conditions and that the predictive power of TWD would improve under drier weather conditions for all study species. This hypothesis was based on the relationship between TWD and soil water availability; as soil water depletes, transpiration will deplete internally stored water resulting in increased TWD. We hypothesised that MDS would have the strongest relationship with sap flux density compared to TWD and GRO for all study species regardless of climatic conditions. This hypothesis was based on the relationship between MDS and transpiration; when the stomata are open and transpiration is occurring, MDS should increase. We also hypothesised that the relationship between MDS and sap flux density would be stronger under wetter annual weather conditions, including high rainfall and soil moisture, as cumulative water stress would become more important under drier conditions. We hypothesised that more sap flux density variation would be explained by including climate variables alongside dendrometer variables in a model, compared to a model with only dendrometer variables. This was expected due to the differences in tissues being measured by the sap flow meters and electronic point dendrometers, as well as the strong influence of climate on all sap flux density, GRO, TWD, and MDS.

4.2 Methods

4.2.1 Site and species

This chapter utilised the same site and species (Table 4.1), climate, soil moisture, electronic point dendrometer, sap flow measurements, and initial data processing as described in Chapter 2 and Chapter 3. In addition, soil moisture and textural property measurements were taken. To gain a proxy understanding of soil moisture and textural properties (Anon, 2014; McNeill, 1980), soil apparent electrical conductivity (EC_a , $mS\ m^{-1}$) was measured using a portable electromagnetic induction sensor (DUALEM-1, Dualem Incorporated, Milton, Canada). Soil EC_a measurements were taken during site setup in January and May of 2022. Measurements were taken in the centre and four corners of each plot, with two measurements perpendicular to each other at each

location. Each measurement provides estimates of EC_a at two cumulative depths simultaneously (0.5 m and 1.6 m), and these were averaged per plot. In general, coarser soils have lower EC_a than finer textured soils (Abdu et al., 2007).

Table 4.1: Study species including taxonomic groupings and status.

	Species	Family	Status
Angiosperms	<i>Fuscospora fusca</i> (Hook.f.) Heenan et Smissen	Nothofagaceae	Indigenous
	<i>Fuscospora solandri</i> (Hook.f.) Heenan et Smissen	Nothofagaceae	Indigenous
	<i>Lophozonia menziesii</i> (Hook.f.) Heenan et Smissen	Nothofagaceae	Indigenous
	<i>Eucalyptus fastigata</i> H.Deane & Maiden	Myrtaceae	Exotic
Conifers	<i>Podocarpus totara</i> G.Benn. ex D.Don var. totara	Podocarpaceae	Indigenous
	<i>Prumnopitys taxifolia</i> (D.Don) de Laub.	Podocarpaceae	Indigenous
	<i>Pinus radiata</i> D.Don	Pinaceae	Exotic
	<i>Sequoia sempervirens</i> (D.Don) Endl.	Cupressaceae	Exotic

4.2.2 Statistical analysis

Statistical analysis was undertaken in RStudio version 2024.12.1+563 (Posit Software, 2024) using R Version 4.4.1 (R Core Team, 2024). To test the effects of depth, EC_a, plot, and species on soil volumetric water content, ANOVA was performed using the ‘aov’ function (R Core Team, 2024).

The Anderson-Darling test was used to determine the normality of the sap flux density, GRO, MDS, and TWD data. As the data were not normally distributed, Spearman correlation was used to test for correlations between sap flux density and the growth variable GRO, and shrinkage variables TWD and MDS. This was done using the ‘cor.test’ function and the ‘spearman’ method (R Core Team, 2024).

Linear mixed effects models (LMMs) were used to assess the relationships between the dendrometer and climate variables and sap flux density in each of the two study years. Sap flux density, the response variable, was log transformed using the ‘log1p()’ function from base R (R Core Team, 2024) to reduce skew of the residuals (Appendix H). All the predictor variables were standardised within each growing year using z-score scaling (mean = 0, SD = 1) to facilitate comparison of effect sizes across predictors.

Dendrometer variables included GRO, TWD, and MDS. Climate variables, rainfall, soil volumetric water content (soil VWC), and potential evapotranspiration (PET) were included to test whether the dendrometer variables alone were enough to explain sap flux density variation. LMMs were fitted using the 'lme4' package using the 'lmer' function (Bates et al., 2015). Two models were fitted for each study year, one with dendrometer variables only and a full model with climate variables included. Fixed predictors included the three dendrometer variables and the three climate variables. Species was included as a random effect as differences between species means were tested in Chapter 2 and Chapter 3. Random slopes were specified using '(GRO + TWD + MDS || Species)', so that each species would have its own intercept and slope for each of the dendrometer variables and to estimate uncorrelated random effects to reduce overparameterisation and singular fits. Models were fitted using restricted maximum likelihood (REML) for parameter estimation, and maximum likelihood (ML) for model comparison using 'anova' (R Core Team, 2024). The dendrometer-only model was compared to the full model in either study year using likelihood ratio tests via the 'anova' function and Akaike's Information Criterion (AIC). Marginal and conditional R^2 values were calculated using the 'r.squaredGLMM' function from the 'MuMIn' package (Bartoń, 2024). Marginal R^2 estimates the variance explained by fixed effects. Conditional R^2 estimates the variance explained by the fixed plus the random effects. Species-specific coefficients were extracted. To quantify uncertainty around species-specific slopes, parametric bootstrapping was performed using the 'bootMer' function from the 'lme4' package. Percentile confidence intervals were calculated from the bootstrap distribution for each species-specific slope.

The Spearman correlations and LMMs were run for each of the two study years. Year 1 was between 21/06/2022 and 21/06/2023. Year 2 was between 22/06/2023 and 21/06/2024. Each test or model was also run on two different timescales, daily or weekly, as the sensitivity of sap flux density, GRO, and MDS to current weather conditions was expected to affect the relationships between the dendrometer variables and sap flux density. For the weekly tests and models, sap flux density, GRO, and where applicable the climate variables were averaged per week, and both TWD and MDS were summed per week. The timescale, weekly or daily, that gave the highest R^2 was retained for interpretation. Spearman correlations were also run in Dry Period 1

(01/01/2023-31/03/2023) and Dry Period 2 (01/01/2024-31/03/2024) but were excluded from further analysis due to lower R^2 than the study year level correlations.

4.3 Results

4.3.1 Climate and soil

As outlined in Chapter 2, there were clear differences in climate between Year 1 and Year 2. Air temperatures were similar between study years and to climate normal levels (Figure 2.4). Mean air temperature was 12.72 °C in Year 1 and 12.45 °C in Year 2. The minimum air temperature in Year 1 was 2.95 °C, recorded on 06/09/2022. The minimum air temperature in Year 2 was 3.59 °C, recorded on 10/08/2023. The maximum air temperature in Year 1 was 23.08 °C, recorded on 04/02/2023. The maximum air temperature in Year 2 was 23.97 °C, recorded on 19/01/2024. Potential evapotranspiration was similar between study years until the summer months; the average was 2 mm day⁻¹ in Year 1 and 3 mm day⁻¹ in Year 2 (Figure 2.4). Aside from late summer into early autumn in Year 1, total monthly rainfall was below climate normal levels in both study years (Figure 2.5). Total annual rainfall was 1543 mm in Year 1 and 829 mm in Year 2. Soil volumetric water content appeared to be near field capacity for the duration of Year 1, while a clear seasonal pattern was observed in Year 2 (Figure 2.5). Of all the species, *F. solandri* and *E. fastigata* experienced the lowest soil volumetric water content in both years. *Pinus radiata* and *S. sempervirens* experienced the highest soil volumetric water content in both years, alongside *F. fusca* in Year 2. The wettest soil was observed in the *P. radiata* plots in Year 1 (Average sVWC = 0.35 m³ m⁻³) and the driest soil was observed in the *E. fastigata* plots in Year 2 (Average sVWC = 0.19 m³ m⁻³). Apparent conductivity was highest for *S. sempervirens* at both depths, and lowest for *L. menziesii* at the 1.60 m cumulative depth, and *P. totara* at the 0.50 m cumulative depth (Table 4.2). Soil depth, the two EC_a signals, plot, and species had significant effects on soil volumetric water content at Rewanui ($p < 0.01$; Table 4.3). Climate differences between Year 1 and Year 2 were partially driven by Cyclone Gabrielle, which caused high rainfall at the study site in February 2023 (Year 1).

Table 4.2: Average EC_a by species at both cumulative depths.

Species	EC _a 1.6 m (mS m ⁻¹)	EC _a 0.5 m (mS m ⁻¹)
<i>F. fusca</i>	5.59 ± 0.16	2.02 ± 0.13
<i>F. solandri</i>	15.49 ± 9.39	3.90 ± 1.19
<i>L. menziesii</i>	5.22 ± 0.48	1.98 ± 0.27
<i>P. totara</i>	5.74 ± 1.36	1.86 ± 0.08
<i>P. taxifolia</i>	8.21 ± 0.43	2.07 ± 0.06
<i>E. fastigata</i>	8.12 ± 3.07	2.64 ± 0.95
<i>P. radiata</i>	20.57 ± 1.55	6.33 ± 1.91
<i>S. sempervirens</i>	32.98 ± 1.28	13.95 ± 0.31

Table 4.3: Results of ANOVA testing the effects of soil depth, apparent electrical conductivity at 1.6 m (EC_a 160), apparent electrical conductivity at 0.5 m (EC_a 50), plot, and species on soil VWC.

Variable	Df	Sum Sq	Mean Sq	F	p	Significance
Soil Depth	1	0.95	0.95	171.40	<0.01	***
EC _a 160	1	4.55	4.55	820.50	<0.01	***
EC _a 50	1	8.83	8.83	1592.60	<0.01	***
Plot	1	0.32	0.32	57.10	<0.01	***
Species	7	46.18	6.60	1189.40	<0.01	***
Residuals	43449	240.99	0.01			

4.3.2 Stem growth, shrinkage and sap flux density

There were clear differences between species and study years in GRO, TWD, MDS, and sap flux density (Figure 4.1). For all species, GRO (Figure 4.1b), MDS (Figure 4.1d), and sap flux density (Figure 4.1a) showed a clear seasonal pattern in both study years, increasing in the warmer months and decreasing in the colder months. GRO was generally highest for *S. sempervirens*, with the highest recorded mean daily GRO of 0.11 mm in January 2023. GRO was generally lowest for *F. solandri* and *P. taxifolia*. In June 2022, GRO of 0.00 mm was recorded for *F. fusca*, *F. solandri*, and *L. menziesii*. All study species demonstrated a larger TWD peak in Year 2; this peak was higher for the exotic species and indigenous conifer species than the indigenous angiosperm species (Figure 4.1c). Total TWD was generally highest for the exotic species, particularly *E. fastigata*. The highest total TWD was recorded for *E. fastigata* in December of 2023 (total = 67.84 mm). Total MDS was generally higher for the exotic species. The highest

total MDS was recorded for *S. sempervirens* in March 2024 (total = 121.97 mm). Total MDS and total TWD of 0.00 mm were recorded for *P. taxifolia* in April, May and June of 2024 and for *F. fusca* in June 2024. All study species followed a general trend of increased sap flux density in the spring and summer months, and decreased rates in the winter months. *Eucalyptus fastigata* demonstrated the highest sap flux density ranging from $6.33 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$ (May 2023) to $17.64 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$ (November 2022) in Year 1 and from $2.45 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$ (March 2024) to $15.79 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$ (November 2023) in Year 2, and *P. taxifolia* demonstrated the lowest ranging from $0.18 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$ (June 2022) to $0.96 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$ (December 2022) in Year 1 and from $0.23 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$ (November 2023) to $1.29 \text{ cm}^3 \text{ cm}^{-2} \text{ h}^{-1}$ (December 2023) in Year 2. The remaining species demonstrated moderate sap flux density.

Cumulative water transpired varied across species and time periods (Figure 4.2). Cumulative water transpired was lowest for *P. taxifolia* in both study years (Year 1 total = 2069.45 L, Year 2 total = 2040.41 L) alongside *L. menziesii* in Year 1 (total = 3038.23 L), and Year 2 (total = 2158.43 L). *Fuscospora solandri* had the highest cumulative water transpired of the indigenous species in both study years (Year 1 total = 5134.25 L, Year 2 total = 8926.42 L). The exotic species demonstrated higher cumulative water transpired than the indigenous species.

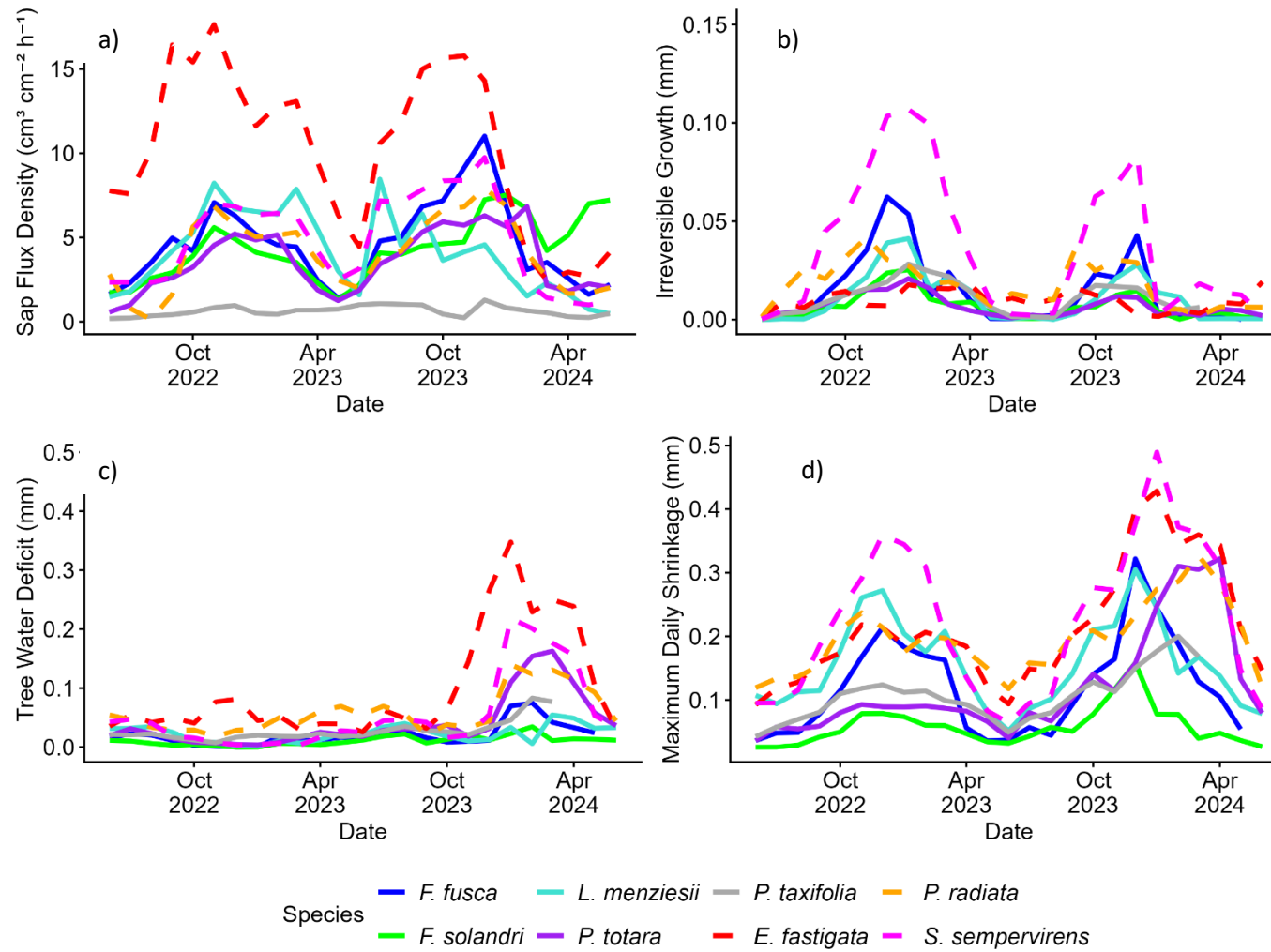


Figure 4.1: Monthly average sap flux density (a), average irreversible growth (GRO; b), total tree water deficit (TWD; c), total maximum daily shrinkage (MDS; d). Exotic species indicated by dashed lines, indigenous species indicated by solid lines.

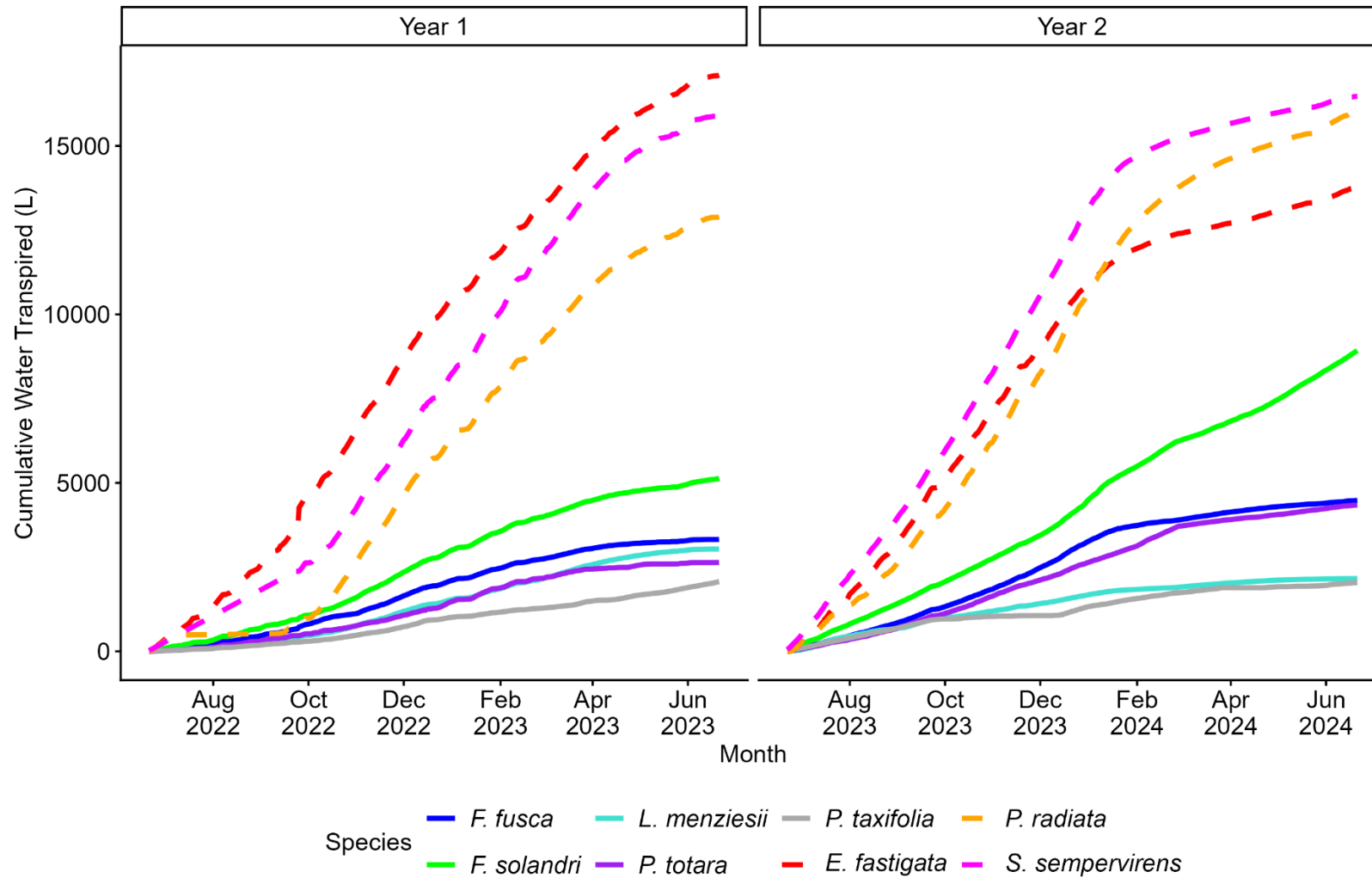


Figure 4.2: Cumulative water transpired (L) in Year 1 (21/06/2022-21/06/2023) and Year 2 (22/06/2023-21/06/2024) for each species. Exotic species indicated with dashed lines.

4.3.3 Correlations between sap flux density and stem shrinkage

Correlations between sap flux density and the dendrometer variables, GRO, TWD, and MDS, varied across time periods and species (Table 4.4). Correlations between sap flux density and GRO were non-significant for *E. fastigata* in both study years (Year 1 $p = 0.08$, Year 2 $p = 0.55$). Sap flux density and GRO correlations were higher in Year 1 for most species. Exceptions to this were *P. radiata* (Year 1 coefficient = 0.16, Year 2 coefficient = 0.37) and *P. taxifolia* for which the Year 1 correlation was non-significant ($p = 0.16$). Of the significant correlations, most were positive, except for *P. taxifolia* in Year 2 (coefficient = -0.33). Correlations between GRO and sap flux density were generally stronger for the indigenous angiosperms, particularly in Year 1.

TWD correlations were generally stronger in Year 1 compared to Year 2. Exceptions to this were in cases where correlations were non-significant, or in the case of *S. sempervirens*, the Year 2 correlation (coefficient = -0.20) was stronger than the Year 1 correlation (coefficient = -0.14). Non-significant correlations were observed in Year 2; all correlations were significant in Year 1. Of the significant correlations, negative correlations were observed for *F. fusca* and *S. sempervirens* in Year 1 and Year 2 and for *F. solandri* in Year 1. Correlations were generally stronger for the angiosperm species than the coniferous species. The strongest correlations were generally observed for *E. fastigata* (Year 1 coefficient = 0.55). Of the significant correlations, the weakest were observed for *P. taxifolia* (Year 1 coefficient = 0.13) and *F. solandri* (Year 2 coefficient = 0.08).

Correlations between sap flux density and MDS were generally more positive and more likely to be significant compared to the other two dendrometer variables. Correlations were generally stronger for the angiosperm species in Year 2. Strong correlations were observed in Year 1 except for *P. taxifolia* (coefficient = 0.42, $p = <0.01$). In contrast, correlations were either weaker or non-significant in Year 2. Correlations between MDS and sap flux density were generally positive in both study years.

Using weekly data for GRO and MDS resulted in higher R^2 , whereas using daily data for TWD resulted in higher R^2 . Daily correlations for GRO and MDS and weekly correlations for TWD were excluded from further analysis.

Table 4.4: Spearman rank correlation coefficients between sap flux density and GRO, TWD, and MDS for each study species and year. Correlations with GRO and MDS were calculated using weekly data (mean sap flux density and GRO, and cumulative MDS). Correlations with TWD were calculated using daily data. Exotic species are indicated in red. Significant p values indicated in bold.

Variable	Species	Study Year	Coefficient	p	n
GRO	<i>F. fusca</i>	1	0.74	<0.01	162
GRO	<i>F. fusca</i>	2	0.69	<0.01	144
GRO	<i>F. solandri</i>	1	0.64	<0.01	216
GRO	<i>F. solandri</i>	2	0.15	0.03	210
GRO	<i>L. menziesii</i>	1	0.77	<0.01	216
GRO	<i>L. menziesii</i>	2	0.23	<0.01	197
GRO	<i>P. totara</i>	1	0.66	<0.01	212
GRO	<i>P. totara</i>	2	0.17	0.01	220
GRO	<i>P. taxifolia</i>	1	0.10	0.16	216
GRO	<i>P. taxifolia</i>	2	-0.33	<0.01	168
GRO	<i>E. fastigata</i>	1	-0.12	0.08	216
GRO	<i>E. fastigata</i>	2	0.04	0.55	214
GRO	<i>P. radiata</i>	1	0.16	0.02	216
GRO	<i>P. radiata</i>	2	0.37	<0.01	216
GRO	<i>S. sempervirens</i>	1	0.69	<0.01	216
GRO	<i>S. sempervirens</i>	2	0.32	<0.01	220
TWD	<i>F. fusca</i>	1	-0.35	<0.01	1002
TWD	<i>F. fusca</i>	2	-0.27	<0.01	819
TWD	<i>F. solandri</i>	1	-0.22	<0.01	1452
TWD	<i>F. solandri</i>	2	0.08	<0.01	1379
TWD	<i>L. menziesii</i>	1	-0.33	<0.01	1403
TWD	<i>L. menziesii</i>	2	<0.01	1.00	1205
TWD	<i>P. totara</i>	1	0.20	<0.01	1244
TWD	<i>P. totara</i>	2	0.01	0.81	1432
TWD	<i>P. taxifolia</i>	1	0.13	<0.01	1411
TWD	<i>P. taxifolia</i>	2	0.03	0.35	997
TWD	<i>E. fastigata</i>	1	0.55	<0.01	1456
TWD	<i>E. fastigata</i>	2	0.10	<0.01	1363
TWD	<i>P. radiata</i>	1	0.20	<0.01	1420
TWD	<i>P. radiata</i>	2	0.04	0.18	1412
TWD	<i>S. sempervirens</i>	1	-0.14	<0.01	1456
TWD	<i>S. sempervirens</i>	2	-0.20	<0.01	1444
MDS	<i>F. fusca</i>	1	0.80	<0.01	162
MDS	<i>F. fusca</i>	2	0.37	<0.01	165
MDS	<i>F. solandri</i>	1	0.62	<0.01	216
MDS	<i>F. solandri</i>	2	0.08	0.25	220
MDS	<i>L. menziesii</i>	1	0.84	<0.01	216
MDS	<i>L. menziesii</i>	2	0.39	<0.01	221
MDS	<i>P. totara</i>	1	0.74	<0.01	212
MDS	<i>P. totara</i>	2	0.18	0.01	220
MDS	<i>P. taxifolia</i>	1	0.42	<0.01	216
MDS	<i>P. taxifolia</i>	2	0.26	<0.01	212
MDS	<i>E. fastigata</i>	1	0.65	<0.01	216
MDS	<i>E. fastigata</i>	2	-0.03	0.66	220
MDS	<i>P. radiata</i>	1	0.74	<0.01	216
MDS	<i>P. radiata</i>	2	0.02	0.81	216
MDS	<i>S. sempervirens</i>	1	0.74	<0.01	216
MDS	<i>S. sempervirens</i>	2	0.12	0.09	220

4.3.4 Stem growth, shrinkage, and climate predictors of sap flux density

The linear mixed effects models showed differences between study years and species in terms of the responses of sap flux density to the dendrometer obtained variables and climate variables. A larger conditional R^2 and lower AIC were observed in Year 1 for the weather inclusive model ($R^2 = 0.80$, AIC = 2532.00) compared to the dendrometer only model ($R^2 = 0.75$, AIC = 3712.60). A larger conditional R^2 and lower AIC were also observed in Year 2 for the weather inclusive model ($R^2 = 0.76$, AIC = 2537.80) compared to the dendrometer only model ($R^2 = 0.53$, AIC = 3813.50). Based on these model fit metric results, the climate inclusive models were selected for further analysis.

Of the dendrometer variables, MDS had the highest overall estimate in Year 1 and Year 2 (Table 4.5). The direction of the overall estimate was positive for MDS and TWD and negative for GRO in both study years. In the combined model, the climate variables generally had higher estimates and t-values than the dendrometer obtained variables in both study years.

The species rankings of species-specific estimates were variable across the dendrometer obtained variables and study years (Figure 4.3). Overall, MDS had the most consistently positive species-specific estimates across the study species in both study years, followed by TWD in Year 2. Not all species followed this general trend. In both study years, a larger estimate was observed for GRO for *E. fastigata*. In Year 2, a larger estimate was observed for TWD for *F. solandri*, *P. totara*, and *P. taxifolia*. Unlike the other species, the estimate for MDS was negative for *P. taxifolia* in both study years. The direction of the estimate was also variable across species for both GRO and TWD.

Table 4.5: Summary of fixed-effect predictor estimates from linear mixed-effects models for Year 1 and Year 2 examining the relationship between log-transformed sap flux density and dendrometer (GRO, TWD, MDS) and climate (Rainfall, PET, soil VWC) variables. Predictor variables were standardised (mean = 0, SD = 1). Estimates represent fixed-effect coefficients (β) with associated standard errors and t-values. Number of observations = 2750.

Study Year	Variable	Estimate	SE	t
1	Intercept	4.41	0.19	7.50
	GRO	-0.05	0.04	-1.14
	TWD	0.04	0.02	2.29
	MDS	0.19	0.08	2.28
	Rainfall	-0.10	0.01	-11.79
	PET	0.30	0.01	29.85
	Soil VWC	-0.09	0.01	-6.28
2	Intercept	1.57	0.19	8.06
	GRO	-0.02	0.03	-0.60
	TWD	0.06	0.05	1.15
	MDS	0.11	0.04	2.52
	Rainfall	-0.07	0.01	-7.89
	PET	0.21	0.01	21.50
	Soil VWC	0.33	0.01	33.82

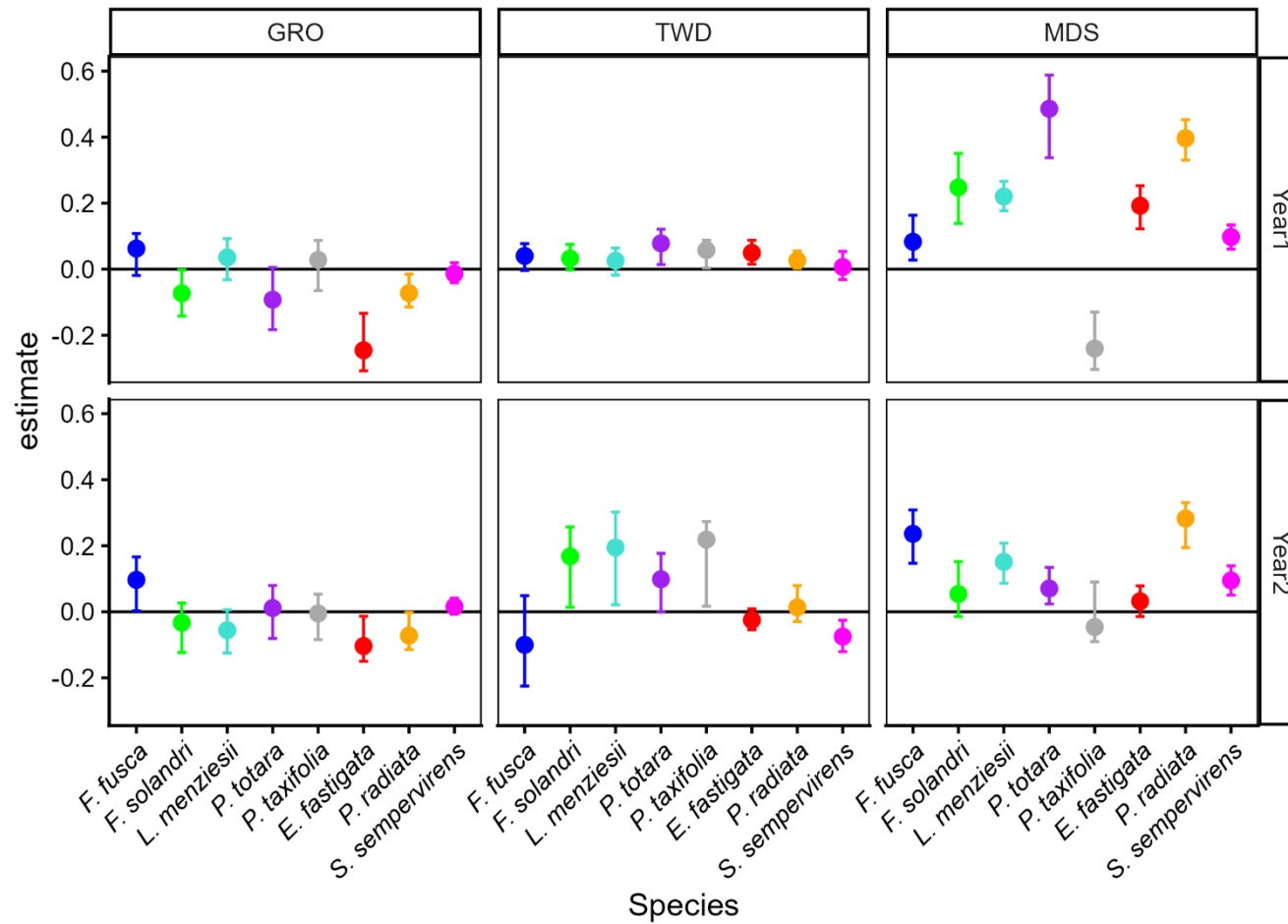


Figure 4.3: Species-specific standardised slope estimates ($\pm$ 95 % bootstrap confidence intervals) for the relationships between sap flux density and dendrometer obtained variables (GRO, TWD, and MDS) in Year 1 and Year 2. Species-specific estimates were extracted from the combined dendrometer and climate models. Slopes represent conditional mixed-effects model estimates (fixed + random effects). Predictors were standardised (mean = 0, SD = 1) prior to analysis.

4.4 Discussion

The weather conditions were different between study years. In particular, the weather in Year 1 had higher rainfall, particularly between January and March, compared to Year 2. This rainfall difference was one of the drivers of the differences in the relationships between the dendrometer variables and sap flux density between study years. The study species also had differing traits as well as differing microsite conditions. These differences are explored in the sections below.

4.4.1 GRO

In partial support of our hypothesis, GRO had a weaker relationship than MDS with sap flux density in both study years and a stronger relationship than TWD in Year 1 for most species. A stronger relationship between GRO and sap flux density than TWD and sap flux density in Year 1 likely reflects the higher rainfall between January and March. Higher rainfall during this period resulted in a longer growing season for all study species (Chapter 2) likely due to maintained turgor and favourable conditions for photosynthesis and transpiration (Lockhart, 1965). These results suggest that under wetter conditions, when turgor is maintained, the relationship between GRO and sap flux density is stronger. These results also suggest that under wetter conditions, GRO could be used in conjunction with other variables to help explain sap flux density variation.

Our results revealed that GRO had a weaker relationship with sap flux density in Year 2 and the weakest relationship of the dendrometer variables. Spearman correlation coefficients were higher in Year 1 compared to Year 2. GRO also had a lower overall estimate and lower species-specific coefficients for most species than both MDS and TWD. It is likely that in Year 2, these results reflect turgor limitations for GRO and sap flux density maintained at similar levels to Year 1 due to the balance between increased VPD and stomatal limitations (Will et al., 2013).

The direction of the relationship between GRO and sap flux density was suggested to be positive for most study species in both study years by the Spearman correlation results. However, the LMM results suggested an overall negative relationship, and a negative relationship for most species in both study years. These results imply that the

positive relationship suggested by the Spearman correlation results is driven by shared responses to external drivers. For example, both GRO and sap flux density may increase when soil moisture is high (Will et al., 2013; Zweifel et al., 2016). The generally negative relationship suggested by the LMM results likely highlights the differences in timing between GRO and sap flux density. GRO occurs when soil moisture is high and evaporative demand is lower, favouring higher turgor and tissue water potentials (Lockhart, 1965; Zweifel et al., 2016), whereas higher sap flux density tends to occur when evaporative demand is higher and tissue water potentials are reduced during the day (Thürmer et al., 1999).

4.4.2 TWD

In support of our hypothesis, the predictive power of TWD improved under the drier weather conditions of Year 2 compared to the wetter weather conditions of Year 1. Results from the LMMs revealed that TWD had the weakest overall relationship in Year 1, and in Year 2 TWD had a weaker overall relationship compared to MDS but a stronger relationship than GRO with sap flux density. The Year 1 result likely reflects soil VWC being near field capacity for the duration of Year 1, which limited the Year 1 summer TWD peak for all study species. The Year 2 result likely reflects the depletion of soil VWC starting in spring, the increased transpiration drivers in the drier conditions, and large TWD peak for all study species in Year 2.

Spearman correlation results were either weak or non-significant between TWD and sap flux density for most species in both study years. This result likely highlights the differences between TWD and sap flux density. TWD is a cumulative variable, integrating stem water status across time (Zweifel et al., 2016). In contrast, sap flux density reflects instantaneous movement of sap. Together, these results indicated that TWD could be used in conjunction with other variables to predict sap flux density under drier weather conditions.

Both the Spearman correlations and the LMMs suggested a positive relationship between TWD and sap flux density for most study species in both study years. This result highlights the relationship between increased transpiration and increased depletion of stored water from the stem (Zweifel et al., 2016), even under wetter weather conditions.

In Year 2, TWD had a larger LMM coefficient than GRO and MDS for several species. These species include *F. solandri*, *L. menziesii*, *P. totara*, and *P. taxifolia*. Interestingly, all four of these species are indigenous to New Zealand. These results suggest that under drier weather conditions TWD could be used to help explain sap flux density and water use for some New Zealand indigenous species. These species could include those occurring at sites with low soil VWC or high competition for soil water (*F. solandri* and *P. totara*), those with short growing seasons (*L. menziesii*), or those with low rates of growth, shrinkage, or sap flow (*P. taxifolia*). Previous studies on New Zealand native trees have also found increased TWD under drier weather conditions and have suggested that elastic storage associated with TWD may help buffer against drought stress and embolism formation under drought conditions, especially for species with vulnerable xylem (Cranston & Macinnis-Ng, 2025) such as *L. menziesii*.

4.4.3 MDS

In partial support of our hypothesis, MDS had the strongest relationship with sap flux density for most study species compared to GRO and TWD in both study years. The LMM results showed that MDS had the highest overall estimate in both study years. This result likely highlights the controls of both sap flux density and MDS. MDS is a measurement of short-term tissue water deficits and sap flux density is a measurement of the water movement causing tissue water deficits in the stem tissue, both as a result of transpiration (Güney et al., 2019). Therefore, both variables should respond to variables that influence transpiration, including evaporative demand, soil moisture, and stomatal conductance (Güney et al., 2019).

In partial support of our hypothesis, the relationship between MDS and sap flux density was stronger in Year 1 compared to Year 2 for most study species. This finding was likely due to water stress accumulating under the drier weather and soil conditions in Year 2, with reduced stomatal conductance or leaf area causing reductions in the amplitude of fluctuations in tissue water potential during periods of water stress (Will et al., 2013). The Spearman correlation coefficients were moderate to strong for most species in Year 1, and weak or non-significant for most species in Year 2. The LMM results showed that MDS had the highest overall estimate of the three dendrometer

variables in both study years. This result was reflected in the Year 1 species-specific coefficients, whereas the Year 2 species coefficients were more variable.

The direction of the relationship between MDS and sap flux density was generally positive. The Spearman correlations indicated a positive relationship for all study species in both study years. The LMMs indicated a positive overall estimate, and a positive species-specific coefficient for all but one species in both study years. These results suggest that the species-specific positive relationship was not influenced by external drivers and highlight the instantaneous nature of both variables (Güney et al., 2019). These results potentially give more evidence for MDS being a suitable proxy variable for sap flux density.

4.4.4 Species differences

Some of the study species did not follow the general trends for the relationships between the dendrometer variables and sap flux density. These differences were likely driven by differences in size, microsite conditions, and species traits. The species with the strongest correlation between GRO and sap flux density in Year 1 also had relatively short growing seasons (Chapter 2). These species included *F. fusca*, *L. menziesii*, and *S. sempervirens*. This result suggests that for species with short growing seasons, GRO could be used to help explain sap flux density and help predict water use when GRO is not limited by soil water.

One of the exotic conifer species, *P. radiata*, demonstrated a stronger correlation between GRO and sap flux density under the drier weather conditions of Year 2 compared to the wetter weather conditions of Year 1. This result likely reflects the wetter microsite conditions measured for this species, and limitation of GRO in Year 1 due to high soil VWC.

The results for *E. fastigata* could reflect high leaf area, canopy closure, and dry microsite conditions. *Eucalyptus fastigata* demonstrated non-significant Spearman correlation results between GRO and sap flux density in both study years. This result likely reflects both high leaf area and canopy closure. High leaf area likely drove higher transpiration and sap flux density, but canopy closure and dry soil in mid-summer likely limited GRO when sap flux density was highest, resulting in poor correlation. This species also demonstrated a larger LMM coefficient for GRO in Year 1 compared to

both TWD and MDS. This coefficient was negative, potentially giving further evidence for the differing drivers and limitations between GRO and sap flux density for *E. fastigata*, even under wetter conditions like those in Year 1. In contrast, a moderately positive Spearman correlation between TWD and sap flux density in Year 1 suggests soil drying, water deficits, and peak rates of sap flow coincided in that year. In Year 2, *E. fastigata* had a negative LMM coefficient between TWD and sap flux density, suggesting stomatal closure during late summer drought stress in combination with the lack of stem water refilling due to depleted soil VWC (Zweifel et al., 2007).

One of the indigenous conifer species, *P. taxifolia*, consistently demonstrated results that differed from the general trend. For example, *P. taxifolia* was the only species with a negative LMM coefficient for MDS in both study years and demonstrated a stronger correlation between GRO and sap flux density in the drier conditions of Year 2 compared to the wetter conditions of Year 1. These results likely reflect the transitional life stage and could potentially indicate that, at this life stage, our sensors and calculations were not sensitive enough for this species.

4.4.5 Influence of weather and climate

In support of our hypothesis, more sap flux density variation was explained by including climate variables in the LMMs. This result was particularly prominent in Year 2, the drier study year. This result likely reflects the increased transpiration drivers and the increased constraints such as depleting soil VWC. These climate drivers and constraints likely exacerbated differences in the timing of the dendrometer variables compared to sap flux density. It is likely that GRO stopped earlier in the summer than sap flux density due to loss of turgor (Lockhart, 1965). It is also likely that TWD continued after sap flux density reduced due to stomatal closure and drought stress avoidance, due to limited soil VWC for stem refilling (Zweifel et al., 2007). Previous studies have also found weather and climate to affect the relationships between TWD and MDS and sap flux density or sap flow. Donfack et al. (2024) found that under drought conditions, TWD had a non-linear relationship with sap flux density. Tian et al. (2019) found that low air temperature and high cloud cover reduced the correlation strength between TWD and sap flow. Climate and dendrometer variables are likely to be complementary when trying to predict sap flux density. Climate variables including

PET have been proven to drive transpiration (Jarvis & McNaughton, 1986; Monteith, 1995). However, these variables do not describe how individual trees are responding to current climatic conditions. Utilising dendrometer variables in conjunction with climate variables can add valuable information about how each tree or species is responding to the same conditions, for example, continued growth or stomatal closure.

4.4.6 Conclusions

Our results suggest that dendrometer variables could be used to help explain sap flux density and help predict water use. The use of climate variables in conjunction with dendrometer variables would likely provide a more accurate estimate of water use. Of the three dendrometer variables, MDS gave the overall best prediction of sap flux density. However, this result was variable across species. For some of the indigenous species, TWD emerged as a stronger predictor under drier weather conditions.

Our results also highlight the importance of size, species traits, and microsite conditions. For example, the large size, high leaf area, and dry microsite conditions for *E. fastigata* affected the relationships between sap flux density and both TWD and GRO. The wet microsite conditions for *P. radiata* also affected the relationship between sap flux density and GRO.

Together, our results highlight the complex nature of the relationships between growth, shrinkage, transpiration, species traits, microsite conditions, and size. Our results also highlight that electronic point dendrometers could be used as practical alternatives to sap flow meters to give an indication of water status, especially when used in conjunction with climate and soil moisture variables.

4.5 References

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Chapter 5: Synthesis

5.1 Thesis summary

This thesis aimed to measure and compare growth, shrinkage, and sap flow of eight study species, using electronic point dendrometers and heat ratio method sap flow meters. This thesis also aimed to understand the environmental and species-specific drivers of growth and transpiration. Another aim of this thesis was to assess the suitability of electronic point dendrometers as practical alternatives to sap flow meters for measuring estimates of transpiration and giving insight into tree water status. There were three experimental chapters included in this thesis:

Chapter 2: Comparison of growth rate and growing season duration between exotic and indigenous planted trees

Chapter 3: Comparison of sap flow between exotic and indigenous planted trees

Chapter 4: Can electronic point dendrometers be used as accessible alternatives to sap flow meters for estimating transpiration?

Eight study species were selected to cover a range of phylogenetic traits. These species included three exotic species, *Eucalyptus fastigata* (Myrtaceae), *Pinus radiata* (Pinaceae), and *Sequoia sempervirens* (Cupressaceae), and five indigenous species *Fuscospora fusca* (Nothofagaceae), *Fuscospora solandri* (Nothofagaceae), *Lophozonia menziesii* (Nothofagaceae), *Podocarpus totara* (Podocarpaceae), and *Prumnopitys taxifolia* (Podocarpaceae). The indigenous species were selected to represent the dominant families in the two main zonal forest types in New Zealand, southern beech and podocarp broadleaf forest. Our study site, Rewanui Forest Park, in the Wairarapa region, was selected due to the replicated planting design and production forestry management techniques not often found for indigenous species in New Zealand. The major results and findings of the three chapters are presented below.

5.1.1 Chapter 2

The aim of Chapter 2 was to measure and compare growth and shrinkage of our eight study species at our study site. To achieve this, electronic point dendrometers were deployed over a two-year study period. Growth and shrinkage variables were calculated from the raw dendrometer data using the Zweifel et al. (2016) method. The Gompertz equation was used to model the growing season duration for each species in both study years (Tjørve & Tjørve, 2017; Wang et al., 2024), and Generalised Additive

Models were used to examine the relationship between environmental drivers and the three dendrometer-derived response variables.

We hypothesised that there would be higher GRO and MDS and lower TWD for the exotic species compared to the indigenous species, and longer growing seasons for the conifer species compared to the angiosperm species. We also expected that weather conditions would affect our results, including warmer spring air temperatures resulting in earlier growth initiation, and that soil volumetric water content (soil VWC) would have the highest F statistic of the climate variables in the GRO and TWD models and potential evapotranspiration (PET) the highest in the MDS models.

Electronic point dendrometers were an effective tool for studying growth and shrinkage responses to climate and site conditions. There were clear differences between species in their stem growth and shrinkage responses to weather differences between the two study years and to microsite effects (Figure 5.1). Rainfall, soil VWC, and PET were important drivers of differences in growth and shrinkage between study years.

Unexpectedly, only one exotic study species, *S. sempervirens*, exhibited higher GRO and MDS than the indigenous study species (Figure 5.1). The differences in weather conditions between the two study years resulted in low TWD in Year 1, which was wetter, whereas significant TWD developed under the drier weather conditions of Year 2 for all study species. Larger size and more leaf area, although not directly measured, likely resulted in higher TWD for the three exotic species compared to the indigenous species.

Growing season duration was longer in Year 1, which was wetter, compared to Year 2, which was drier (Figure 5.1) for all study species. Across the study species, growing season duration was variable and there was no clear pattern of conifer species demonstrating a longer growing season duration than the angiosperm species. This result highlights the key role of species-specific traits in predicting growth patterns. Average spring air temperature was similar between study years and when compared to climate normal levels, resulting in similar growth initiation timing between the two study years. Consistent with the findings of Bose et al. (2025), the lower rainfall and

soil VWC in the summer of Year 2 resulted in earlier growth cessation for all species compared to Year 1.

The climate variables, rainfall, soil VWC, and PET, were important drivers of the growth and shrinkage variables, GRO, TWD, and MDS, with varying effects in each study year. Rainfall was the key driver of GRO in both study years, reflecting the lack of soil VWC limitation in Year 1 and the importance of periodic rainfall inputs in promoting GRO in Year 2. Rainfall was the key negative driver of TWD in Year 1, reflecting the high water availability limiting TWD. Soil VWC was the key negative driver of TWD in Year 2, reflecting increasing drought stress as the soils dried out in Year 2, which was drier. Previous studies have also found variable drivers of TWD based on climate; these variables include VPD, soil water potential, air temperature, solar radiation, and precipitation depending on climate (e.g. Güney et al., 2020; Oogathoo et al., 2024; Zweifel et al., 2016). Together these results highlight the complex role of climate variables and current weather conditions in predicting TWD. Potential evapotranspiration was the key driver of MDS in both study years, supporting our hypothesis and previous findings linking MDS and transpiration (Zweifel & Häsler, 2000). Included in the PET calculation were air temperature and relative humidity, which are both related to shared drivers between sap flow and MDS in previous studies, including air temperature and VPD (Dong et al., 2019; Güney et al., 2020; Paltineanu et al., 2020).

Chapter 2 contributed to the limited quantitative growth data for New Zealand indigenous species (Upton, 2025) and highlighted the important roles of microsite effects, species traits, weather, and climate in predicting growth rate, growing season duration, and both daily and cumulative water stress. Microsite effects and species differences are discussed in Section 5.3 below.

5.1.2 Chapter 3

The aim of Chapter 3 was to measure and compare sap flow between our study species at our study site. To achieve this, heat ratio method sap flow meters were deployed over a two-year study period. From the raw sap flow data, we calculated sap flow rate, sap flux density, and cumulative water transpired.

We hypothesised that our results would vary across the study species; the exotic species would exhibit higher sap flow rates, cumulative water transpired, and sap flux density compared to the indigenous species. We also hypothesised the exotic angiosperm species would exhibit higher daily mean sap flux density than the exotic conifer species, and the indigenous angiosperm species would exhibit higher daily mean sap flux density than the indigenous conifer species. We hypothesised that the climate variables would explain more sap flux density variation under the wetter weather conditions of Year 1 compared to the drier Year 2. Of the climate variables, PET was hypothesised to be a significant predictor of sap flux density under all weather conditions, whereas rainfall and soil VWC were hypothesised to be significant predictors in Year 2 only.

Heat ratio sap flow meters were effective for estimating transpiration and water status and assessing responses to climate and site conditions. There were clear differences between species in their sap flow responses to weather conditions and microsite effects (Figure 5.1). Rainfall, soil VWC, and PET were important drivers of differences in sap flow between study years.

The three exotic study species generally demonstrated higher sap flow rates and cumulative water transpired but only *E. fastigata* exhibited higher sap flux density compared to the indigenous study species, especially in the wetter time periods (Year 1 and Dry Period 1; Figure 5.1). The sap flow rate and cumulative water transpired results were driven by the larger size of the exotic species, a result also found in previous studies (Butz et al., 2018; Kaptein et al., 2023). The sap flux density results were driven by differences in microsite and species effects, discussed in Section 5.3 below.

Weather variables were important drivers of sap flux density in both study years. However, these relationships were also affected by species traits and microsite conditions. For example, more sap flux density variation was explained by the climate variables in Year 1, which was wetter, indicating that under the drier conditions of Year 2, species traits became more important. Potential evapotranspiration was a significant predictor of sap flux density for all study species in both study years, supporting our hypothesis and previous findings (e.g. Sun et al., 2022). This result also highlights the link between sap flow and transpiration, as transpiration is driven by VPD, which

encapsulates air temperature and relative humidity as in the PET calculation used in this thesis.

The two exotic conifer species, *P. radiata* and *S. sempervirens*, followed the trend of rainfall being a significant predictor of sap flux density in Year 2, which was drier, but not in Year 1, which was wetter. These two species had the highest soil VWC in Year 1. Overall, these results indicate that due to high soil VWC in Year 1, rainfall inputs did not significantly affect sap flux density for these two exotic conifer species. One of the indigenous conifer species, *P. totara*, followed the expected trend of soil VWC being a non-significant predictor of sap flux density in Year 1, which was wetter. Previous studies have found soil VWC to have a strong effect on transpiration even under wetter weather conditions (Fang et al., 2024). Interestingly, rainfall was not a significant predictor of sap flux density in either study year for *L. menziesii* and *P. totara*, highlighting the role of microsite effects.

Previously, sap flow measurements for New Zealand indigenous species have been limited to dominant trees within old growth forests (Barbour et al., 2005; Bowman et al., 2005; Cranston, 2022; Kostner et al., 1992; Zhao et al., 2020). Chapter 3 contributes to the limited sap flow data available for indigenous species and highlights the role of stem size, leaf area, microsite effects, and species traits in predicting water use.

5.1.3 Chapter 4

The aim of Chapter 4 was to test whether electronic point dendrometers could be used as a more practical alternative to the commonly used sap flow meters for estimating transpiration and water use. This was achieved by utilising the dendrometer data from Chapter 2 and the sap flow data from Chapter 3. Linear mixed effects models were used to test the relationships between dendrometer variables, GRO, TWD, and MDS, and sap flux density, as well as the influence of species on this relationship.

Electronic point dendrometers showed promise as practical alternatives to sap flow meters for estimating transpiration and giving insight into tree water status. There were clear differences between species in the relationships between the dendrometer variables and sap flux density. Weather conditions and climate variables (rainfall, soil VWC, and PET) aided in further understanding these relationships.

The strength of the relationship between sap flux density and each of GRO, TWD, and MDS was variable and affected by weather conditions. GRO had a weaker relationship with sap flux density than MDS in both study years for most of the study species, highlighting the links between MDS, sap flux density, and transpiration. Under the wetter conditions of Year 1, GRO had a stronger relationship with sap flux density compared to TWD for most species, a result not reflected in Year 2, which was drier. This result reflects positive turgor pressure in Year 1 promoting GRO, and reduced soil VWC in Year 2 inhibiting GRO. The wetter conditions in Year 1 resulted in high soil VWC reducing the development of TWD, a result reflected in increased predictive power for TWD in the drier Year 2 compared to Year 1, supporting our hypothesis. The drier conditions in Year 2, including seasonal soil drying in the warmer months, resulted in the development of greater TWD.

Maximum daily shrinkage had the strongest relationships with sap flux density for most of the study species in both study years compared to GRO and TWD. The relationship between MDS and sap flux density was stronger for most study species in Year 1 compared to Year 2. However, for most of the indigenous species (*F. solandri*, *L. menziesii*, *P. totara*, and *P. taxifolia*), TWD emerged as the strongest predictor of sap flux density under the drier conditions of Year 2. Taken together, these results show that, of the dendrometer variables, MDS is the best at predicting sap flux density for most of our study species due to the shared drivers, such as PET, and links with transpiration. However, under drier conditions, TWD is likely to be a better predictor for some species, including *F. solandri*, *L. menziesii*, *P. totara*, and *P. taxifolia*, which had differing limitations generally linked with water availability. *Fuscospora solandri* had low soil VWC, *L. menziesii* demonstrated a short growing season and occurs naturally in high rainfall locations, *P. totara* was limited by high competition for soil water, and *P. taxifolia* was transitioning from an early divaricating life stage. These results are in partial contrast with international studies that found TWD had a stronger relationship with sap flux density under most weather conditions (Tian et al., 2019) and that TWD does not have a strong relationship with sap flow under drought conditions (Donfack et al., 2024).

Including climate variables in the LMMs resulted in higher R^2 and lower AIC, compared to the models with dendrometer variables only. This result suggests that climate

variables, such as rainfall, soil VWC, and PET, can improve the prediction of tree water status and transpiration. Improvement of R^2 was only marginal in Year 1 but substantial in Year 2, reflecting increased atmospheric demand and soil water constraints in Year 2 driving higher transpiration and subsequently sap flux density. This disparity in R^2 improvement between study years highlights the importance of including climate variables when weather conditions are drier. Including more variables in a statistical model will inherently affect model fit metrics such as R^2 and AIC. However, our results show that the relationships between sap flux density and the dendrometer variables are weather dependent and including climate variables under drier weather conditions can improve prediction strength. Including both dendrometer and climate variables can give valuable insight into tree-level transpiration and water status and responses to the environment. Climate variables represent external drivers of transpiration, whereas dendrometer variables reflect tree-level responses to those drivers. Evaluating dendrometer variables in the first instance will give an understanding of internal constraints on sap flow that are likely to be variable from tree to tree; evaluating climate variables subsequently will give an understanding of external demand and constraints which will become more important under drier conditions.

Despite being widely accepted as the current best method for measuring estimates of transpiration, sap flow meters are prone to errors (Flo et al., 2019) and are known to be difficult to install and maintain. The sap flow meters used in this thesis required significant solar panel infrastructure which increased the cost. Installation of the solar panels was difficult due to the remote location and access difficulties of our study site. The need for solar panels also resulted in large lengths of cable being used which had to be buried and checked regularly for damage from rodents and ungulates present at the site. The high cost of the devices reduced the amount of possible replication at our study site to compensate for any measurement and installation errors. Our sap flow meters could not be connected to a cell-phone network, meaning that data had to be manually downloaded and device status could not be assessed remotely. Installation and maintenance were difficult due to the delicate nature of the probes and issues with drill bits not fitting into drills with high enough power and long enough charge. The sap flow meters required re-installation several times across the study period due to the stems growing around the probes and device failure. In comparison, re-setting

the dendrometer devices only required the unscrewing of wingnuts, the internal batteries did not require power from solar panels, the devices were less prone to failure, and device status could be assessed remotely.

There have been few studies assessing the use of electronic point dendrometers as cost-effective alternatives to sap flow meters in estimating water status and transpiration (e.g. Biel et al., 2012; Conejero et al., 2007; Donfack et al., 2024; Tian et al., 2019). The results from Chapter 4 contribute to this small pool of knowledge and further highlight the complex nature of species traits and the influence of climate. Our results show that when used in conjunction with meteorological measurements, dendrometers are a practical alternative to sap flow meters for estimating transpiration and water status. This finding along with the installation, maintenance, infrastructure, remote connectivity, and cost benefits demonstrates the possibilities of utilising dendrometers for large-scale projects with remote site locations and a need for near real-time monitoring. Overall, MDS in conjunction with climate variables emerged as the best predictor of water status and transpiration, especially under wetter weather conditions. Under drier weather conditions, TWD emerged as the best proxy for some of our study species. It is possible that after further testing and development, TWD could emerge as the overall best dendrometer variable for predicting transpiration and tree water status under drier weather conditions. Further testing and development of TWD should include the complete separation of GRO and TWD (Zweifel et al., 2016), and direct tests of what TWD is actually measuring. These results also highlight the need for selecting the right variables and methods for each species based on species traits and microsite conditions.

5.2 Limitations

Rewanui Forest Park was selected for our study as it is one of the few available sites in New Zealand with a range of indigenous species planted in a replicated design utilising plantation management techniques. However, the site proved quite challenging, with access complicated by distance from the University, high rainfall, poor condition of access tracks, and erosion of the tracks during the study period. Electronic point dendrometers and heat ratio method sap flow meters were effective for measuring and assessing the growth, shrinkage, and sap flow dynamics for our study as they allowed

for unattended monitoring. Additional measurements, such as photosynthesis, stomatal conductance, water potentials, water use efficiency, leaf area, and drought tolerance (e.g. P_{50}), would have aided in our understanding of the growth and water use dynamics of our study species. However, the site's remoteness and difficult access prevented more regular measurements and the use of bulky portable equipment. As the study progressed it was also noted that microsite differences, particularly differences in soil depth and soil moisture, were having significant effects on tree responses. These differences appeared to be related to differences in the topographic position of the various species plots. The limited replication of plots for some species meant that it was challenging to separate plot effects from species effects. Rewanui Forest Park is a rare example of a forestry trial including both indigenous and exotic tree species. More trial sites at a wide range of locations and age classes are needed to develop a more diversified and sustainable forestry sector. A more diversified forestry sector could include a range of indigenous and exotic species that could be used for a variety of purposes.

5.3 Implications

There were clear differences in results across the study species. These were driven by differences in size, leaf area, species traits, and microsite conditions. Weather also affected the results for all study species; for example, all species had a longer growing season duration in Year 1, which was wetter, compared to Year 2, which was drier (Figure 5.1). These varied results highlight the importance of species selection for achieving afforestation project goals and for achieving goals at each planting site. Project goals could include erosion control, carbon sequestration, increasing biodiversity, or wood production. Afforestation projects could have short-term (e.g. up to 25 years), medium-term (e.g. between 25 and 75 years), or long-term (e.g. more than 75 years) goals.

5.3.1 Implications for exotic species

All three of the exotic study species had larger stem diameters at the start of the study period compared to the indigenous study species despite being planted at about the same time. Their faster growth suggests that the exotic species are better suited to projects with short-term goals. The exotic species generally demonstrated higher

growth, shrinkage, and sap flow rates compared to the indigenous species, with a few exceptions, further highlighting the importance of species selection for afforestation projects.

Eucalyptus fastigata had the second largest diameter of the study species at the start of the study period. Canopy closure and dry microsite conditions affected the results for this species. Canopy closure limited GRO. Dry microsite conditions resulted in higher TWD compared to the other study species. Large leaf area resulted in high sap flow, including high sap flux density and cumulative water transpired. *Eucalyptus fastigata* also demonstrated a long growing season, especially in Year 1, suggesting that this species can grow nearly year-round at our study site. Together, these results indicate that *E. fastigata* can successfully reach canopy closure at water-limited sites. However, for projects where high water use is of concern, *E. fastigata* may not be the most suitable option. Our results suggest that *E. fastigata* will be a suitable candidate for projects with short-term goals such as erosion control, carbon sequestration, or wood production.

Pinus radiata had the largest stem diameter at the start of the study period compared to the other species. This large stem size supported high sap flow including sap flow rate and cumulative water transpired. Wet microsite conditions limited GRO for this species. *Pinus radiata*, like *E. fastigata*, had a longer growing season, especially in Year 1, with growth continuing nearly year-round. Collectively, these results indicate that when the project goals require *P. radiata* to reach its full growing potential, a drier site than ours will be advantageous. These results also indicate that *P. radiata* will be a suitable candidate for projects with short-term goals such as erosion control, carbon sequestration, or wood production.

Sequoia sempervirens had the smallest stem diameter at the start of the study period of the exotic species. This species also demonstrated higher rates of all the dendrometer and sap flow variables compared to most of the indigenous species in both study years. However, *S. sempervirens* demonstrated a moderate growing season duration in Year 1 and a shorter growing season duration in Year 2 compared to the other study species. This result suggests some climate sensitivity and could be due to the differences in climate between the natural range for this species and our study site.

Together our results suggest that *S. sempervirens* would be a suitable candidate for projects with both short-term and long-term goals such as erosion control, carbon sequestration, or wood production. *Sequoia sempervirens* would also be suitable for planting at wetter sites; this would increase growing season duration, improve overall growth performance, and account for any lack of the high humidity and summer fog that occurs in this species' natural range.

5.3.2 Implications for indigenous species

The three indigenous angiosperm species were selected for this thesis to represent the dominant families from one of the two main zonal forest types in New Zealand, southern beech forest. *Fuscospora fusca* demonstrated high GRO and sap flux density compared to the other indigenous species. However, this species demonstrated a short growing season, particularly in Year 2, low cumulative water transpired and low shrinkage, relative to the other study species. Collectively these results suggest high climate sensitivity and high instantaneous GRO and sap flux density in response to increased water availability. Our results suggest that *F. fusca* is not likely to be as successful as a more drought-tolerant species at a water-limited site. Our results also suggest that due to the short growing season and relatively low cumulative water transpired, this species could be a suitable candidate for projects where late summer water use is of concern. However, this would need to be balanced with the drought tolerance of *F. fusca* to ensure survival and allow the individual trees to reach their growing potential. *Fuscospora fusca* will be an ideal candidate for projects with long-term goals including carbon sequestration and increasing biodiversity. The high instantaneous growth rate of *F. fusca* and highly stable timber make this species a contender as being a popular timber species, especially in regions that are less prone to drought.

Fuscospora solandri had the largest stem diameter at the start of the study period of the indigenous species and demonstrated unique traits compared to the other two indigenous angiosperm species, namely a long growing season and higher cumulative water transpired. These results suggest that *F. solandri* does not exhibit high instantaneous growth or transpiration but grows and uses water at a more consistent rate across a longer time period. Our results suggest that *F. solandri* would be a

suitable candidate for planting sites where high water use over short periods of time is of concern and for long-term projects targeting biodiversity and carbon sequestration goals. *Fuscospora solandri* could be a popular timber species in regions with naturally fewer indigenous conifers due to the high durability and ability to continue growth under drier weather conditions.

Lophozonia menziesii had the smallest stem diameter at the start of the study period compared to all other study species. This indigenous angiosperm appeared to be the most weather and climate sensitive of the study species, demonstrating the shortest growing season duration and low species rankings for all the dendrometer and sap flow variables in Year 2, which was drier. The short growing season was also reflected in the low cumulative water transpired species ranking in Year 1. Similar to *F. fusca*, *L. menziesii* may be a suitable candidate for projects where late summer water use is of concern so long as the planting site is not drought prone to keep within this species' natural high rainfall climate distribution. This species will also be a suitable candidate for projects with long-term goals for carbon sequestration and increasing biodiversity. *Lophozonia menziesii* has the potential to be a key timber species for indoor applications in regions with high rainfall, due to the consistent high quality but low durability timber.

The two indigenous conifer species were selected to represent the co-dominant species in one of the two main zonal forest types in New Zealand, podocarp broadleaf forest. *Podocarpus totara* had the second smallest starting diameter of the study species and generally ranked low to moderate in the dendrometer and sap flow species rankings, including GRO and cumulative water transpired. In the Year 2 species rankings for TWD, *P. totara* ranked moderately. This result likely reflects the high planting density which increased intraspecific competition for water. This species also demonstrated a relatively long growing season duration in both study years. Taken together, these results indicate that *P. totara* will be a suitable candidate for drier sites where high water use is of concern. This species will also be a suitable candidate for projects with longer-term goals for carbon sequestration and increasing biodiversity. *Podocarpus totara* should be a key indigenous timber species due to its high quality and durable timber, ability to tolerate a range of site conditions, wide range of historic uses, and relatively low water use.

Prumnopitys taxifolia had the second largest stem diameter at the start of the study period compared to the other indigenous species. This species generally ranked the lowest for most of the dendrometer and sap flow variables and had a relatively moderate growing season duration. Together, our results indicated that *P. taxifolia* would be a suitable candidate for planting sites where high water use is of concern and for afforestation projects with long-term goals for carbon sequestration and increasing biodiversity. It is unlikely that *P. taxifolia* can be a key timber species due to slow growth rates and low durability; however, excellent stability and hardness, low water use, and high cultural value mean this species should be considered a minor timber species especially at sites where high water use is of concern.

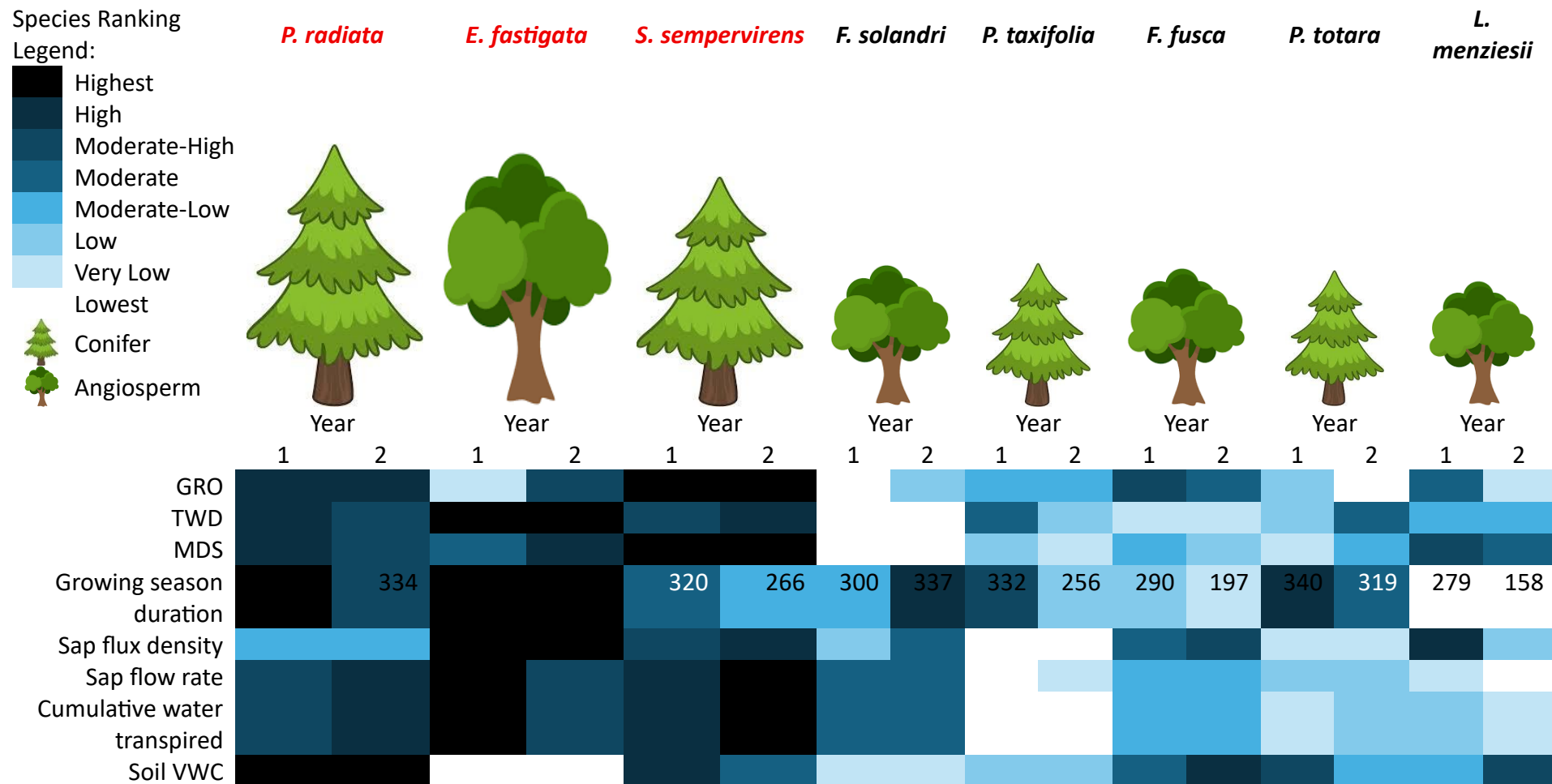


Figure 5.1: Summary of the Year 1 and Year 2 results including species rankings for irreversible growth (GRO), tree water deficit (TWD), maximum daily shrinkage (MDS), growing season duration (days), sap flux density, sap flow rate, cumulative water transpired, and soil volumetric water content (soil VWC). Species rankings are represented using a common colour scale across all variables, with darker colours indicating higher rankings. Order of species from left to right is based on stem diameter, with larger trees to the left of the graphic. Exotic species indicated in red font.

5.3.3 Implications for angiosperm and conifer species

Due to differences in hydraulic architecture, angiosperm species can have higher hydraulic conductivity than conifer species (Hacke & Sperry, 2001). Our results indicated that the exotic angiosperm species, *E. fastigata*, could have higher hydraulic conductance than the exotic conifer species, *P. radiata* and *S. sempervirens*. *Eucalyptus fastigata* demonstrated higher mean sap flux density and higher cumulative water transpired in the wetter time periods than the exotic conifer species. Aside from higher daily mean sap flux density in Year 2, these results were not reflected in the drier time periods. These drier time period results were likely more of a reflection of low soil VWC as opposed to lower hydraulic conductance, a theory potentially supported by soil VWC being a stronger predictor of sap flux density for *E. fastigata* than PET. The indigenous angiosperm species, *F. fusca*, *F. solandri*, and *L. menziesii* could have higher hydraulic conductance than the indigenous conifer species, *P. totara* and *P. taxifolia*. The indigenous angiosperm species generally ranked higher in daily mean sap flux density and cumulative water transpired than the indigenous conifer species. For *F. fusca* and *L. menziesii*, these results were not reflected at the dry period level (January through March), likely reflecting climate sensitivity and stomatal behaviour. One of the indigenous conifer species, *P. taxifolia*, likely had the lowest hydraulic conductance of the indigenous species, consistently ranking low in sap flux density and cumulative water transpired, and weak coupling with PET. Together, these results potentially indicate that within the exotic and indigenous groups, the angiosperm species could have higher hydraulic conductivity, as well as the complex influence of microsite and weather conditions.

5.3.4 Implications for forest hydrology

Our results demonstrate the benefits of measuring estimates of transpiration as opposed to inferring plant water use in traditional catchment water balance methods (e.g. Duncan, 1995). The study species demonstrated variable results despite being planted at the same time and at the same site. Microsite conditions were variable across study species, with a range of soil VWC levels, planting densities, soil depths, and positions on the slope. These conditions interacted with species traits to affect our results. For example, due to differences in size, leaf area, and water use strategies, low

soil VWC was not associated with low transpiration or cumulative water use at our study site. The exotic study species demonstrated higher transpiration and cumulative water use due to faster early growth rates and large stem sizes and leaf area than the indigenous species. Together, our results highlight the importance of species traits and microsite conditions in predicting tree water use as well as the complex interplay between all variables. Measuring estimates of transpiration directly gives a clearer understanding of species effects on the hydrology of a particular catchment.

5.3.5 Implications for afforestation

Our results highlighted the differences in growth and water use between the study species and have implications for both new and existing forests. The exotic study species grew faster between planting and the study period (Figure 5.1); therefore, the exotic species will be favourable when short-term productivity is the goal. The exotic study species also demonstrated higher cumulative water use compared to the indigenous study species. In this thesis, size and leaf area were discussed as being key drivers of higher water use for the exotic species. However, our study was comparing indigenous and exotic species planted at the same time and not indigenous and exotic species of the same size. This leaves room to question whether the exotic species use more water across their lifetime compared to the indigenous species and if this result will change once the indigenous species reach similar stem sizes to the exotic species. There is potential for indigenous species to be more efficient in their water use over their much longer life cycles and demonstrate lower peaks of water use even after canopy closure compared to exotic species. Regardless of these currently unanswered questions, when effects on local hydrology such as reduced streamflow are of concern, the indigenous species will be favourable. This is due to slower growth rates resulting in slower increases in water loss from the hydrological cycle through ET. However, the slower growth rates and limited quantitative growth and water use data for the indigenous species present challenges for their use in afforestation projects. Indigenous species are currently considered not economically viable for timber and carbon sequestration objectives. Establishment is also difficult and expensive due to competition with weeds as a result of slow early growth and the need for high planting densities or the use of nurse crops (Rolando et al., 2025). Regardless of the current

views and lack of data, indigenous tree species can add value in a range of afforestation projects due to their high-quality timber, cultural and ecological value, lower total water use, and longer life span. Indigenous species afforestation projects could include the retirement of unproductive land, small-scale timber production, and planting to increase biodiversity and reintroduce locally extinct species both in new and existing forests, especially on land where the impacts on local hydrology are of concern. These implications for afforestation, together, exemplify the debate on the effects of indigenous versus exotic species on catchment hydrology (e.g. Lima et al., 1990; Little et al., 2009; White et al., 2021), the importance of selecting the best species for each project, and the need for more investment in future research.

5.4 Future work

Establishment of more forestry trial sites similar to Rewanui Forest Park in New Zealand.

There is a lack of quantitative data on growth, shrinkage, and water use for New Zealand indigenous species and an urgent need for more investment in research on alternative species for afforestation, particularly indigenous species (Upton, 2025).

There is also an urgent need for more data on the performance and environmental impact of indigenous species, especially in comparison with exotic plantation species. Rewanui Forest Park is a rare example of a range of indigenous species being planted in a forestry trial setting with replication. To gain a better understanding of performance and environmental impact, there is a need for investment in replicated planting trials at multiple locations across the country. There is also a need for within-site replication for each species, to cover any site-related covariates such as soil depth, slope, and aspect.

Establishment of a growth and water use sensor network in New Zealand.

In the northern hemisphere, networks of sensors for monitoring growth and water use dynamics in near real time have been established (e.g. Zweifel et al., 2021). For example, the TreeNet network utilises point dendrometers and microclimate measurements as indicators of growth performance and drought stress (Zweifel et al., 2021). In New Zealand, the Forest Flows programme implemented the first large-scale network of forest hydrology sensors, including point dendrometers and sap flow meters, for near real-time monitoring in the country (Meason et al., 2020). However,

the programme was largely limited to *P. radiata*. Expanding the Forest Flows network in conjunction with the establishment of forestry trial sites similar to Rewanui Forest Park would allow for near real-time monitoring and easier communication of results with key stakeholders.

How do our indigenous and exotic study species compare when at the same life stage?

The results from our study demonstrated that, when planted at the same time, our exotic study species will grow to larger stem sizes faster than our indigenous study species, resulting in higher total water use. Future research could take growth and sap flow measurements when our study species are at comparable stem sizes, meaning that the trees would have to have been planted at different times. This would give a better understanding of growth and water use at comparable life stages.

*Were our measurements and calculations sensitive enough for *P. taxifolia*?*

One of our study species, *P. taxifolia*, was transitioning from a divaricating life stage during our study period. It is possible that our measurements were not sensitive enough for this species. Future research could test different device calibration or methods such as external heat pulse sap flow meters to gain a better understanding of growth and sap flow for *P. taxifolia* at this transitional life stage.

Do electronic point dendrometer measurements directly on the sapwood improve correlation strength between dendrometer variables and sap flux density?

Dendrometers measure the cumulative effect of multiple processes including xylem and phloem transport, as well as tissues with differing elastic properties, sapwood and bark (Steppe et al., 2015). Future work could install electronic point dendrometers directly on the sapwood (e.g. Oberhuber et al., 2023) to give a closer estimate of transpiration to that recorded by sap flow meters.

Are daily oscillations in raw electronic point dendrometer data due to device malfunctions or are they a quirk of the New Zealand climate?

Electronic point dendrometer data from several of the study trees were excluded from analysis due to unexplained daily oscillations in the raw dendrometer data. Future research could assess these daily oscillations to confirm if they are due to sensor

malfunctions or if they are due to the unique growth and shrinkage behaviour of our study species or because of the New Zealand climate.

Can MDS and TWD be used as a proxy for sap flux density for other New Zealand indigenous species?

Our results suggested that MDS was the best overall dendrometer variable for predicting transpiration and water status. However, for many of the indigenous species, TWD emerged as the best variable under drier weather conditions. Future research could test these results on a wider range of indigenous species as well as our study species at a range of study sites with differing climate including rainfall, soil properties, and elevation, to determine if this result was due to microsite conditions or is a result common to New Zealand indigenous species.

Are other dendrometer variables suitable for our indigenous species?

Novel uses for dendrometers are being explored. For example, normalised TWD could be a valuable in situ drought stress indicator as opposed to ex situ laboratory methods such as turgor loss point and xylem vulnerability (P_{50} ; Peters et al., 2025). Novel approaches like this have the potential to give a better understanding of the dynamic responses of plants to the environment. When used in conjunction with a network of sensors, this could also be done in near real-time. Tree water deficit emerged as a strong predictor of water status for most of our indigenous study species under drier weather conditions. Normalised TWD could be tested on our indigenous species to determine if this variable is a suitable predictor of drought stress or if differing standardisation is required across differing families.

5.5 Concluding comments

This thesis strongly indicated that, when planted at the same time, exotic tree species including *E. fastigata*, *P. radiata*, and *S. sempervirens* will grow faster and use more water than indigenous tree species including *F. fusca*, *F. solandri*, *L. menziesii*, *P. totara*, and *P. taxifolia*, approximately 15 years after planting. It also revealed that when used in conjunction with climate variables, MDS and, for some species, TWD may be used as a proxy measure for sap flux density to estimate water status and transpiration, making electronic point dendrometers an accessible alternative to sap flow meters. Future

research can help determine differences in growth, shrinkage, and sap flow of our study species when at similar life stages as well as their responses to differing planting sites and management techniques.

5.6 References

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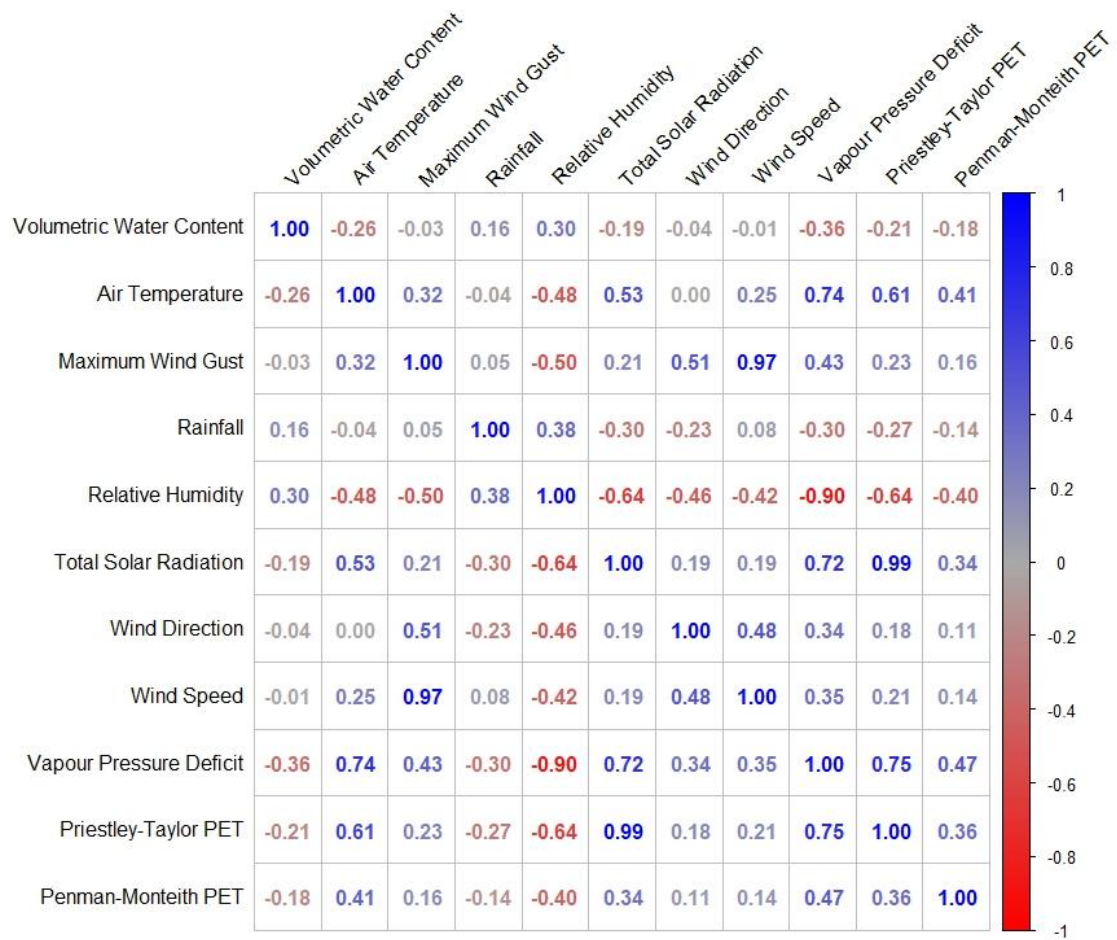
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Appendix A: Correlation matrix used for determining which climate variables were used in the statistical analyses for Chapters 2, 3, and 4.



Appendix B: Estimated marginal means of irreversible growth in Year 1 (Chapter 2), derived from generalised additive models, with Tukey-adjusted pairwise comparisons among study species.

Contrast	Estimate	SE	df	T	p
<i>P. radiata</i> – <i>E. fastigata</i>	0.50	0.023	20899	22.42	<0.01
<i>P. radiata</i> – <i>F. fusca</i>	0.18	0.030	20899	5.93	<0.01
<i>P. radiata</i> – <i>F. solandri</i>	0.60	0.024	20899	24.45	<0.01
<i>P. radiata</i> – <i>L. menzeisii</i>	0.38	0.027	20899	13.93	<0.01
<i>P. radiata</i> – <i>P. totara</i>	0.49	0.022	20899	22.21	<0.01
<i>P. radiata</i> – <i>P. taxifolia</i>	0.46	0.023	20899	19.75	<0.01
<i>P. radiata</i> – <i>S. sempervirens</i>	-0.76	0.019	20899	-40.17	<0.01
<i>E. fastigata</i> - <i>F. fusca</i>	-0.32	0.031	20899	-10.53	<0.01
<i>E. fastigata</i> - <i>F. solandri</i>	0.09	0.022	20899	4.18	<0.01
<i>E. fastigata</i> - <i>L. menzeisii</i>	-0.13	0.027	20899	-4.67	<0.01
<i>E. fastigata</i> - <i>P. totara</i>	-0.01	0.023	20899	-0.57	1.00
<i>E. fastigata</i> - <i>P. taxifolia</i>	-0.05	0.023	20899	-2.09	0.42
<i>E. fastigata</i> - <i>S. sempervirens</i>	-1.27	0.023	20899	-56.37	<0.01
<i>F. fusca</i> - <i>F. solandri</i>	0.42	0.032	20899	12.85	<0.01
<i>F. fusca</i> - <i>L. menzeisii</i>	0.20	0.035	20899	5.72	<0.01
<i>F. fusca</i> - <i>P. totara</i>	0.31	0.031	20899	9.91	<0.01
<i>F. fusca</i> - <i>P. taxifolia</i>	0.28	0.031	20899	8.82	<0.01
<i>F. fusca</i> - <i>S. sempervirens</i>	-0.94	0.031	20899	-30.51	<0.01
<i>F. solandri</i> - <i>L. menzeisii</i>	-0.22	0.029	20899	-7.58	<0.01
<i>F. solandri</i> - <i>P. totara</i>	-0.11	0.025	20899	-4.18	<0.01
<i>F. solandri</i> - <i>P. taxifolia</i>	-0.14	0.025	20899	-5.69	<0.01
<i>F. solandri</i> - <i>S. sempervirens</i>	-1.36	0.024	20899	-56.11	<0.01
<i>L. menzeisii</i> - <i>P. totara</i>	0.11	0.028	20899	4.05	<0.01
<i>L. menzeisii</i> - <i>P. taxifolia</i>	0.08	0.028	20899	2.85	0.08
<i>L. menzeisii</i> - <i>S. sempervirens</i>	-1.14	0.028	20899	-41.40	<0.01
<i>P. totara</i> - <i>P. taxifolia</i>	-0.03	0.024	20899	-1.42	0.85
<i>P. totara</i> - <i>S. sempervirens</i>	-1.25	0.023	20899	-55.69	<0.01
<i>P. taxifolia</i> - <i>S. sempervirens</i>	-1.22	0.024	20899	-51.78	<0.01

Appendix C: Estimated marginal means of irreversible growth in Year 2 (Chapter 2), derived from generalised additive models, with Tukey-adjusted pairwise comparisons among study species.

Contrast	Estimate	SE	df	T	p
<i>P. radiata</i> – <i>E. fastigata</i>	0.10	0.024	18460	4.41	<0.01
<i>P. radiata</i> – <i>F. fusca</i>	0.19	0.036	18460	5.37	<0.01
<i>P. radiata</i> – <i>F. solandri</i>	0.30	0.025	18460	11.76	<0.01
<i>P. radiata</i> – <i>L. menzeisii</i>	0.32	0.031	18460	10.38	<0.01
<i>P. radiata</i> – <i>P. totara</i>	0.34	0.023	18460	14.50	<0.01
<i>P. radiata</i> – <i>P. taxifolia</i>	0.27	0.028	18460	9.71	<0.01
<i>P. radiata</i> – <i>S. sempervirens</i>	-0.43	0.021	18460	-20.18	<0.01
<i>E. fastigata</i> - <i>F. fusca</i>	0.09	0.038	18460	2.33	0.28
<i>E. fastigata</i> - <i>F. solandri</i>	0.19	0.026	18460	7.38	<0.01
<i>E. fastigata</i> - <i>L. menzeisii</i>	0.21	0.033	18460	6.61	<0.01
<i>E. fastigata</i> - <i>P. totara</i>	0.23	0.025	18460	9.21	<0.01
<i>E. fastigata</i> - <i>P. taxifolia</i>	0.17	0.030	18460	5.63	<0.01
<i>E. fastigata</i> - <i>S. sempervirens</i>	-0.54	0.024	18460	-22.13	<0.01
<i>F. fusca</i> - <i>F. solandri</i>	0.11	0.038	18460	2.78	0.1
<i>F. fusca</i> - <i>L. menzeisii</i>	0.13	0.042	18460	3.04	0.05
<i>F. fusca</i> - <i>P. totara</i>	0.15	0.037	18460	3.96	<0.01
<i>F. fusca</i> - <i>P. taxifolia</i>	0.08	0.040	18460	2.05	0.45
<i>F. fusca</i> - <i>S. sempervirens</i>	-0.62	0.036	18460	-17.22	<0.01
<i>F. solandri</i> - <i>L. menzeisii</i>	0.02	0.034	18460	0.62	1
<i>F. solandri</i> - <i>P. totara</i>	0.04	0.027	18460	1.48	0.82
<i>F. solandri</i> - <i>P. taxifolia</i>	-0.02	0.031	18460	-0.78	1
<i>F. solandri</i> - <i>S. sempervirens</i>	-0.73	0.026	18460	-28.33	<0.01
<i>L. menzeisii</i> - <i>P. totara</i>	0.02	0.032	18460	0.59	1
<i>L. menzeisii</i> - <i>P. taxifolia</i>	-0.05	0.036	18460	-1.27	0.91
<i>L. menzeisii</i> - <i>S. sempervirens</i>	-0.75	0.031	18460	-23.92	<0.01
<i>P. totara</i> - <i>P. taxifolia</i>	-0.06	0.030	18460	-2.16	0.38
<i>P. totara</i> - <i>S. sempervirens</i>	-0.77	0.024	18460	-32.20	<0.01
<i>P. taxifolia</i> - <i>S. sempervirens</i>	-0.71	0.029	18460	-24.32	<0.01

Appendix D: Estimated marginal means of tree water deficit in Year 1 (Chapter 2), derived from generalised additive models, with Tukey-adjusted pairwise comparisons among study species.

Contrast	Estimate	SE	df	T	p
<i>P. radiata</i> – <i>E. fastigata</i>	-0.28	0.024	20900	-11.53	<0.01
<i>P. radiata</i> – <i>F. fusca</i>	0.76	0.033	20900	23.18	<0.01
<i>P. radiata</i> – <i>F. solandri</i>	0.82	0.026	20900	31.27	<0.01
<i>P. radiata</i> – <i>L. menzeisii</i>	0.62	0.029	20900	21.20	<0.01
<i>P. radiata</i> – <i>P. totara</i>	0.63	0.024	20900	26.34	<0.01
<i>P. radiata</i> – <i>P. taxifolia</i>	0.56	0.025	20900	22.16	<0.01
<i>P. radiata</i> – <i>S. sempervirens</i>	0.56	0.021	20900	27.21	<0.01
<i>E. fastigata</i> - <i>F. fusca</i>	1.04	0.033	20900	31.44	<0.01
<i>E. fastigata</i> - <i>F. solandri</i>	1.10	0.024	20900	46.23	<0.01
<i>E. fastigata</i> - <i>L. menzeisii</i>	0.90	0.029	20900	31.02	<0.01
<i>E. fastigata</i> - <i>P. totara</i>	0.91	0.025	20900	36.63	<0.01
<i>E. fastigata</i> - <i>P. taxifolia</i>	0.84	0.024	20900	34.50	<0.01
<i>E. fastigata</i> - <i>S. sempervirens</i>	0.84	0.024	20900	34.51	<0.01
<i>F. fusca</i> - <i>F. solandri</i>	0.06	0.035	20900	1.76	0.65
<i>F. fusca</i> - <i>L. menzeisii</i>	-0.14	0.037	20900	-3.75	<0.01
<i>F. fusca</i> - <i>P. totara</i>	-0.13	0.034	20900	-3.89	<0.01
<i>F. fusca</i> - <i>P. taxifolia</i>	-0.21	0.034	20900	-6.11	<0.01
<i>F. fusca</i> - <i>S. sempervirens</i>	-0.20	0.033	20900	-6.13	<0.01
<i>F. solandri</i> - <i>L. menzeisii</i>	-0.20	0.031	20900	-6.45	<0.01
<i>F. solandri</i> - <i>P. totara</i>	-0.19	0.027	20900	-7.07	<0.01
<i>F. solandri</i> - <i>P. taxifolia</i>	-0.27	0.026	20900	-10.14	<0.01
<i>F. solandri</i> - <i>S. sempervirens</i>	-0.27	0.026	20900	-10.18	<0.01
<i>L. menzeisii</i> - <i>P. totara</i>	0.01	0.030	20900	0.27	1.00
<i>L. menzeisii</i> - <i>P. taxifolia</i>	-0.07	0.030	20900	-2.24	0.33
<i>L. menzeisii</i> - <i>S. sempervirens</i>	-0.06	0.030	20900	-2.18	0.36
<i>P. totara</i> - <i>P. taxifolia</i>	-0.08	0.026	20900	-2.92	0.07
<i>P. totara</i> - <i>S. sempervirens</i>	-0.07	0.024	20900	-3.00	0.05
<i>P. taxifolia</i> - <i>S. sempervirens</i>	0.00	0.026	20900	0.09	1.00

Appendix E: Estimated marginal means of tree water deficit in Year 2 (Chapter 2), derived from generalised additive models, with Tukey-adjusted pairwise comparisons among study species.

Contrast	Estimate	SE	df	T	p
<i>P. radiata</i> – <i>E. fastigata</i>	-0.42	0.021	18461	-19.72	<0.01
<i>P. radiata</i> – <i>F. fusca</i>	0.46	0.032	18461	14.36	<0.01
<i>P. radiata</i> – <i>F. solandri</i>	0.82	0.023	18461	35.60	<0.01
<i>P. radiata</i> – <i>L. menzeisii</i>	0.41	0.028	18461	14.78	<0.01
<i>P. radiata</i> – <i>P. totara</i>	0.22	0.021	18461	10.24	<0.01
<i>P. radiata</i> – <i>P. taxifolia</i>	0.42	0.026	18461	16.54	<0.01
<i>P. radiata</i> – <i>S. sempervirens</i>	-0.01	0.019	18461	-0.70	1.00
<i>E. fastigata</i> - <i>F. fusca</i>	0.89	0.034	18461	26.22	<0.01
<i>E. fastigata</i> - <i>F. solandri</i>	1.24	0.024	18461	52.25	<0.01
<i>E. fastigata</i> - <i>L. menzeisii</i>	0.83	0.029	18461	28.44	<0.01
<i>E. fastigata</i> - <i>P. totara</i>	0.64	0.023	18461	27.93	<0.01
<i>E. fastigata</i> - <i>P. taxifolia</i>	0.84	0.027	18461	31.10	<0.01
<i>E. fastigata</i> - <i>S. sempervirens</i>	0.41	0.022	18461	18.77	<0.01
<i>F. fusca</i> - <i>F. solandri</i>	0.35	0.035	18461	10.17	<0.01
<i>F. fusca</i> - <i>L. menzeisii</i>	-0.05	0.038	18461	-1.41	0.85
<i>F. fusca</i> - <i>P. totara</i>	-0.25	0.033	18461	-7.44	<0.01
<i>F. fusca</i> - <i>P. taxifolia</i>	-0.04	0.036	18461	-1.15	0.95
<i>F. fusca</i> - <i>S. sempervirens</i>	-0.48	0.033	18461	-14.61	<0.01
<i>F. solandri</i> - <i>L. menzeisii</i>	-0.41	0.030	18461	-13.42	<0.01
<i>F. solandri</i> - <i>P. totara</i>	-0.60	0.024	18461	-24.88	<0.01
<i>F. solandri</i> - <i>P. taxifolia</i>	-0.39	0.028	18461	-13.93	<0.01
<i>F. solandri</i> - <i>S. sempervirens</i>	-0.83	0.023	18461	-35.69	<0.01
<i>L. menzeisii</i> - <i>P. totara</i>	-0.19	0.029	18461	-6.75	<0.01
<i>L. menzeisii</i> - <i>P. taxifolia</i>	0.01	0.032	18461	0.36	1.00
<i>L. menzeisii</i> - <i>S. sempervirens</i>	-0.42	0.028	18461	-14.97	<0.01
<i>P. totara</i> - <i>P. taxifolia</i>	0.21	0.027	18461	7.72	<0.01
<i>P. totara</i> - <i>S. sempervirens</i>	-0.23	0.022	18461	-10.63	<0.01
<i>P. taxifolia</i> - <i>S. sempervirens</i>	-0.43	0.026	18461	-16.64	<0.01

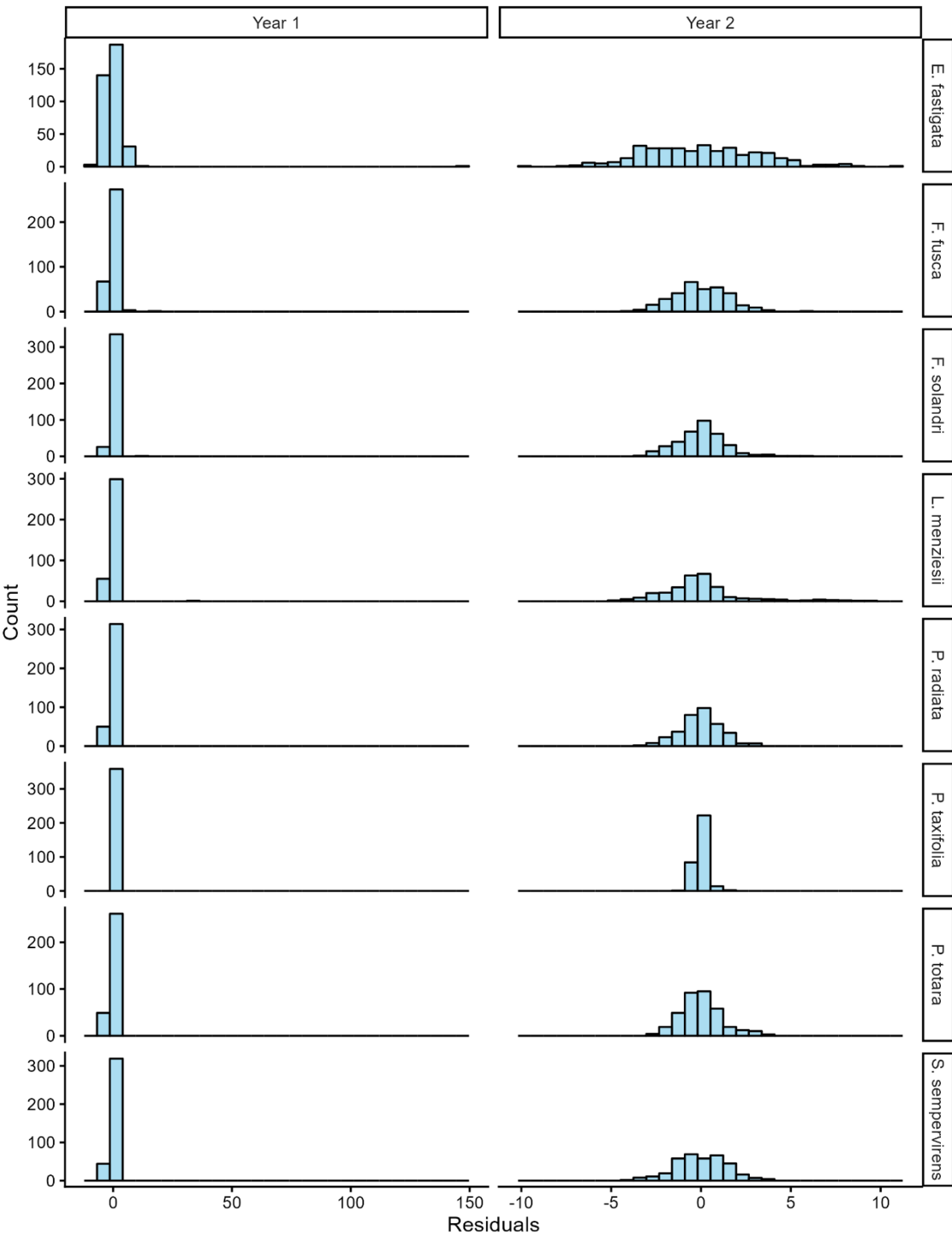
Appendix F: Estimated marginal means of maximum daily shrinkage in Year 1 (Chapter 2), derived from generalised additive models, with Tukey-adjusted pairwise comparisons among study species.

Contrast	Estimate	SE	df	T	p
<i>P. radiata</i> – <i>E. fastigata</i>	0.29	0.018	20900	15.75	<0.01
<i>P. radiata</i> – <i>F. fusca</i>	0.83	0.025	20900	33.28	<0.01
<i>P. radiata</i> – <i>F. solandri</i>	1.49	0.020	20900	75.01	<0.01
<i>P. radiata</i> – <i>L. menzeisii</i>	0.26	0.022	20900	11.87	<0.01
<i>P. radiata</i> – <i>P. totara</i>	1.18	0.018	20900	65.32	<0.01
<i>P. radiata</i> – <i>P. taxifolia</i>	1.04	0.019	20900	54.91	<0.01
<i>P. radiata</i> – <i>S. sempervirens</i>	-0.27	0.016	20900	-17.66	<0.01
<i>E. fastigata</i> - <i>F. fusca</i>	0.54	0.025	20900	21.42	<0.01
<i>E. fastigata</i> - <i>F. solandri</i>	1.20	0.018	20900	66.52	<0.01
<i>E. fastigata</i> - <i>L. menzeisii</i>	-0.03	0.022	20900	-1.21	0.93
<i>E. fastigata</i> - <i>P. totara</i>	0.89	0.019	20900	47.55	<0.01
<i>E. fastigata</i> - <i>P. taxifolia</i>	0.75	0.018	20900	41.01	<0.01
<i>E. fastigata</i> - <i>S. sempervirens</i>	-0.56	0.018	20900	-30.70	<0.01
<i>F. fusca</i> - <i>F. solandri</i>	0.67	0.026	20900	25.17	<0.01
<i>F. fusca</i> - <i>L. menzeisii</i>	-0.56	0.028	20900	-20.02	<0.01
<i>F. fusca</i> - <i>P. totara</i>	0.36	0.026	20900	13.97	<0.01
<i>F. fusca</i> - <i>P. taxifolia</i>	0.21	0.026	20900	8.37	<0.01
<i>F. fusca</i> - <i>S. sempervirens</i>	-1.10	0.025	20900	-43.64	<0.01
<i>F. solandri</i> - <i>L. menzeisii</i>	-1.23	0.024	20900	-52.12	<0.01
<i>F. solandri</i> - <i>P. totara</i>	-0.31	0.021	20900	-14.97	<0.01
<i>F. solandri</i> - <i>P. taxifolia</i>	-0.45	0.020	20900	-22.58	<0.01
<i>F. solandri</i> - <i>S. sempervirens</i>	-1.77	0.020	20900	-89.50	<0.01
<i>L. menzeisii</i> - <i>P. totara</i>	0.92	0.023	20900	40.50	<0.01
<i>L. menzeisii</i> - <i>P. taxifolia</i>	0.78	0.023	20900	34.33	<0.01
<i>L. menzeisii</i> - <i>S. sempervirens</i>	-0.54	0.023	20900	-23.86	<0.01
<i>P. totara</i> - <i>P. taxifolia</i>	-0.14	0.020	20900	-7.34	<0.01
<i>P. totara</i> - <i>S. sempervirens</i>	-1.46	0.018	20900	-79.16	<0.01
<i>P. taxifolia</i> - <i>S. sempervirens</i>	-1.31	0.019	20900	-68.28	<0.01

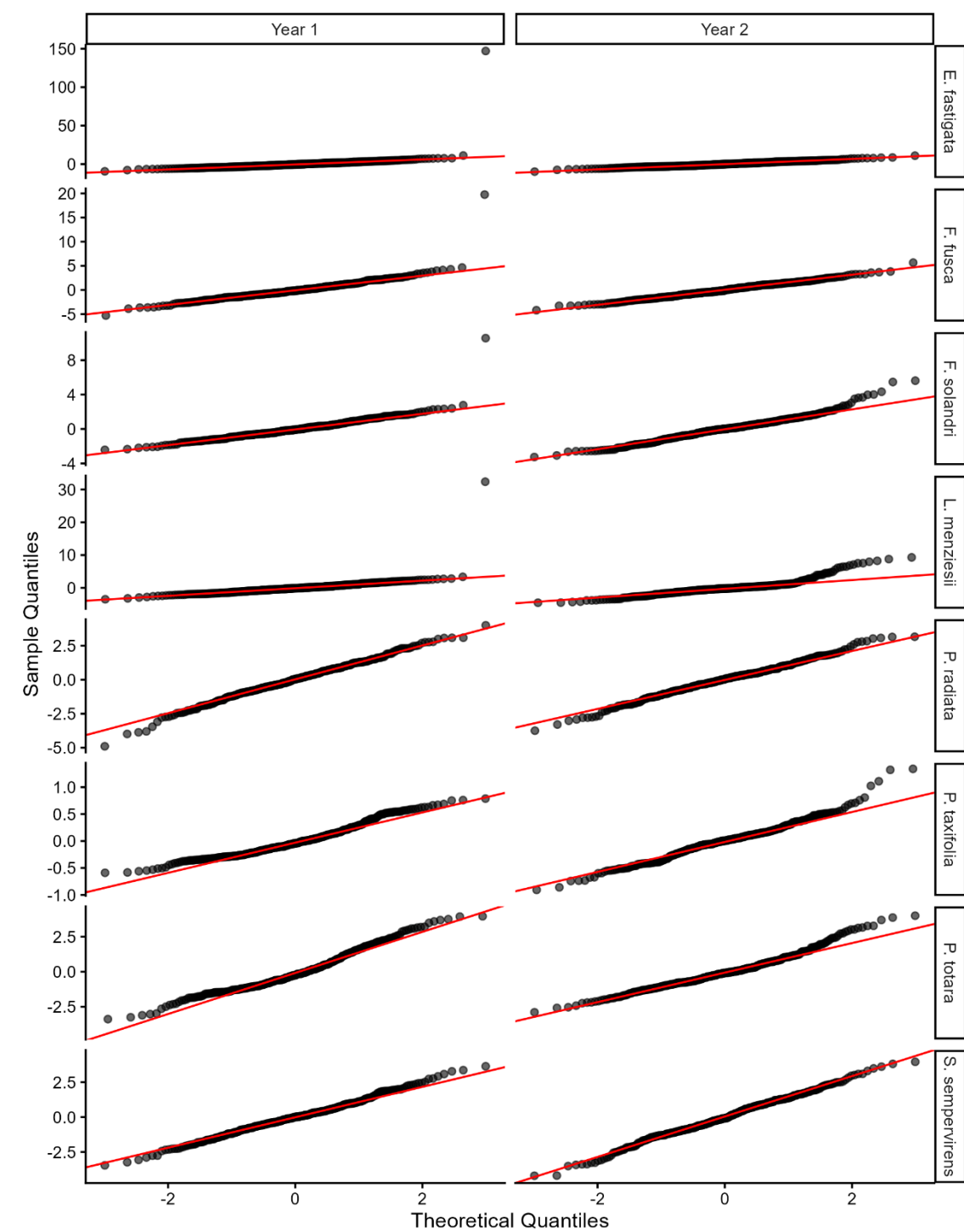
Appendix G: Estimated marginal means of maximum daily shrinkage in Year 2 (Chapter 2), derived from generalised additive models, with Tukey-adjusted pairwise comparisons among study species.

Contrast	Estimate	SE	df	T	p
<i>P. radiata</i> – <i>E. fastigata</i>	-0.04	0.018	18464	-2.29	0.30
<i>P. radiata</i> – <i>F. fusca</i>	0.76	0.027	18464	27.55	<0.01
<i>P. radiata</i> – <i>F. solandri</i>	1.38	0.020	18464	70.93	<0.01
<i>P. radiata</i> – <i>L. menzeisii</i>	0.47	0.024	18464	19.70	<0.01
<i>P. radiata</i> – <i>P. totara</i>	0.55	0.018	18464	30.90	<0.01
<i>P. radiata</i> – <i>P. taxifolia</i>	0.85	0.022	18464	39.36	<0.01
<i>P. radiata</i> – <i>S. sempervirens</i>	-0.17	0.016	18464	-10.34	<0.01
<i>E. fastigata</i> - <i>F. fusca</i>	0.80	0.029	18464	27.75	<0.01
<i>E. fastigata</i> - <i>F. solandri</i>	1.42	0.020	18464	70.63	<0.01
<i>E. fastigata</i> - <i>L. menzeisii</i>	0.51	0.025	18464	20.35	<0.01
<i>E. fastigata</i> - <i>P. totara</i>	0.59	0.019	18464	30.59	<0.01
<i>E. fastigata</i> - <i>P. taxifolia</i>	0.89	0.023	18464	38.74	<0.01
<i>E. fastigata</i> - <i>S. sempervirens</i>	-0.13	0.019	18464	-6.87	<0.01
<i>F. fusca</i> - <i>F. solandri</i>	0.63	0.030	18464	21.24	<0.01
<i>F. fusca</i> - <i>L. menzeisii</i>	-0.29	0.032	18464	-9.04	<0.01
<i>F. fusca</i> - <i>P. totara</i>	-0.20	0.028	18464	-7.17	<0.01
<i>F. fusca</i> - <i>P. taxifolia</i>	0.10	0.031	18464	3.14	0.04
<i>F. fusca</i> - <i>S. sempervirens</i>	-0.93	0.028	18464	-33.35	<0.01
<i>F. solandri</i> - <i>L. menzeisii</i>	-0.92	0.026	18464	-35.66	<0.01
<i>F. solandri</i> - <i>P. totara</i>	-0.83	0.021	18464	-40.40	<0.01
<i>F. solandri</i> - <i>P. taxifolia</i>	-0.53	0.024	18464	-21.98	<0.01
<i>F. solandri</i> - <i>S. sempervirens</i>	-1.55	0.020	18464	-78.52	<0.01
<i>L. menzeisii</i> - <i>P. totara</i>	0.09	0.025	18464	3.59	0.01
<i>L. menzeisii</i> - <i>P. taxifolia</i>	0.39	0.027	18464	14.20	<0.01
<i>L. menzeisii</i> - <i>S. sempervirens</i>	-0.63	0.024	18464	-26.36	<0.01
<i>P. totara</i> - <i>P. taxifolia</i>	0.30	0.023	18464	13.21	<0.01
<i>P. totara</i> - <i>S. sempervirens</i>	-0.72	0.018	18464	-39.42	<0.01
<i>P. taxifolia</i> - <i>S. sempervirens</i>	-1.02	0.022	18464	-45.97	<0.01

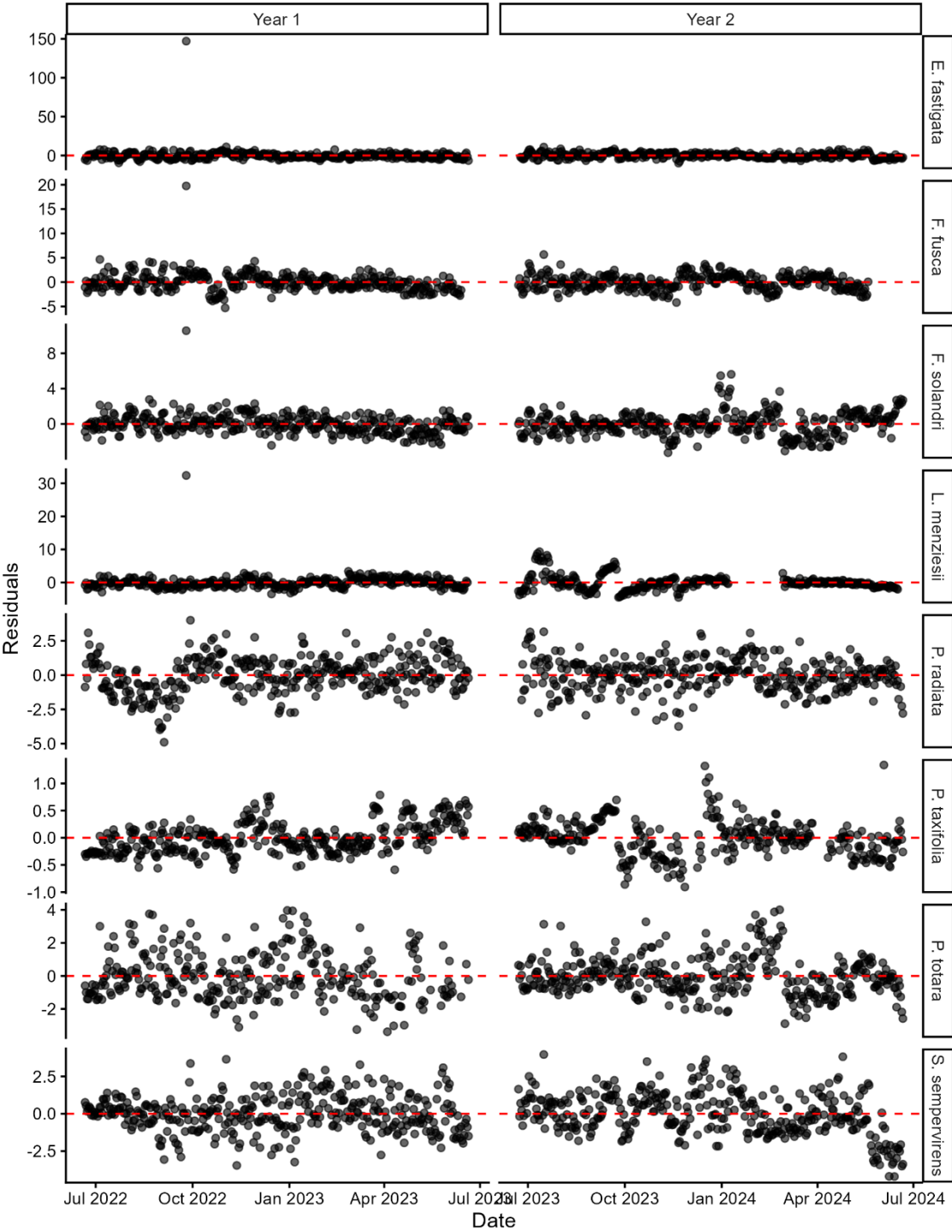
Appendix H: Histograms of residuals for generalised additive models of sap flux density (Chapter 3) and linear mixed effects models of sap flux density and both dendrometer and climate variables (Chapter 4). Shown separately for Year 1 and Year 2 across the eight study species. Residual distributions were inspected for skewness.



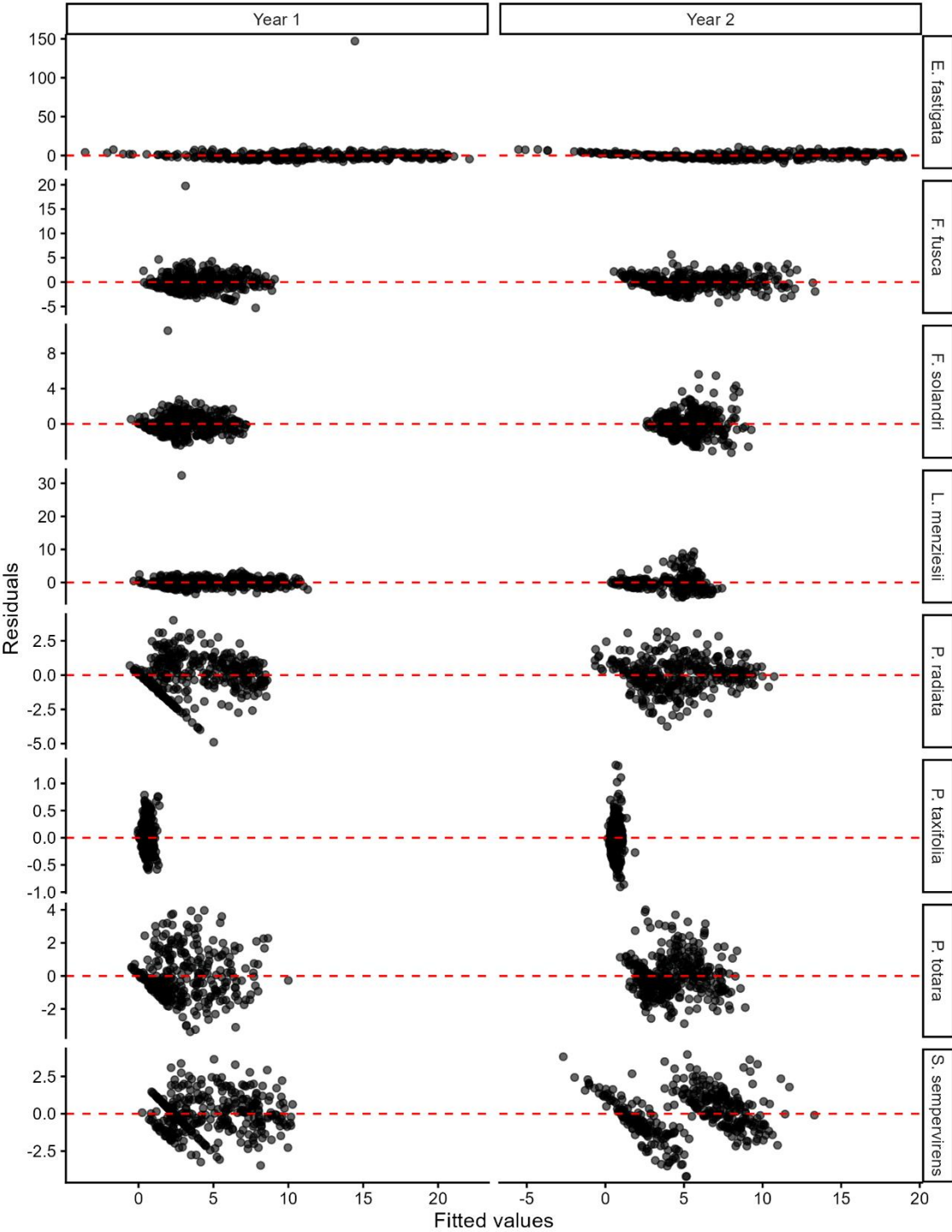
Appendix I: Quantile-quantile plots of residuals from generalised additive models of sap flux density (Chapter 3), shown separately for Year 1 and Year 2 across the eight study species. Residual distributions were assessed for normality.



Appendix J: Residuals versus date from generalised additive models of sap flux density (Chapter 3), shown separately for Year 1 and Year 2 across the eight study species. Residual distributions were assessed for heteroscedasticity.



Appendix K: Residuals versus fitted values from generalised additive models of sap flux density (Chapter 3), shown separately for Year 1 and Year 2 across the eight study species. Residual distributions were assessed for heteroscedasticity.



Appendix L: Post-hoc Dunn test results for pairwise comparisons of cumulative water transpired (Chapter 3) among species in Year 1 and Year 2.

Comparison	Year 1			Year 2		
	z	p unadjusted	p adjusted	z	p unadjusted	p adjusted
<i>E. fastigata</i> – <i>F. fusca</i>	16.00	<0.01	<0.01	13.33	<0.01	<0.01
<i>E. fastigata</i> – <i>F. solandri</i>	12.06	<0.01	<0.01	8.23	<0.01	<0.01
<i>F. fusca</i> - <i>F. solandri</i>	-3.94	<0.01	<0.01	-5.10	<0.01	<0.01
<i>E. fastigata</i> – <i>L. menziesii</i>	19.20	<0.01	<0.01	20.16	<0.01	<0.01
<i>F. fusca</i> - <i>L. menziesii</i>	3.21	<0.01	0.04	6.84	<0.01	<0.01
<i>F. solandri</i> - <i>L. menziesii</i>	7.15	<0.01	<0.01	11.93	<0.01	<0.01
<i>E. fastigata</i> – <i>P. radiata</i>	7.07	<0.01	<0.01	-0.24	0.81	1.00
<i>F. fusca</i> - <i>P. radiata</i>	-8.93	<0.01	<0.01	-13.57	<0.01	<0.01
<i>F. solandri</i> - <i>P. radiata</i>	-4.99	<0.01	<0.01	-8.47	<0.01	<0.01
<i>L. menziesii</i> - <i>P. radiata</i>	-12.13	<0.01	<0.01	-20.40	<0.01	<0.01
<i>E. fastigata</i> – <i>P. totara</i>	19.75	<0.01	<0.01	14.85	<0.01	<0.01
<i>F. fusca</i> - <i>P. totara</i>	3.75	<0.01	<0.01	1.53	0.13	1.00
<i>F. solandri</i> - <i>P. totara</i>	7.69	<0.01	<0.01	6.63	<0.01	<0.01
<i>L. menziesii</i> - <i>P. totara</i>	0.54	0.59	1.00	-5.31	<0.01	<0.01
<i>P. radiata</i> - <i>P. totara</i>	12.68	<0.01	<0.01	15.10	<0.01	<0.01
<i>E. fastigata</i> – <i>P. taxifolia</i>	23.89	<0.01	<0.01	21.91	<0.01	<0.01
<i>F. fusca</i> - <i>P. taxifolia</i>	7.89	<0.01	<0.01	8.58	<0.01	<0.01
<i>F. solandri</i> - <i>P. taxifolia</i>	11.83	<0.01	<0.01	13.68	<0.01	<0.01
<i>L. menziesii</i> - <i>P. taxifolia</i>	4.68	<0.01	<0.01	1.75	0.08	1.00
<i>P. radiata</i> - <i>P. taxifolia</i>	16.82	<0.01	<0.01	22.15	<0.01	<0.01
<i>P. totara</i> - <i>P. taxifolia</i>	4.14	<0.01	<0.01	7.06	<0.01	<0.01
<i>E. fastigata</i> – <i>S. sempervirens</i>	2.48	0.01	0.37	-3.34	<0.01	0.02
<i>F. fusca</i> - <i>S. sempervirens</i>	-13.52	<0.01	<0.01	-16.66	<0.01	<0.01
<i>F. solandri</i> - <i>S. sempervirens</i>	-9.58	<0.01	<0.01	-11.57	<0.01	<0.01
<i>L. menziesii</i> - <i>S. sempervirens</i>	-16.73	<0.01	<0.01	-23.50	<0.01	<0.01
<i>P. radiata</i> - <i>S. sempervirens</i>	-4.59	<0.01	<0.01	-3.10	<0.01	0.05
<i>P. totara</i> - <i>S. sempervirens</i>	-17.27	<0.01	<0.01	-18.19	<0.01	<0.01
<i>P. taxifolia</i> - <i>S. sempervirens</i>	-21.41	<0.01	<0.01	-25.25	<0.01	<0.01

Appendix M: Post-hoc Dunn test results for pairwise comparisons of cumulative water transpired (Chapter 3) among species in Dry Period 1 and Dry Period 2.

Comparison	Dry Period 1			Dry Period 2		
	z	p unadjusted	p adjusted	z	p unadjusted	p adjusted
<i>E. fastigata</i> – <i>F. fusca</i>	7.87	<0.01	<0.01	5.29	<0.01	<0.01
<i>E. fastigata</i> – <i>F. solandri</i>	4.99	<0.01	<0.01	-0.81	0.42	1.00
<i>F. fusca</i> - <i>F. solandri</i>	-2.87	<0.01	0.11	-6.10	<0.01	<0.01
<i>E. fastigata</i> – <i>L. menziesii</i>	8.12	<0.01	<0.01	10.72	<0.01	<0.01
<i>F. fusca</i> - <i>L. menziesii</i>	0.25	0.80	1.00	5.43	<0.01	<0.01
<i>F. solandri</i> - <i>L. menziesii</i>	3.13	<0.01	0.05	11.53	<0.01	<0.01
<i>E. fastigata</i> – <i>P. radiata</i>	-0.31	0.76	1.00	-5.16	<0.01	<0.01
<i>F. fusca</i> - <i>P. radiata</i>	-8.18	<0.01	<0.01	-10.45	<0.01	<0.01
<i>F. solandri</i> - <i>P. radiata</i>	-5.30	<0.01	<0.01	-4.36	<0.01	<0.01
<i>L. menziesii</i> - <i>P. radiata</i>	-8.43	<0.01	<0.01	-15.88	<0.01	<0.01
<i>E. fastigata</i> – <i>P. totara</i>	7.26	<0.01	<0.01	3.92	<0.01	<0.01
<i>F. fusca</i> - <i>P. totara</i>	-0.61	0.54	1.00	-1.37	0.17	1.00
<i>F. solandri</i> - <i>P. totara</i>	2.27	0.02	0.65	4.73	<0.01	<0.01
<i>L. menziesii</i> - <i>P. totara</i>	-0.86	0.39	1.00	-6.80	<0.01	<0.01
<i>P. radiata</i> - <i>P. totara</i>	7.57	<0.01	<0.01	9.08	<0.01	<0.01
<i>E. fastigata</i> – <i>P. taxifolia</i>	12.22	<0.01	<0.01	8.56	<0.01	<0.01
<i>F. fusca</i> - <i>P. taxifolia</i>	4.35	<0.01	<0.01	3.27	<0.01	0.03
<i>F. solandri</i> - <i>P. taxifolia</i>	7.22	<0.01	<0.01	9.37	<0.01	<0.01
<i>L. menziesii</i> - <i>P. taxifolia</i>	4.10	<0.01	<0.01	-2.16	0.03	0.86
<i>P. radiata</i> - <i>P. taxifolia</i>	12.53	<0.01	<0.01	13.72	<0.01	<0.01
<i>P. totara</i> - <i>P. taxifolia</i>	4.96	<0.01	<0.01	4.64	<0.01	<0.01
<i>E. fastigata</i> – <i>S. sempervirens</i>	-1.35	0.18	1.00	-3.19	<0.01	0.04
<i>F. fusca</i> - <i>S. sempervirens</i>	-9.21	<0.01	<0.01	-8.49	<0.01	<0.01
<i>F. solandri</i> - <i>S. sempervirens</i>	-6.34	<0.01	<0.01	-2.39	0.02	0.47
<i>L. menziesii</i> - <i>S. sempervirens</i>	-9.47	<0.01	<0.01	-13.92	<0.01	<0.01
<i>P. radiata</i> - <i>S. sempervirens</i>	-1.04	0.30	1.00	1.97	0.05	1.00
<i>P. totara</i> - <i>S. sempervirens</i>	-8.61	<0.01	<0.01	-7.12	<0.01	<0.01
<i>P. taxifolia</i> - <i>S. sempervirens</i>	-13.56	<0.01	<0.01	-11.76	<0.01	<0.01

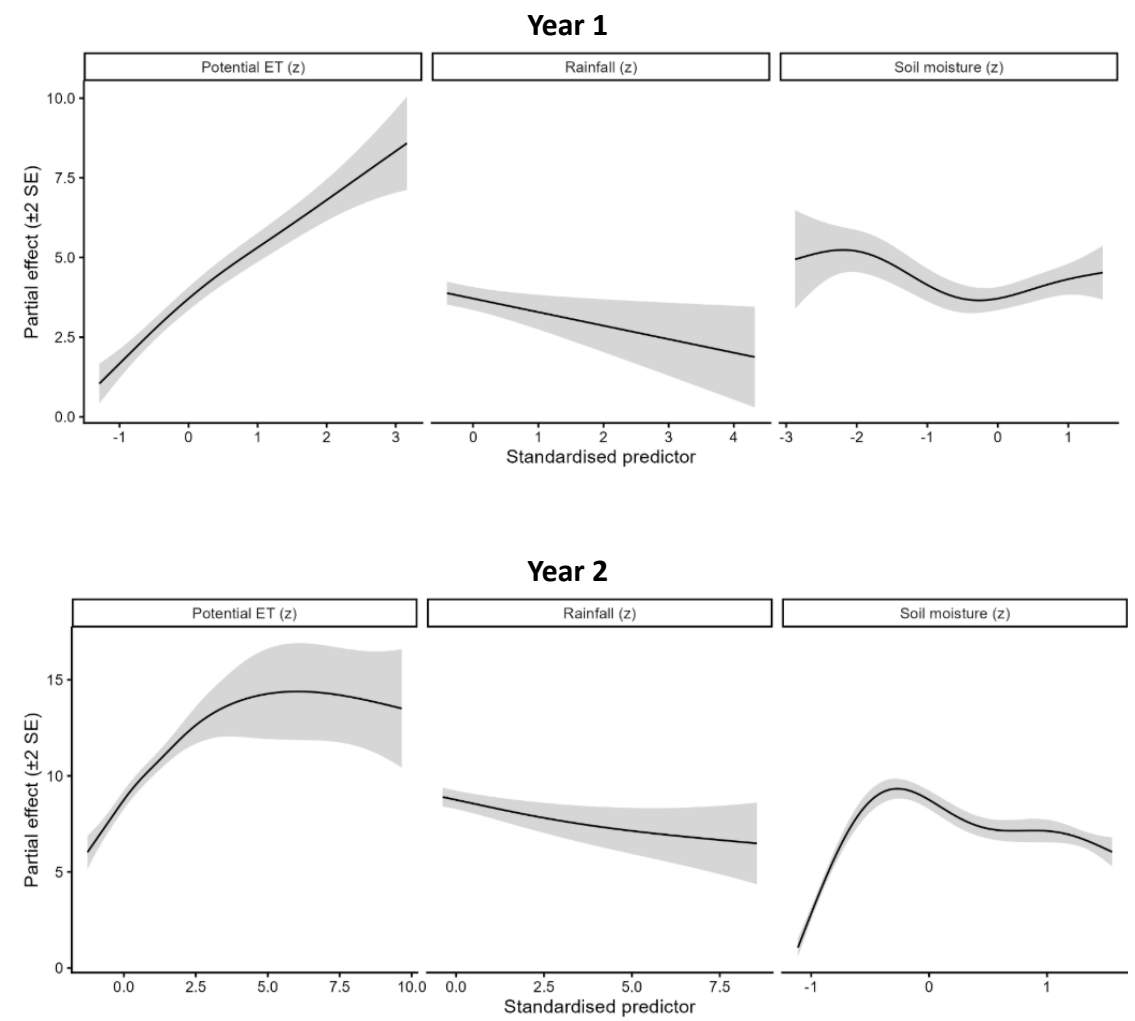
Appendix N: Post-hoc Dunn test results for pairwise comparisons of sap flux density (Chapter 3) among species in Year 1 and Year 2.

Comparison	Year 1			Year 2		
	z	p	p adjusted	z	p	p adjusted
<i>E. fastigata</i> – <i>F. fusca</i>	13.62	<0.01	<0.01	10.16	<0.01	<0.01
<i>E. fastigata</i> – <i>F. solandri</i>	17.13	<0.01	<0.01	9.23	<0.01	<0.01
<i>F. fusca</i> - <i>F. solandri</i>	3.28	<0.01	0.03	-1.01	0.31	1.00
<i>E. fastigata</i> – <i>L. menziesii</i>	11.00	<0.01	<0.01	13.94	<0.01	<0.01
<i>F. fusca</i> - <i>L. menziesii</i>	-2.70	0.01	0.20	3.71	<0.01	0.01
<i>F. solandri</i> - <i>L. menziesii</i>	-6.04	<0.01	<0.01	4.75	<0.01	<0.01
<i>E. fastigata</i> – <i>P. radiata</i>	16.81	<0.01	<0.01	11.54	<0.01	<0.01
<i>F. fusca</i> - <i>P. radiata</i>	2.95	<0.01	0.09	1.33	0.18	1.00
<i>F. solandri</i> - <i>P. radiata</i>	-0.35	0.73	1.00	2.35	0.02	0.53
<i>L. menziesii</i> - <i>P. radiata</i>	5.71	<0.01	<0.01	-2.39	0.02	0.47
<i>E. fastigata</i> – <i>P. totara</i>	17.74	<0.01	<0.01	12.51	<0.01	<0.01
<i>F. fusca</i> - <i>P. totara</i>	4.43	<0.01	<0.01	2.52	0.01	0.33
<i>F. solandri</i> - <i>P. totara</i>	1.29	0.20	1.00	3.53	<0.01	0.01
<i>L. menziesii</i> - <i>P. totara</i>	7.09	<0.01	<0.01	-1.11	0.27	1.00
<i>P. radiata</i> - <i>P. totara</i>	1.62	0.10	1.00	1.23	0.22	1.00
<i>E. fastigata</i> – <i>P. taxifolia</i>	30.94	<0.01	<0.01	33.51	<0.01	<0.01
<i>F. fusca</i> - <i>P. taxifolia</i>	16.94	<0.01	<0.01	23.35	<0.01	<0.01
<i>F. solandri</i> - <i>P. taxifolia</i>	13.84	<0.01	<0.01	24.52	<0.01	<0.01
<i>L. menziesii</i> - <i>P. taxifolia</i>	19.80	<0.01	<0.01	19.80	<0.01	<0.01
<i>P. radiata</i> - <i>P. taxifolia</i>	14.20	<0.01	<0.01	22.14	<0.01	<0.01
<i>P. totara</i> - <i>P. taxifolia</i>	12.01	<0.01	<0.01	20.44	<0.01	<0.01
<i>E. fastigata</i> – <i>S. sempervirens</i>	12.30	<0.01	<0.01	9.08	<0.01	<0.01
<i>F. fusca</i> – <i>S. sempervirens</i>	-1.49	0.14	1.00	-1.17	0.24	1.00
<i>F. solandri</i> – <i>S. sempervirens</i>	-4.84	<0.01	<0.01	-0.16	0.87	1.00
<i>L. menziesii</i> – <i>S. sempervirens</i>	1.23	0.22	1.00	-4.92	<0.01	<0.01
<i>P. radiata</i> – <i>S. sempervirens</i>	-4.50	<0.01	<0.01	-2.51	0.01	0.34
<i>P. totara</i> – <i>S. sempervirens</i>	-5.94	<0.01	<0.01	-3.69	<0.01	0.01
<i>P. taxifolia</i> – <i>S. sempervirens</i>	-18.68	<0.01	<0.01	-24.70	<0.01	<0.01

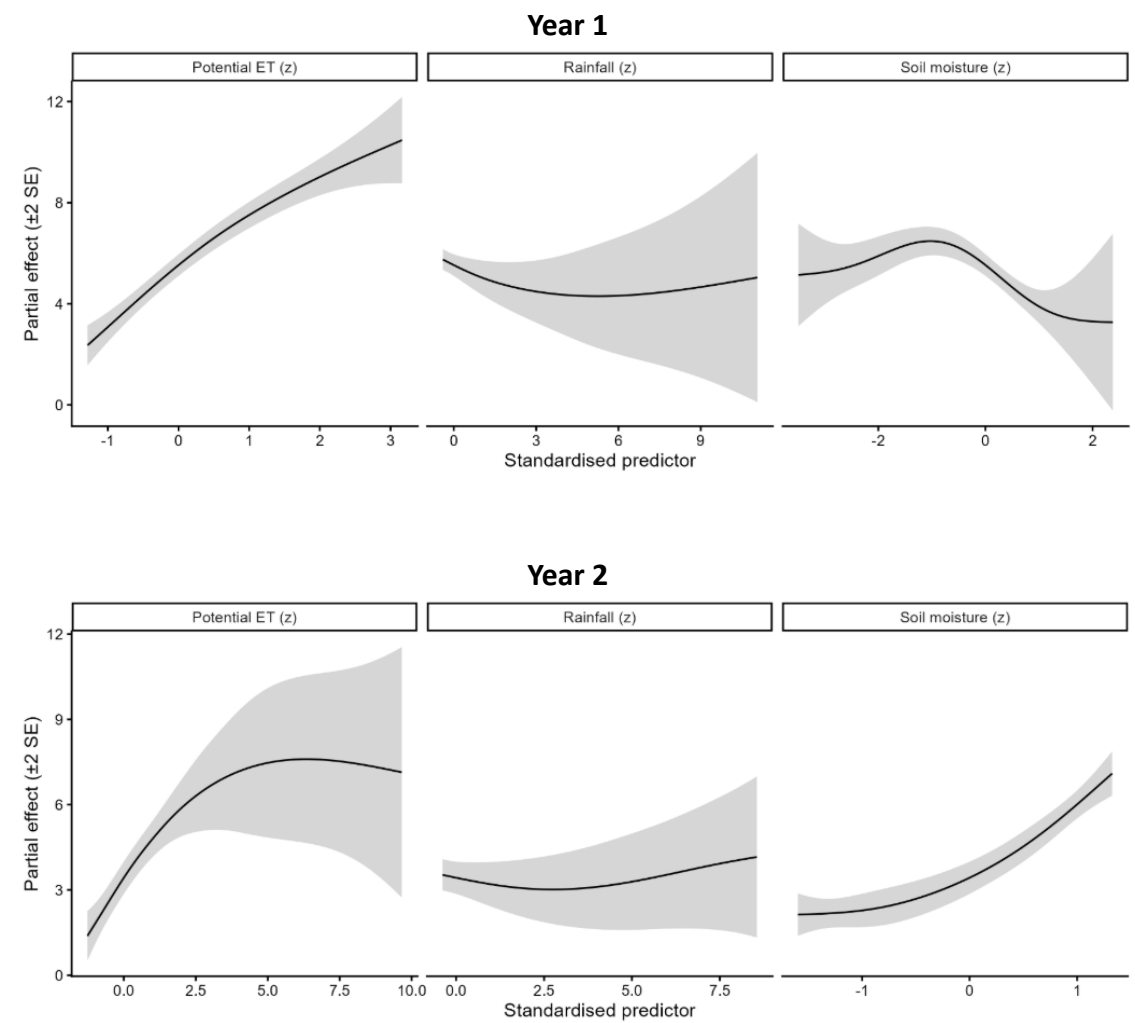
Appendix O: Post-hoc Dunn test results for pairwise comparisons of sap flux density (Chapter 3) among species in Dry Period 1 and Dry Period 2.

Comparison	Dry Period 1			Dry Period 2		
	z	p	p adjusted	z	p	p adjusted
<i>E. fastigata</i> – <i>F. fusca</i>	8.79	<0.01	<0.01	0.25	0.80	1.00
<i>E. fastigata</i> – <i>F. solandri</i>	10.84	<0.01	<0.01	-3.63	<0.01	0.01
<i>F. fusca</i> - <i>F. solandri</i>	2.02	0.04	1.00	-3.87	<0.01	<0.01
<i>E. fastigata</i> – <i>L. menziesii</i>	4.35	<0.01	<0.01	6.57	<0.01	<0.01
<i>F. fusca</i> - <i>L. menziesii</i>	-4.44	<0.01	<0.01	6.30	<0.01	<0.01
<i>F. solandri</i> - <i>L. menziesii</i>	-6.48	<0.01	<0.01	10.20	<0.01	<0.01
<i>E. fastigata</i> – <i>P. radiata</i>	7.80	<0.01	<0.01	-0.06	0.95	1.00
<i>F. fusca</i> - <i>P. radiata</i>	-1.04	0.30	1.00	-0.31	0.75	1.00
<i>F. solandri</i> - <i>P. radiata</i>	-3.07	<0.01	0.06	3.57	<0.01	0.01
<i>L. menziesii</i> - <i>P. radiata</i>	3.43	<0.01	0.02	-6.63	<0.01	<0.01
<i>E. fastigata</i> – <i>P. totara</i>	9.09	<0.01	<0.01	-0.42	0.67	1.00
<i>F. fusca</i> - <i>P. totara</i>	0.66	0.51	1.00	-0.67	0.50	1.00
<i>F. solandri</i> - <i>P. totara</i>	-1.27	0.20	1.00	3.20	<0.01	0.04
<i>L. menziesii</i> - <i>P. totara</i>	4.92	<0.01	<0.01	-6.97	<0.01	<0.01
<i>P. radiata</i> - <i>P. totara</i>	1.66	0.10	1.00	-0.36	0.72	1.00
<i>E. fastigata</i> – <i>P. taxifolia</i>	17.17	<0.01	<0.01	12.43	<0.01	<0.01
<i>F. fusca</i> - <i>P. taxifolia</i>	8.33	<0.01	<0.01	12.15	<0.01	<0.01
<i>F. solandri</i> - <i>P. taxifolia</i>	6.32	<0.01	<0.01	16.03	<0.01	<0.01
<i>L. menziesii</i> - <i>P. taxifolia</i>	12.80	<0.01	<0.01	5.94	<0.01	<0.01
<i>P. radiata</i> - <i>P. taxifolia</i>	9.42	<0.01	<0.01	12.50	<0.01	<0.01
<i>P. totara</i> - <i>P. taxifolia</i>	7.32	<0.01	<0.01	12.82	<0.01	<0.01
<i>E. fastigata</i> – <i>S. sempervirens</i>	5.61	<0.01	<0.01	4.16	<0.01	<0.01
<i>F. fusca</i> – <i>S. sempervirens</i>	-3.23	<0.01	0.03	3.90	<0.01	<0.01
<i>F. solandri</i> – <i>S. sempervirens</i>	-5.27	<0.01	<0.01	7.79	<0.01	<0.01
<i>L. menziesii</i> – <i>S. sempervirens</i>	1.24	0.22	1.00	-2.41	0.02	0.45
<i>P. radiata</i> – <i>S. sempervirens</i>	-2.20	0.03	0.77	4.22	<0.01	<0.01
<i>P. totara</i> – <i>S. sempervirens</i>	-3.76	<0.01	<0.01	4.57	<0.01	<0.01
<i>P. taxifolia</i> – <i>S. sempervirens</i>	-11.62	<0.01	<0.01	-8.32	<0.01	<0.01

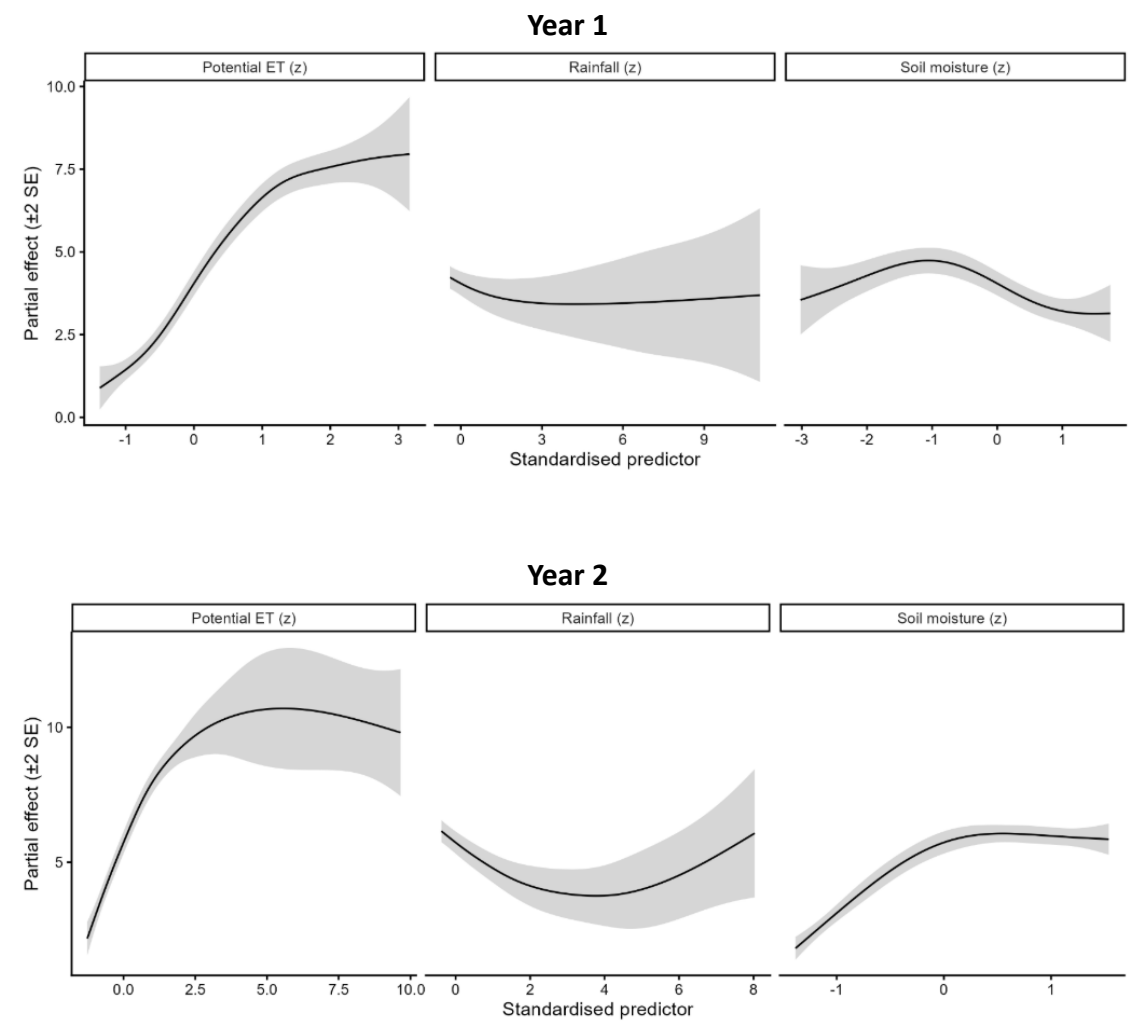
Appendix P: Partial effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *F. solandri* in Year 1 and Year 2. Each panel shows the estimated nonlinear relationship between sap flux density and soil moisture (soil VWC), rainfall, and Potential ET (PET), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.



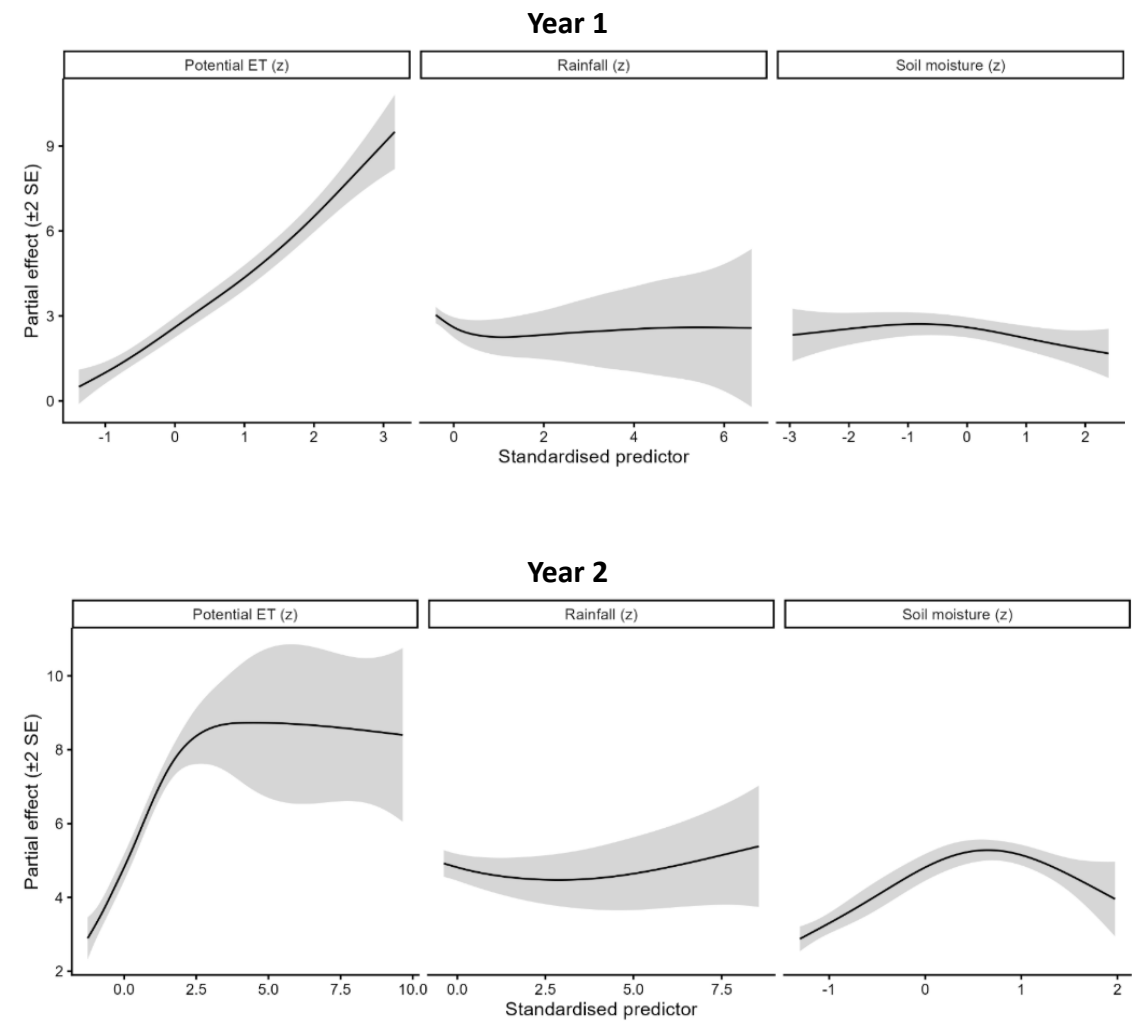
Appendix Q: Partial effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *P. totara* in Year 1 and Year 2. Each panel shows the estimated nonlinear relationship between sap flux density and soil moisture (soil VWC), rainfall, and Potential ET (PET), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.



Appendix R: Partial effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *P. taxifolia* in Year 1 and Year 2. Each panel shows the estimated nonlinear relationship between sap flux density and soil moisture (soil VWC), rainfall, and Potential ET (PET), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.



Appendix S: Partial effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *P. radiata* in Year 1 and Year 2. Each panel shows the estimated nonlinear relationship between sap flux density and soil moisture (soil VWC), rainfall, and Potential ET (PET), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.



Appendix T: Partial effect smooths (± 2 SE) from the Gaussian GAM (REML smoothing) for sap flux density of *S. sempervirens* in Year 1 and Year 2. Each panel shows the estimated nonlinear relationship between sap flux density and soil moisture (soil VWC), rainfall, and Potential ET (PET), with predictors standardised (mean = 0, SD = 1) and other variables held at their mean values.

