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# **Tree species sorting along temperature gradients: How do frost-resistant traits influence competitive ability in the forest environment?**

A thesis submitted in partial fulfilment

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*Te Whare Wānanga o Waikato*

# Abstract

To thrive in the forest environment a species must be able to pass each of three filters: first it must reach a site (the historical filter), then it must be able to tolerate the physical environment (the physiological filter) and finally it must be able to cope with biotic interactions at the site (the biotic filter). This thesis comprises of two complementary studies that explore the role temperature gradients play in determining a species ability to pass the physiological and biotic filters of a temperate rainforest. These studies were conducted using the seedlings of New Zealand warm- and cool- temperate tree species. The first study addresses how the trade-off in shade tolerance vs. growth rate found throughout closed-canopy forests changes from warm-temperate to cool-temperate environments using a transplant experiment. The second study aims to determine the implications of climate-related variation in xylem anatomy for morphological and physiological traits related to competitive ability. Warm-temperate species were found to be both faster-growing and more shade-tolerant than the cool-temperate species, indicating that cold resistant traits reduce competitive ability in warmer environments. This was supported by findings that the warm-temperate species had more conductive xylem and correspondingly higher levels of leaf area deployed than the cool species, indicating that cold resistance indirectly reduces the leafiness of a species. These cool-temperate species with less leaf surface area are less effective at intercepting light, resulting in lower growth rates and reduced shade tolerance which are important components of competitive ability in tree species. This may explain their absence from warmer forest environments, and their restriction to colder environments.

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# 1 General Introduction

A major goal of forest ecology is to determine what drives species sorting and community composition. Early authors in this field proposed a number of models of forest community composition that focus mainly on the competitive abilities of plant species mediated by resource availability and disturbance, with light being a key resource (Whittaker, 1956; Austin, 1986; Keddy & Maclellan, 1990). Since then, temperature extremes, light and water availability have been emphasized as key abiotic factors (Valladares & Niinemets, 2008; Martinez-Tilleria *et al.*, 2012) and species-specific differences in performance along these environmental gradients are considered an important determinant of plant community structures and dynamics (Silvertown, 2004). These differences in performance are the result of trade-offs that inevitably determine the space that can be occupied by a species along gradients of abiotic conditions (Sack, 2004; Seiwa, 2007).

Lambers *et al.* (1998) proposed a ‘triple filter’ model that offered three filters that restrict species establishment in a given environment. These three filters are the historical filter (the species must overcome dispersal barriers to reach the site), the physiological filter (the species must be able to cope with the physical environment) and the biotic filter (the species must be able to cope with biotic interactions at the site). The relative importance of these three filters varies over environmental gradients and these changes can be used to explain species composition and the limits of species distribution. Loehle (1998) attempted to explain the equatorial and polar limits of tree species distributions, hypothesising that maximum growth rate, an important competitive trait, determines a species’ equatorial limit while frost-resistance is the primary determinant of the polar limit. This idea was further developed by Lusk *et al.* (2013), considering growth rate and shade tolerance to both be important competitive traits, and hypothesising that species sorting along temperature gradients reflects a shift in the relationship between shade tolerance and maximum growth rate. The equatorial and polar limits of tree species distributions can also be likened to the altitudinal limits as both involve strong temperature gradients. These strong temperature gradients have been shown to play an important role in driving species turnover and

community composition with increasing altitude on non-arid mountains throughout the world (Korner, 1998).

For a long time, growth rate has been seen as a fundamental aspect of competitive ability, facilitating the occupation of space and, by extension, resources (Lambers & Poorter, 1992). In a more direct competitive sense faster growth rates allow trees to overtop their neighbours, serving to increase light interception whilst limiting the light available to competing saplings. This is known as asymmetrical competition for light as a taller plant will shade a shorter plant while the shorter plant will have no shading effect on the taller plant (Schwinning & Weiner, 1998), which has led to an evolutionary 'arms race' for light (Falster & Westoby, 2003). In order to optimise growth rates a species can invest in several traits, such as higher specific leaf area (SLA) and leaf area ratio (LAR) to increase light interception, high leaf nitrogen content to increase photosynthetic efficiency, faster leaf turnover, greater ability to adjust allocation and metabolic rates of respiration (Lambers & Poorter, 1992). However, if competition in forest environments was driven solely by growth rate we would not see the range of height and growth rates that are commonly observed in forests. This can be explained by a strategy to specialize in efficient growth and reproduction at light levels that are not tolerated by other species, facilitating the completion of a species life cycle without being out-competed by taller and faster-growing species (Kohyama *et al.*, 2003).

Shade tolerance is also considered an important aspect of competitive ability in forest environments (Valladares & Niinemets, 2008). Specifically in late-successional forests, shade tolerance is thought to play a major role as seedlings that are more shade tolerant are able survive and grow despite decreasing light availability (Shugart, 1984). Shade tolerance has several similar definitions that all revolve around a plants' ability to maintain positive net carbon gain under long-term low-light conditions (Givnish, 1988; Kobe *et al.*, 1995), with an explicit measurement of this being the whole-plant compensation point which is the minimum amount of light required to achieve zero net growth (Baltzer & Thomas, 2007). However, a species' shade tolerance is the result of a wide range of

physiological, biochemical, morphological and whole plant traits that all contribute to the ability to survive in low-light (Valladares & Niinemets, 2008). There are, however, two hypotheses for which suite of traits are of primary importance in determining a species' shade tolerance: the carbon gain hypothesis Givnish (1988) and the stress tolerance hypothesis (Kitajima, 1994). The carbon gain hypothesis proposes that shade tolerance is derived from traits that improve light-use efficiency such as higher leaf chlorophyll content and photosynthetic capacity at the leaf scale and greater leaf area at the whole-plant scale. The stress tolerance hypothesis on the other hand proposes that survival in low-light was more related to traits that improve resistance to biotic and abiotic stresses such as wood density, pathogen resistance and higher leaf mass per area (Augsburger, 1984; Walters & Reich, 1996). When considering these hypotheses it is also important to note that ontogenic changes can alter many of the traits that influence a species shade tolerance, adding an additional layer of variation (Bond, 2000; Lusk, 2004; Niinemets, 2006).

Many traits that increase a species' tolerance of particular abiotic or biotic stressors can negatively affect other traits that improve the tolerance of other limiting factors (e.g. shade, drought, waterlogging) (Valladares & Niinemets, 2008). A fundamental trade-off within forest communities is between growth rate and shade tolerance, two traits that provide a competitive advantage but are thought to be mutually incompatible. This trade-off has been observed in a variety of tropical, subtropical and temperate biomes (Hubbell & Foster, 1992; Pacala *et al.*, 1994; Kobe, *et al.*, 1995; Gilbert *et al.*, 2006; Sterck *et al.*, 2006; Seiwa, 2007), indicating that it may be a pervasive driver of species turnover within forest communities. Faster-growing light-demanding species and slower-growing shade-tolerant species can be distinguished based on many traits at both leaf- and plant-levels (Givnish, 1988), with light-demanding species utilising traits that maximise photosynthetic return while shade-tolerant species utilise traits that aid in maintaining a net positive carbon balance in resource poor environments. The trade-off between growth rate and shade tolerance may not be as straight-forward as expected however, as recent research has indicated that there may be a shift in

the growth rate vs. shade tolerance relationship with increasing cold stress (Lusk, *et al.*, 2013).

Although biotic interactions are invoked as determinants of the equatorial limit of tree species distributions, the abiotic aspects of decreasing temperature are considered more significant in determining the poleward distributional limit (Loehle, 1998). Freeze-thaw embolisms occur when air is released from solution during freezing and subsequently block the xylem, restricting water from flowing through (Tyree *et al.*, 1994). Plant cells are dehydrated during freezing as the intercellular spaces are filled with ice (Kozlowski & Pallardy, 2002). Deformation of leaves may also occur during freezing, damaging tissues and causing cells to burst (Loehle, 1998). The combination of all of these effects makes frost-resistant traits more valuable with decreasing temperatures and increasing frost incidence.

There are a number of mechanisms tree species use to cope with the challenges provided by a colder environment. Narrower conduits have been shown to reduce the incidence of cavitation after freeze-thaw events as they produce smaller bubbles that are less likely to give rise to embolisms (Sperry *et al.*, 1994; Davis *et al.*, 1999). Structural investments such as increased lignification and internal structural supports can be used to reduce deformation during freezing (Loehle, 1998). Low temperatures induce the production of dehydrins and similar proteins in the stem, flowers and roots which helps reduce the dehydrating effects of freezing in the intercellular space (Muthalif & Rowland, 1994; Wisniewski *et al.*, 1996). Other cryoprotectants that are used by cold-tolerant species include unsaturated lipids, sugars, membrane proteins and ATP (Santarius, 1984; Woodward & Williams, 1987; Loehle, 1998). Conservative growth strategies play an integral role as younger leaves, buds and reproductive organs tend to be more vulnerable to freezing as they have not developed cold hardiness and saplings and seedlings tend to be more vulnerable due to earlier flushing times (Vitasse *et al.*, 2014). It is often difficult to predict frost events on daily and year-to-year time-scales (Larcher & Bauer, 1981) which, when combined with the higher costs of frost-resistant traits, encourages growth strategies that minimise losses.

However there are costs associated with utilising these cold resistance strategies that can negatively impact a species' competitive ability. There are three types of costs associated with cold resistance: allocation, specialization and opportunity costs. Allocation costs include factors such as investing more in xylem production due to selection for narrower vessels and the production of cryoprotectants (Loehle, 1998; Peppe *et al.*, 2011). An examples of a specialization cost is the production of smaller, denser leaves that are more resistant to frost damage but are less productive (Chabot & Hicks, 1982). Lastly, opportunity costs are those associated with the inherently conservative growth strategies that, while reducing risk of loss to unexpected frost events, also reduce a species ability to take advantage of early season opportunities and ephemeral favourable growing conditions (Loehle, 1998; Saxe *et al.*, 2001).

This thesis attempts to discern the role cold resistance traits, particularly narrower conduits, have in influencing a species' competitiveness in warmer environments. In Chapter 2 I test the hypothesis that there is a shift in the relationship between growth rate and shade tolerance between warm- and cool-temperate tree species assemblages using a transplant experiment. To assess this basal stem diameter and height growth were measured across a range of light environments in a common warm-temperate forest environment for five warm- and five cool-temperate species. This data was then used to calculate relative growth rates and light compensation points for each species and test for relationships between them and the two assemblages. Then, in Chapter 3 I explore the effect of interspecific variation in conduit diameter on leaf area deployment and photosynthetic capacity in warm- and cool-temperate tree species. Five warm- and five cool-temperate species grown in a shadehouse environment were used to measure xylem anatomy (conduit diameter), leaf area deployment (LAR, SLA and leaf mass fraction) and gas exchange rates (photosynthetic capacity and stomatal conductance). Two main hypotheses were tested: that differences in hydraulic capacity translate into differences in leaf area deployment, or into variation in photosynthetic capacity per unit leaf area. Differences between the warm- and cool-temperate assemblages were also tested for. Finally, in Chapter 4 the results of the two primary chapters are integrated and assessed as a whole. The results are discussed in terms of their

relation to the overall idea that frost-resistant traits influence competitive ability in warmer forest environments and how these studies fit into the bigger picture of species turnover along temperature gradients.

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## **2 The relationship between shade tolerance and growth rate in warm- and cool-temperate rainforest assemblages**

### **2.1 Abstract**

Much research has been conducted into the mechanisms underlying tree species sorting along temperature gradients, and it has been hypothesised that a trade-off between growth rate and cold resistance plays a significant role. A recent study proposed that a shift in the relationship between shade tolerance and growth in high light could be more relevant than a simple trade-off model. This study uses a transplant experiment to test the hypothesis that there will be a shift in the relationship between shade tolerance and growth in high light between warm-temperate and cool-temperate assemblages. Seedlings of warm- and cool-temperate tree species were grown in a common forest environment in order to examine the shade tolerance vs. maximum growth rate trade-off within the two species assemblages. Basal stem diameter and stem height growth measurements across a range of light environments were used to calculate light compensation points for growth of each species, which were used as a measure of shade tolerance. Major axis tests and t-tests were then used to compare relationships between compensation points and maximum growth rate of warm- and cool-temperate species. These showed that, on average, warm-temperate species were faster-growing and had lower compensation points than cool-temperate species. The ability to exploit opportunities presented by canopy gaps with a high growth rate, and the ability to tolerate shade, become more important in warmer environments where abiotic restrictions are lessened and competitive biotic interactions are more significant. Conversely, adaptation to cooler environments negatively impacts juvenile performance due to the investments required to tolerate cold-related stresses.

## 2.2 Introduction

A number of biotic and abiotic factors might drive species turnover along temperature gradients and their relative importance in different environments has been a sustained focus of research (Woodward & Williams, 1987; Brown *et al.*, 1996; Guisan & Thuiller, 2005). It has long been suggested that the equatorial limit for a species' distribution is determined by biotic factors and the poleward limit determined by abiotic factors, specifically those associated with lower temperatures (Dobzhansky, 1950; MacArthur, 1972). Loehle (1998) developed this idea more explicitly, hypothesising that tree species sorting along temperature gradients was driven by a trade-off between growth rate and cold resistance, growth rate reflecting the importance of biotic interactions in warmer climates and cold resistance reflecting the increasing physical stress associated with colder climates. This idea was supported by Pither (2003) and similar relationships have been hypothesized to explain species distributions over other geographical gradients associated with environmental factors such as elevation, water availability and nutrient availability (Brown, *et al.*, 1996). If the trade-off proposed by Loehle (1998) exists then we would expect to be able to grow woody perennials on sites warmer than those found within their natural distribution but not on sites that are significantly colder. Although this has been supported by recent research (Vetaas, 2002), more research is required to verify Loehle's original hypothesis. That being said, ecophysiological studies have supported the idea that there is a trade-off between resistance to environmental stressors and a species' ability to intercept light and acquire carbon (Lambers & Poorter, 1992; Reich *et al.*, 2003; Baltzer & Thomas, 2007).

A variety of structural investments, physiological responses and growth strategies enable plants to cope with cold; these undoubtedly have significant resource costs and so could potentially underlie a trade-off between growth and cold resistance (Loehle, 1998). A well-researched example is the trade-off between stem conductivity and resistance to freezing-induced embolism, where wider vessels are more conductive and efficient (Tyree & Ewers, 1991; Lewis & Boose, 1995) but are more vulnerable to cavitation following freeze-thaw cycles vessels (Sperry

& Sullivan, 1992; Davis, *et al.*, 1999; Choat *et al.*, 2011), leading to a selection for thinner vessels in colder environments. Sclerophyllous leaves with high construction costs are common in particularly cold regions as they resist wind stress, ice abrasion and deformation when frozen (Korner & Larcher, 1988; Atkin *et al.*, 1996; Loehle, 1998). Conservative growth strategies in the early growing season such as late budburst and early cessation of growth serve to reduce the risk of frost damage during periods of unpredictable temperatures (Sakai, 1987). Also, many cold-adapted species synthesize cryoprotectants that reduce the frequency and extent of frost damage (Sakai, 1987).

Growth has long been considered the primary determinant of competitive viability but recently other factors have also been proposed to play a potentially significant role. Shade tolerance has been proposed as a primary determinant of competitive hierarchies (Keddy & Maclellan, 1990), particularly in late successional forests where light availability often limits seedling growth (Canham *et al.*, 1994; Pacala, *et al.*, 1994). Shade tolerance allows a seedling to invade existing vegetation and pre-empt the seedlings of competing species prior to the formation of canopy gaps, increasing its likelihood of eventual recruitment into the canopy (Brown & Whitmore, 1992; Canham, *et al.*, 1994). Partial support for the model used by Keddy and Maclellan (1990) was found as shade-tolerant species dominated the most productive sites within a region but tree-fall gap provide opportunities for more light-demanding species. This mixture of shade-tolerant and light-demanding species in many forests is the result of a widely established performance trade-off between shade tolerance and maximum growth rate (Bazzaz, 1979; Hubbell & Foster, 1992; Kobe, *et al.*, 1995; Lin *et al.*, 2002; Gilbert, *et al.*, 2006; Poorter & Bongers, 2006; Lusk & Jorgensen, 2013). However, despite extensive research into the shade-tolerance and growth rate trade-off itself, little is known about how this trade-off might vary along environmental gradients. This is important as there are examples of tree species that are both light demanding and slow growing existing in very cold or resource-poor environments (Read, 1985; Lusk *et al.*, 1997). Smith and Huston (1989) addressed an analogous problem in their examination of the effect of water-availability gradients on this trade-off: they hypothesized that the woody species

that can grow in semi-arid sites would be slower growing and/or less shade-tolerant than those in mesic environments.

Lusk, *et al.* (2013) hypothesized that tree species sorting on temperature gradients reflects shifts in the growth vs shade tolerance trade-off, challenging the idea of a single, universal trade-off. However, that study quantified species' shade tolerance only where they were found naturally and made comparisons across differing growing environments. While this method accurately measures growth responses as they would occur in the species' natural environment, it potentially confounds inherent differences between species with plastic responses to the environment (cf. Wright *et al.*, 1998). For this reason it is important to compare the performance trade-offs of species grown in a common environment in order to reduce this potential source of variability.

As suggested by Lusk, *et al.* (2013), it is hypothesised that the cost of cold-resistant traits limit shade tolerance and/or growth rate which in turn limits a species ability to compete in a warmer environment. This idea is assessed with a transplant experiment growing warm- and cool-temperate species in a common warm-temperate environment. It is hypothesised that there will be a shift in the relationship between shade-tolerance and maximum growth rate between the warm- and cool- temperate assemblages. The alternate hypothesis is that the warm- and cool- temperate species will fall along the same shade tolerance vs. growth rate trade-off axis.

## **2.3 Methods**

### **2.3.1 Species and study site**

Five warm-temperate and five cool-temperate tree species were used in this study (Table 1). The tree species chosen represent a variety of expected growth responses ranging from shade-tolerant to light-demanding (Grubb *et al.*, 2013; Lusk & Jorgensen, 2013; Lusk *et al.*, 2015). Seedlings were obtained from nurseries and grown in a shade house to acclimate for two months prior to transplantation in July 2013 (winter).



The study was conducted in the northern enclosure of Maungatautari Ecological Island, a temperate rainforest ecological reserve surrounded by a predator-proof fence to exclude invasive mammalian species (McQueen, 2004).

Maungatautari is an extinct andesite-dacite composite volcano that last erupted 1.8 million years ago (Cole, 1978; Briggs, 1986). The study site on Maungatautari lies at latitude 38.00 S and longitude 175.57 E with an altitude of approximately 340m asl. It receives approximately 1300mm mean annual rainfall, and has a mean annual

temperature of 13°C (NIWA, 2014). The topography of the study site varies from moderately to strongly rolling slopes (McQueen, 2004).



**Figure 1: Seedling planting scheme in high-light plot**

The forest types represented at Maungatautari are primarily rimu-tawa (*Dacrydium cupressium* and *Beilschmiedia tawa*) warm-temperate lowland forest below 600m and tawari (*Ixerba brexioides*), kamahi (*Weinmannia racemosa*) and tawheowheo (*Quintinia serrata*) dominated cool-temperate upland forest above 600m (Clarkson, 2002). The Northern Enclosure of Maungatautari where this experiment was conducted is composed of the warm-temperate rimu-tawa forest and includes other canopy species such as *Litsea calicaris*, *Knightia excelsa* and *Laurelia novae-zelandiae*. The understory of the warm-temperate forest in the Northern Enclosure is composed of shrubs and small trees including five-finger (*Pseudopanax arboreus*), pigeonwood (*Hedycarya arborea*), *Coprosma grandifolia*, *Schefflera digitata* and raukawa (*Raukawa edgerleyi*), and soft tree fern (*Cyathea smithii*). The ground cover is primarily crown fern (*Blechnum discolor*), *Microlaena avenacea* and hook-seeded sedges (*Uncinia* spp.).

### 2.3.2 Experimental design

This experiment was aimed to measure growth responses of ten tree species to a range of light environments. High, intermediate and low-light environments were found for the study, designated gap, intermediate and understory: these three light environments were replicated in eight different stands throughout the enclosure. The gap environments were located beneath treefall gaps and on forest margins, and then corresponding intermediate- and understory environments were found as close as possible to each gap. One seedling of each of the 10 species were planted in a random position within each 5x2 plot although in some cases the plot layout was changed to 1x12 or 3x4 to accommodate the surrounding understorey vegetation (Figure 1). Monthly visits were made to monitor the seedlings' development and clear any debris that may have fallen on them.

### 2.3.3 Data collection

Both RGR of stem volume and height growth rate were measured. Relative growth rate (RGR) for each seedling was calculated as per Equation 1. (Baltzer & Thomas, 2007). Although this does not calculate actual whole-plant RGR it has been shown to correlate well with more direct measurements (Kohyama & Hotta, 1990). For the purposes of basal measurements a point was marked using white acrylic paint at which all further basal measurements were made. Digital callipers were used to measure basal diameter and for each seedling two measurements were taken at 90° angles and the average used. Stem length was measured from ground level to the tip of the longest stem. Length and basal diameter of the longest stem were measured at the time of planting and after 12 months to calculate growth rates of each seedling over a year.

$$RGR_{\text{stem}} = \frac{(\ln(l_f \times \pi(d_f/2)^2) - (\ln(l_i \times \pi(d_i/2)^2))}{t_f - t_i} \quad \text{Equation 1}$$

Light availability was calculated using hemispherical photographs taken above each seedling at the time of planting and then again six months into the growth period (Figure 2). The average of the two photographs was used to account for changes in canopy structure over the duration of the experiment. Photographs

were taken with a Nikon D5100 digital camera and a Sigma 4.5mm F2.8 EX DC HSM Circular Fisheye lens. To facilitate analysis the camera was oriented north with a compass and levelled using a spirit level. The images were then processed using Gap Light Analyzer (Frazer *et al.*, 1999), using cloud cover frequency estimates from MODIS satellite photos for cloudiness index (Kt), beam fraction and spectral fraction by month (Iqbal, 1983). This provided an estimate of mean daily photon flux for each seedling over a 12 month period, ranging from 0.5 to 22% canopy light transmission and 0.1 to 6 mol m<sup>-2</sup> mean daily photosynthetic photon flux.



**Figure 2: Examples of hemispherical photographs taken in high-light (left), intermediate-light (centre), and low-light (right) environments**

RGR and height growth rates at 20% light transmission were calculated using a regression across a range of light environments. Light compensation points of stem growth were used as a measure of shade tolerance as they correlate well with both understorey mortality rates and minimum light requirements for juvenile tree species (Lusk & Jorgensen, 2013). Compensation points are calculated by measuring the stem relative growth rate of seedlings over a range of light environments to calculate the light level at which net growth equals zero (Baltzer & Thomas, 2007).

This study used a regression against log(light) model which is one of two functions that have been commonly used to model the response of relative growth rate to light availability and accurately approximate growth responses to light, the other being a Michaelis-Menten-type response (Sack & Grubb, 2001; Kitajima & Bolker, 2003). The use of regression against log(light) in this study is supported

by Lusk and Jorgensen (2013) who found regression against log(light) to slightly better explain growth than the Michaelis-Menten model.

Two-tailed t-tests were used to compare compensation points and high-light growth in warm- and cool-temperate assemblages. A major axis test was then used to analyse the relationship between compensation point and growth in high light (Warton *et al.*, 2006).

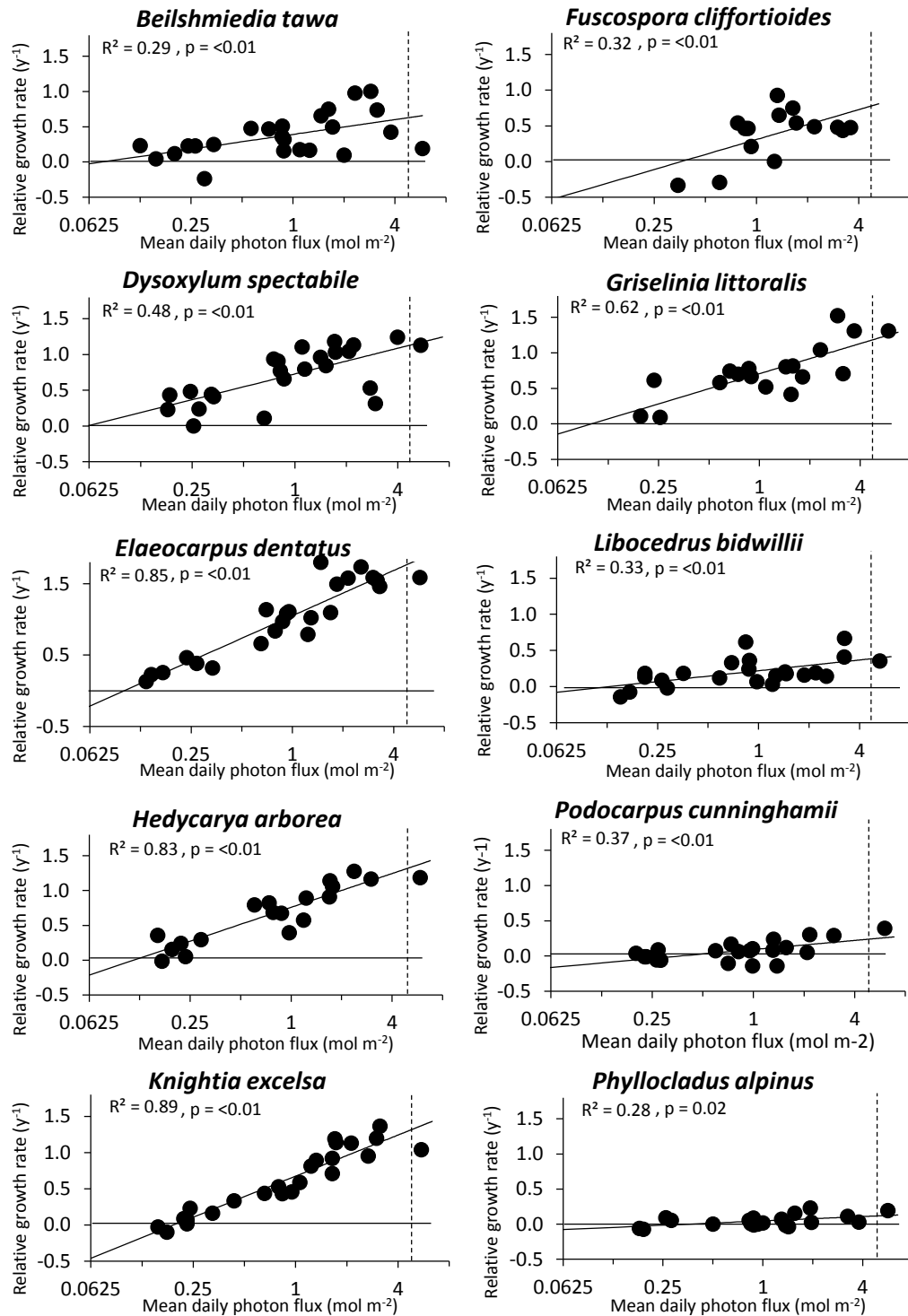
**Table 1. Species included in experiment**

| Origin         | Species                          | Family         | Height (mm) |
|----------------|----------------------------------|----------------|-------------|
| Warm-temperate | <i>Beilshmedia tawa</i>          | Lauraceae      | 382 ± 10    |
| Warm-temperate | <i>Dysoxylum spectabile</i>      | Meliaceae      | 382 ± 14    |
| Warm-temperate | <i>Hedycarya arborea</i>         | Monimiaceae    | 602 ± 13    |
| Warm-temperate | <i>Elaeocarpus dentatus</i>      | Elaeocarpaceae | 489 ± 12    |
| Warm-temperate | <i>Knightia excelsa</i>          | Proteaceae     | 403 ± 9     |
| Cool-temperate | <i>Griselinia littoralis</i>     | Griselinaceae  | 376 ± 6     |
| Cool-temperate | <i>Fuscospora cliffortioides</i> | Nothofagaceae  | 501 ± 23    |
| Cool-temperate | <i>Libocedrus bidwillii</i>      | Cupressaceae   | 417 ± 8     |
| Cool-temperate | <i>Podocarpus cunninghamii</i>   | Podocarpaceae  | 592 ± 24    |
| Cool-temperate | <i>Phyllocladus alpinus</i>      | Podocarpaceae  | 532 ± 15    |

## 2.4 Results

Relative growth rates for all species were significantly correlated with log mean daily photon flux, facilitating the calculation of compensation points for each species ( ). Species responses to light varied substantially both between and within the warm- and cool-temperate assemblages (Figures 4-5). Maximum relative growth rates ranged from 0.63 (*Beilshmedia tawa*) to 1.80 (*Elaeocarpus*

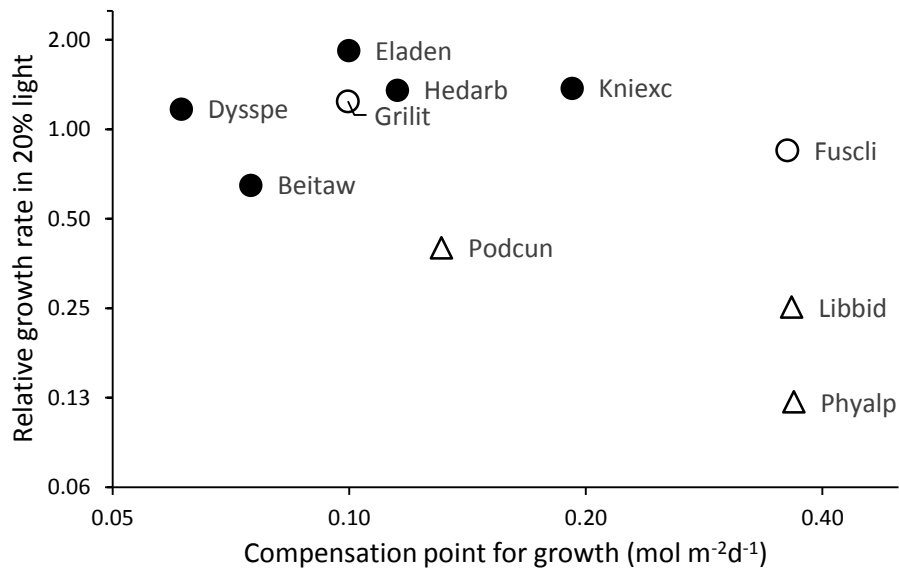
*dentatus*) for the warm-temperate species and from 0.12 (*Phyllocladus alpinus*) to 1.20 (*Griselinia littoralis*) for the cool-temperate species. Maximum height growth rates showed a similar trend with warm-temperate species ranging from 130 mm y<sup>-1</sup> (*Beilshmiadia tawa*) to 570 mm y<sup>-1</sup> (*Elaeocarpus dentatus*) for the warm-temperate species and from 12 mm y<sup>-1</sup> (*Phyllocladus alpinus*) to 260 mm y<sup>-1</sup> (*Griselinia littoralis*) for the cool-temperate species. These growth measurements were compared with compensation points, which ranged from 0.06 mol m<sup>-2</sup> (*Dysoxylum spectabile*) to 0.19 mol m<sup>-2</sup> (*Knightia excelsa*) for the warm-temperate species and from 0.10 mol m<sup>-2</sup> (*Griselinia littoralis*) to 0.37 mol m<sup>-2</sup> (*Fuscospora cliffortioides*) for the cool-temperate species.



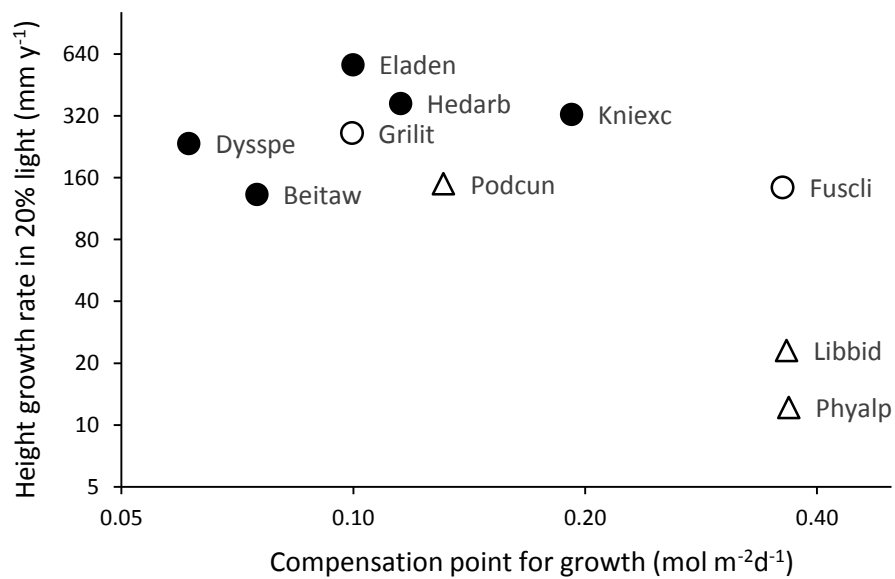
**Figure 3: Regressions of stem relative growth rate and mean daily photon flux for warm-temperate (left) and cool-temperate (right) tree species. The dashed line indicates the mean daily photon flux that is the equivalent of 20% light availability at the site.**

A major axis test of the relative growth rate and compensation point data (Figures 4-5) revealed a significant overall negative relationship between relative growth rate at 20% light and compensation point. The major axis test showed no difference in slope ( $p=0.56$ ) and no shift in elevation ( $=0.91$ ), but a significant shift along a common slope ( $p=0.02$ ). The major axis test for height growth rate at 20% light and compensation point showed the same relationship with no difference in slope ( $p=0.48$ ) and no shift in elevation ( $=0.91$ ), but the same significant shift along a common slope ( $p=0.02$ ). This indicates that the warm-temperate species are on average both faster-growing in high light and more shade-tolerant than the cool-temperate species.

The common axis shared by both assemblages is an unexpected result as the overall relationship between shade tolerance and maximum growth rate has a negative slope – the opposite of conventional shade tolerance-growth rate trade-offs. Also, the originally hypothesized model predicted two separate axes for the warm- and cool-temperate assemblages. Instead they were found to exist on the same axis but as significantly separate groups, the two assemblages being significantly different in terms of both compensation point ( $p=0.044$ ) and RGR at 20% light ( $p=0.046$ ); height growth at 20% light differed only marginally between the two assemblages ( $p=0.056$ ). This reflects a lack of strong relationships within groups but confirms the overall expectation that the shade tolerance-growth rate relationship differs between groups.



**Figure 4: Relationship between relative growth rate in high light and compensation point for angiosperms (circle), conifers (triangle), warm-temperate (black) and cool-temperate (white) species.**



**Figure 5: Relationship between height growth rate in high light and compensation point for angiosperms (circle), conifers (triangle), warm-temperate (black) and cool-temperate (white) species.**



## 2.5 Discussion

This study revealed significant differences between warm- and cool-temperate tree species in terms of their shade tolerance and growth rate. The warm-temperate species were both faster-growing and more shade-tolerant than their cool-temperate counterparts, traits that likely contribute to their competitive ability in warmer forest environments (Keddy & Maclellan, 1990; Loehle, 1998). The observed differences in growth rate support the general hypothesis of (Loehle, 1998) that there is a trade-off between maximum growth rate in warmer environments and tolerance of abiotic stressors in colder environments. These results also support the hypothesis of Lusk, *et al.* (2013) in that the relationship between shade tolerance and growth rate changes over temperature gradients. Growth rate and shade tolerance have been separately suggested as determinants of competitive ability (Keddy & Maclellan, 1990; Loehle, 1998) but evidence from this study indicates that shade tolerance and growth rate together play an integral role in determining competitiveness in the New Zealand forest environment. Despite supporting the hypothesis that the warm- and cool-temperate assemblages differ in their growth rate and shade tolerance, neither assemblage showed a distinct trade-off between shade tolerance and growth rate, on face value refuting the hypothesis that a shift in the growth rate vs shade tolerance relationship is associated with temperature gradients.

The lesser shade tolerance and growth rates of the cool-temperate species overall also supports the idea that cold-resistant traits come at the expense of traits that promote competitive ability in warmer environments. Investment in traits such as sclerophyllous leaves and cryoprotectants reduce carbon allocation to productive structures, reducing growth rates (Sakai, 1987; Atkin, *et al.*, 1996; Choat, *et al.*, 2011; Lusk, *et al.*, 2013). Lusk, *et al.* (2013) found cold-tolerant species to have a lower LAR, associated with limited shade tolerance; this probably reflects the importance of LAR for net carbon gain at low light levels (Poorter, 1999). Cold-tolerant species tend to have narrower conduits that are less prone to freeze-thaw embolism (Sperry, *et al.*, 1994), but at the cost of reductions in leaf area and/or photosynthetic capacity due to the associated reductions in hydraulic conductance

(Brodrigg & Feild, 2000; Meinzer, 2002; Mencuccini, 2003). The results of the study shown in Chapter 3 support this, also showing that cold-tolerant tree species have lower LAR and hydraulic conductivity. In a cold environment with frequent frosts these traits would provide a significant advantage over species adapted to warmer climates but in the absence of severe cold stress they restrict competitive ability (Loehle, 1998).

An important aspect of this study is the distribution of gymnosperms and angiosperms within the warm- and cool-temperate groups. Seven of the species used in this study were angiosperms (*B. tawa*, *D. spectabile*, *H. arborea*, *E. dentatus*, *K. excelsa*, *G. littoralis* and *F. cliffortioides*) and 3 were gymnosperms (*L. bidwillii*, *P. cunninghamii*, *P. alpinus*), with all of the gymnosperms belonging to the cool-temperate group. Many New Zealand forests have a canopy of broadleaved angiosperm trees with an emergent layer of gymnosperms. Conifers are typically cold-tolerant due to their tracheids that are naturally limited in diameter, an important cold resistance trait (Sperry & Sullivan, 1992; Sperry, *et al.*, 1994; Davis, *et al.*, 1999). Conifers also tend to occupy different niches from angiosperms, typically in emergent roles with long lifespans that utilise large disturbance events to facilitate regeneration (Wardle, 1991; Lusk & Ogden, 1992; Smale *et al.*, 1997). However, New Zealand conifers do not seem to exhibit the characteristics one would expect to find in a pioneer species as they have similar or slower juvenile growth rates than angiosperm canopy species (Lusk & Ogden, 1992; Russo *et al.*, 2010) and some species such as *Dacrydium cupressinum* and *Prumnopitys ferruginea* exhibit shade tolerance more commonly associated with late-successional species (Lusk *et al.*, 2009; Russo, *et al.*, 2010; Carswell *et al.*, 2012). This role difference between angiosperms and conifers may have had a significant impact on the results of this study. A recent study indicated that, while there was evidence of an underlying shade tolerance vs. growth rate trade-off in New Zealand angiosperm species, evidence of a similar relationship within the conifer species was not found (Lusk, *et al.*, 2015). The paper by Lusk, *et al.* (2015) also paralleled the results of this study, finding conifers performed poorly compared to their angiosperm counterparts and below the angiosperms trade-off

line. With this being the case, the inclusion of a more diverse cool-temperate species pool may further increase the representativeness of this study.

Few comparable studies exist within the warm- to cool- temperate rainforest environment but one such study measured growth and low-light mortality rates in two size classes of New Zealand tree species (Kunstler *et al.*, 2009). It was found that when comparing juveniles of the same age group the relationships were poor and only found a trade-off between growth and shade tolerance when comparing seedling shade tolerance and sapling growth rates. Where Kunstler, *et al.* (2009) found little evidence of a shade tolerance vs. growth rate trade-off, this study found no significant trade-off within warm- and cool-temperate assemblages but still found them to be distinctly different groups. As both studies take place in New Zealand temperate rainforest they are particularly relevant to each other, despite only sharing two species (*F. cliffortioides* and *P. cunninghamii*). However, our study only examined the seedling life stage and there is some evidence the light requirements of trees change with age (Kneeshaw *et al.*, 2006; Lusk *et al.*, 2008).

This study serves to reinforce several developing ideas in forest ecology but also provides questions and avenues of potential research that should be addressed. It seems that the results of this study are consistent with Loehle's hypothesis of a biotic equatorial limit and an abiotic poleward limit. Similarly, our results support the idea that both shade tolerance and growth rate play a role in the distribution of species along temperature gradients. However, the lack of a trade-off between shade tolerance and growth rate within the warm- and cool-temperate assemblages is unexpected and is at odds with what was expected at the beginning of this study. A similar study with a larger species pool would help clarify the relationships found in this study, as well as help differentiate between the warm- vs. cool-temperate comparison and the conifer vs. angiosperm comparison. It would also be relevant to extend the scope of this research to include smaller woody trees and shrubs as the different niches that they occupy within the forest environment may lead to similar shifts in the shade tolerance vs. growth rate trade-off.

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# **3 Physiological and morphological implications of climate-related variation in the xylem anatomy of temperate rainforest tree seedlings**

## **3.1 Abstract**

The trade-off between cold resistance and performance has been hypothesized to play a fundamental role in geographic sorting of tree species, where the need to mitigate the impact of frost events necessitates frost-resistant traits that reduce competitiveness in warmer environments. Of these traits conduit diameter is of particular importance as narrow conduits are less prone to embolism during frost events but are also less effective at conducting water to the leaves. This study attempts to elucidate the role of interspecific variation in stem conductivity of New Zealand canopy trees. It is hypothesized that the higher stem conductivity of warm-temperate compared to cool-temperate species could facilitate the deployment of a greater leaf area relative to biomass invested in stem, a higher photosynthetic capacity per unit leaf area, or both. The study was conducted using seedlings of ten New Zealand tree species, five from warm-temperate environments and five from cool-temperate environments. Seedlings were grown together in a shade house for four months before measuring leaf area ratio (LAR), specific leaf area (SLA), leaf mass fraction (LMF), photosynthetic capacity ( $A_{\max}$ ) and stomatal conductance ( $g_s$ ). Potential stem conductivity ( $K_s$ ), an estimate of conducting capacity per unit sapwood area, was calculated from conduit diameters measured on basal stem sections. A positive linear relationship was found between stem conductivity and LAR and SLA, but not LMF,  $A_{\max}$  or  $g_s$ . LAR and stem conductivity were significantly different between the warm and cool-temperate species with the warm-temperate species averaging 370% greater stem conductivity than the cool-temperate species, and c. 100% greater LAR. However, no significant relationships were found between hydraulic conductivity and LMF,  $A_{\max}$  or  $g_s$ . These differences were influenced by the presence of conifers in the

cool-temperate group, lowering the average  $K_s$  and LAR. These results suggest that the higher stem conductivity possible in warm-temperate environments facilitate the deployment of a greater leaf area relative to the total investment in biomass. Having a greater photosynthetic surface area provides a competitive advantage over less leafy species except when abiotic stressors such as frost reduce stem conductivity so that the leaves are limited by their water supply and do not reach their maximum potential level of performance.

### **3.2 Introduction**

Plant survival in any given environment is determined by a species' ability to both tolerate unfavourable conditions and effectively exploit resources to promote growth. These unfavourable conditions are driven by biotic and abiotic factors that vary in their impact over environmental gradients (Brown, *et al.*, 1996). The two strategies of tolerance and exploitation are commonly at odds, however, as traits that promote resistance to unfavourable conditions (such as frost) typically involve an energetic cost and are inefficient under favourable conditions (Larcher & Bauer, 1981; Chabot & Hicks, 1982; Santarius, 1984; Herms & Mattson, 1992; Wright *et al.*, 2001). These costs come in three forms: allocation costs such as the production of cryogenic molecules, specialization costs such as thinner conduits to provide resistance to freeze-thaw embolism, and opportunity costs such as conservative growth strategies (Saxe, *et al.*, 2001; Lusk *et al.*, 2013). This then influences the competitive potential of species along environmental gradients (Leathwick, 2001).

Originally the equatorial limit of a species' distribution was thought to be controlled by increasing temperatures but observations that many species achieved their best growth rates near their equatorial limit led to competition being proposed as the governing force (Schenk, 1996; Loehle, 1998). Loehle (1998) hypothesized that tree species distribution along temperature gradients was driven by a trade-off between growth rate and frost resistance with adaptations to colder climates reducing growth rates and making frost-resistant species less competitive towards their equatorial limit. Frost resistance had been established as important in determining the distribution of trees along temperature gradients

(Sakai, 1978; Bannister, 2007) but the idea that the associated costs affect competitive ability in warmer environments was novel.

A number of traits influence a species' cold resistance and a particularly important and well-studied example is xylem conduit diameter which influences the formation of embolisms during freezing events. Plants with wider xylem are more likely to cavitate after a freeze-thaw cycle because they produce larger bubbles that are more likely to form embolisms (Sperry, *et al.*, 1994; Davis, *et al.*, 1999; Feild & Brodribb, 2001). These embolisms block water transport through the embolised conduit as a continuous water column is necessary to draw water through the xylem (Tyree, *et al.*, 1994). Supporting this theory a correlation between conduit diameter and loss of hydraulic conductivity during freezing has been observed in many studies (Sperry & Sullivan, 1992; Davis, *et al.*, 1999; Pittermann & Sperry, 2003). Similarly, conduit diameter tends to decrease with altitude which is an environmental gradient closely tied with temperature changes (Charra-Vaskou *et al.*, 2012; Charrier *et al.*, 2013).

Conifers are particularly resistant to frost events as they have tracheids which are naturally limited in diameter (Sperry & Sullivan, 1992; Sperry, *et al.*, 1994; Davis, *et al.*, 1999). The narrow tracheids of conifers act to extend the growing season of cool temperate species in environments with extended periods of winter stress (Chabot & Hicks, 1982; Zimmermann, 1983; Sprugel, 1989). This strategy is in contrast with that of deciduous trees which have much wider conduits that are more conductive but also cavitate more easily during frost events (Wang *et al.*, 1992). These species shed their leaves during winter when their wide conduits would embolise and be unable to provide a sufficient water supply (Zimmermann, 1983; Sperry, *et al.*, 1994). In New Zealand however deciduous species are rare, with the majority of angiosperms maintaining their leaves throughout the year. These species would then be expected to potentially utilise the same frost resistant strategy of the coniferous species and have narrower conduits that are less prone to embolism.

Although it has been proposed that highly conductive stems support carbon gain and growth rates there have been conflicting reports on the mechanism by which

this happens. One idea involves the leaf area ratio (LAR) of a plant which represents the ‘leafiness’ of a plant. Ideally a plant would have a high LAR to maximise light interception and growth rates (Veneklaas & Poorter, 1998) but there are limits to the LAR a plant can support. The restriction on leaf area was typically thought to be due to the mechanical limits of the branches supporting the leaves’ weight with a higher LAR being accompanied by an increased weight and mechanical strain (Niklas, 1994). This was followed by another idea that leaf area is linked to the hydraulic supply of the stem with higher stem conductivities required to support higher leaf areas (Zimmermann, 1983; Tyree & Ewers, 1991; Pataki *et al.*, 1998). This coincides with other research that suggests that LAR and SLA are part of a suite of traits that contribute to high growth rates (Poorter & Remkes, 1990; Reich *et al.*, 1992). With this being the case we would expect to see tree species from cooler climates having a correspondingly lower LAR as freezing events necessitate narrower conduits and lower hydraulic conductivity.

Another potential idea is that a higher stem-specific hydraulic conductivity ( $K_s$ ) supports a higher photosynthetic capacity ( $A_{\max}$ ) per unit leaf area. We would expect to see photosynthetic rate be affected by leaf-specific hydraulic conductivity ( $K_l$ ) since evaporative water loss and  $\text{CO}_2$  uptake follow the same pathway (Brodribb & Feild, 2000).  $K_s$  is the conductance of a stem normalized by its cross-sectional area, a useful measure of the conducting efficiency of the xylem.  $K_l$  is a similar measure to  $K_s$  but is instead normalized by the total leaf area supplied by the stem, making it a measure of the stem’s ability to supply water to its leaves. Several studies have shown a correlation between photosynthetic capacity and  $K_l$ , indicating that maximum photosynthetic rate may be restricted by the hydraulic properties of the stem (Brodribb *et al.*, 2002; Santiago *et al.*, 2004; Brodribb *et al.*, 2005; Zhu *et al.*, 2013). Accordingly, significant correlations have also been found between  $K_l$  and stomatal conductance ( $g_s$ ) as the stomata act to maintain a consistent leaf-water status (Meinzer & Grantz, 1990; Sperry & Pockman, 1993; Comstock & Mencuccini, 1998; Meinzer *et al.*, 1999).  $K_s$  is related to photosynthetic capacity through the leaf-area to sapwood-area ratio (LSR), with variation in  $K_s$  influencing  $K_l$ .  $K_l$  can vary with changes in biomass allocation to

stems that alter stem area and the LSR, or with changes in conduit size and frequency, that alter  $K_s$ .

This study explores the relationships between stem hydraulic conductivity and the leaf area and gas exchange rates of New Zealand tree species from both warm- and cool- temperate environments. There are two possible hypotheses in this study. The first is that increased hydraulic conductivity supports greater leaf area relative to plant biomass, increasing the surface area available for light interception and photosynthesis. The second hypothesis is that a greater stem hydraulic conductivity facilitates productive leaf area with a higher photosynthetic capacity per unit area. This study seeks to determine whether these traits are associated with the temperature of the species' native habitat. These hypotheses are assessed using seedlings of New Zealand tree species grown in a shade-house environment.

### **3.3 Methods**

#### **3.3.1 Growing conditions**

For this experiment four seedlings of ten native New Zealand tree species were sourced from commercial nurseries (Table 1). Five of the species used originate from warm-temperate environments and the other five originate from cool-temperate environments (Leathwick, 1995) and represent a range of growth strategies from shade-tolerant to light-demanding (Grubb, *et al.*, 2013; Lusk & Jorgensen, 2013). Prior to examination the seedlings were allowed to acclimatise in a shade house environment for four months.

**Table 2: Species included in experiment**

| Origin         | Species                          | Family         | Main stem length (mm) |
|----------------|----------------------------------|----------------|-----------------------|
| Warm-temperate | <i>Beilshmedia tawa</i>          | Lauraceae      | 380 ± 9               |
| Warm-temperate | <i>Dysoxylum spectabile</i>      | Meliaceae      | 384 ± 11              |
| Warm-temperate | <i>Hedycarya arborea</i>         | Monimiaceae    | 596 ± 13              |
| Warm-temperate | <i>Elaeocarpus dentatus</i>      | Elaeocarpaceae | 490 ± 13              |
| Warm-temperate | <i>Knightia excelsa</i>          | Proteaceae     | 401 ± 8               |
| Cool-temperate | <i>Griselinia littoralis</i>     | Griselinaceae  | 375 ± 6               |
| Cool-temperate | <i>Fuscospora cliffortioides</i> | Nothofagaceae  | 489 ± 16              |
| Cool-temperate | <i>Libocedrus bidwillii</i>      | Cupressaceae   | 419 ± 7               |
| Cool-temperate | <i>Podocarpus cunninghamii</i>   | Podocarpaceae  | 587 ± 18              |
| Cool-temperate | <i>Phyllocladus alpinus</i>      | Podocarpaceae  | 534 ± 13              |

### 3.3.2 Potential hydraulic conductivity

For this study potential stem hydraulic conductivity ( $K_s$ ) was used as a measure of hydraulic conductivity and was calculated using the measured conduit frequency and lumen area of each species. A slide microtome (Reichert, Vienna, Austria) was used to take thin sections from the base of the stem. The sections were then photographed using an epifluorescence microscope (Olympus BH-2, Tokyo, Japan) with UV excitation and a long-pass filter set, enabling identification of conduits as lignin fluoresces brightly when exposed to ultraviolet light (Albinsson *et al.*, 1999). The image analysis program ImageJ (Schneider *et al.*, 2012) was used to measure the area of each conduit lumen within an area extending from the centre of the stem outwards at an angle of 45°, creating a ‘pie-slice’ section that is representative of the whole stem section.

Potential stem-specific conductivity for each stem was calculated using the equation provided by Tyree and Ewers (1991):



$$K_{\text{stem}} = \frac{\pi p}{128 \eta A} \sum_{i=1}^n d_{i=1}^4 \quad (\text{kg m}^{-1}\text{s}^{-1}\text{MPa}^{-1}) \quad \text{Equation 2}$$

Where  $p$  = the density of water ( $\text{kg m}^{-3}$ ),  $\eta$  = the dynamic viscosity of water (MP s),  $A$  = the cross-sectional area of the xylem near the stem base ( $\text{m}^2$ ) and  $d$  = the conduit diameter (m), with effective diameter calculated from lumen area by assuming conduits are circular in cross section.

Potential leaf-specific conductivity ( $K_l$ ) was calculated using a similar equation from Tyree and Ewers (1991):

$$K_{\text{leaf}} = \frac{\pi p}{128 \eta A} \sum_{i=1}^n d_{i=1}^4 \quad (\text{kg m}^{-1}\text{s}^{-1}\text{MPa}^{-1}) \quad \text{Equation 3}$$

Where  $p$  = the density of water ( $\text{kg m}^{-3}$ ),  $\eta$  = the dynamic viscosity of water (MPs),  $A$  = the total leaf area supplied by the stem ( $\text{m}^2$ ) and  $d$  = the conduit diameter (m).

It is important to note that in this study  $K_s$  is not the actual hydraulic conductivity of a stem, it is instead the estimated maximum potential conductivity that could occur through the sapwood in the absence of end-wall resistance. This is important as end-walls have been shown to contribute 50-60% of the total hydraulic resistance in a stem, leading predictions of conductivity based on conduit diameters to overestimate conductivity (Sperry *et al.*, 2006). However, a study by Choat *et al.* (2007) found that potential  $K_s$  correlated well with direct measurements of stem conductivity in tropical *Cordia* species.

Mean conduit hydraulic diameter ( $D_h$ ) was calculated from individual conduit diameters according to Equation 4 (Sperry, et al., 1994). Mean hydraulic diameter is a measure of conduit size weighted towards the diameter of conduit that contributes the most to the total hydraulic conductance of the stem (Davis, *et al.*, 1999).

$$D_h = \sum D^5 / \sum D^4 \quad \text{Equation 4}$$

### 3.3.3 Biomass distribution and leaf area

Leaf area ratio (LAR), specific leaf area (SLA), leaf mass fraction (LMF) and leaf-area to sapwood-area ratio (LSR) were calculated according to Equations 5-8. Total leaf area was measured by removing all leaves from the stem and then passing them through a leaf area meter (3100, Licor Inc., Nebraska). Total plant dry weight was measured by placing the washed roots, leaves and stem in a drying oven at 60°C for 48 hours.

$$\text{LAR} = \frac{\text{Total leaf area (mm}^2\text{)}}{\text{Total plant dry weight (g)}} \quad \text{Equation 5}$$

$$\text{SLA} = \frac{\text{Total leaf area (mm}^2\text{)}}{\text{Total leaf dry weight (g)}} \quad \text{Equation 6}$$

$$\text{LMF} = \frac{\text{Weight of leaves (g)}}{\text{Weight of plant (g)}} \quad \text{Equation 7}$$

$$\text{LSR} = \frac{\text{Total leaf area (m}^2\text{)}}{\text{Total sapwood area (m}^2\text{)}} \quad \text{Equation 8}$$

### 3.3.4 Gas exchange

Photosynthetic capacity ( $A_{\max}$ ) and stomatal conductance ( $g_s$ ) for each species was measured using a gas exchange system (LI-6400XT, Licor Inc., Lincoln, NE, USA) between the hours of 10am and 2pm. Measurements were taken on the most recent fully expanded leaves, avoiding the midrib where possible. For some species it was not possible to fill the 6cm<sup>2</sup> leaf chamber and so the area was measured using a leaf area meter (3100, Licor Inc., Nebraska). Relative humidity was kept at 70%, leaf temperature at 22°C and chamber CO<sub>2</sub> concentration at 400 ppm. Photosynthetically active radiation was increased over 15 minutes from 0 to 1500  $\mu\text{moles m}^{-2} \text{s}^{-1}$  PAR and then maintained until no significant fluctuations in  $A_{\max}$  or stomatal conductance were observed for at least 5 minutes.

### 3.3.5 Data analysis

All variables were log<sub>10</sub>-transformed to normalize the distribution of the data and tested for homogeneity of variances prior to statistical testing. Linear regressions

were used to examine relationships between stem-specific hydraulic conductivity and LAR, SLA, LMF,  $A_{\max}$  and  $g_s$ , leaf-specific conductivity and  $A_{\max}$  and  $g_s$ , and LAR and LSR. T-tests were used to establish significant differences between the warm- and cool-temperate species, as well as between the conifer and angiosperm species.

## 3.4 Results

### 3.4.1 Warm- vs. cool-temperate variation

Physiological measurements taken for this study revealed a wide range of values between species (Table 3). The species with the highest  $D_h$ ,  $K_s$  and  $K_l$  was *Hedycarya arborea* (25.8 $\mu$ m, 7.27 kg s<sup>-1</sup>m<sup>-1</sup>MPa<sup>-1</sup>, 0.135 kg s<sup>-1</sup>m<sup>-1</sup>MPa<sup>-1</sup>) while the species with the lowest  $D_h$ ,  $K_s$  and  $K_l$  was *Phyllocladus alpinus* (7.3 $\mu$ m, 0.004 kg s<sup>-1</sup>m<sup>-1</sup>MPa<sup>-1</sup>, 3x10<sup>-4</sup> kg s<sup>-1</sup>m<sup>-1</sup>MPa<sup>-1</sup>). For measurements of ‘leafiness’ the LAR values ranged from 7.8 cm<sup>2</sup> g<sup>-1</sup> (*P. alpinus*) to 47.6 cm<sup>2</sup> g<sup>-1</sup> (*Knightia excelsa*) while SLA values ranged from 44.0 cm<sup>2</sup> g<sup>-1</sup> (*P. alpinus*) and 154.1 cm<sup>2</sup> g<sup>-1</sup> (*Dysoxylum spectabile*) and LMF values ranged from 0.17 (*P. alpinus*) to 0.43 (*K. excelsa*). Leaf-area to sapwood-area ratio (LSR) values ranged from 15.1 (*Fuscospora cliffortioides*) to 68.4 (*H. arborea*). Leaf level measurements of photosynthesis gave  $A_{\max}$  values between 3.59  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> (*D. spectabile*) and 15.15  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> (*F. cliffortioides*) and  $g_s$  values between 0.04 mmol m<sup>-2</sup> s<sup>-1</sup> (*D. spectabile*) and 0.21 mmol m<sup>-2</sup> s<sup>-1</sup> (*F. cliffortioides*). Therefore, *H. arborea* was the ‘leafiest’ species, while *P. alpinus* was the least ‘leafy’. *F. cliffortioides* had the highest photosynthetic capacity while *D. spectabile* had the lowest.

**Table 3: Mean physiological and morphological measurements for each for each species used in study.**

|                          | $K_s$<br>(kg s <sup>-1</sup><br>m <sup>-1</sup> MPa <sup>-1</sup> ) | $K_l$<br>(kg s <sup>-1</sup><br>m <sup>-1</sup> MPa <sup>-1</sup> ) | $D_h$<br>(μm) | SLA<br>(cm <sup>2</sup> g <sup>-1</sup> ) | LAR<br>(cm <sup>2</sup> g <sup>-1</sup> ) | LMF  | LSR  | $A_{max}$<br>(μmol<br>m <sup>-2</sup> s <sup>-1</sup> ) | $g_s$<br>(mmol<br>m <sup>-2</sup> s <sup>-1</sup> ) |
|--------------------------|---|---|---------------|---|---|------|------|---|---|
| Warm-temperate           |   |   |               |   |   |      |      |   |   |
| <i>B. tawa</i>           | 0.99  | 0.036   | 18.54         | 112.0                                     | 36.7                                      | 0.33 | 29.4 | 5.47  | 0.06  |
| <i>D. spectabile</i>     | 2.43  | 0.061   | 23.42         | 154.1                                     | 35.8                                      | 0.23 | 41.3 | 3.59  | 0.04  |
| <i>E. dentatus</i>       | 0.74  | 0.034   | 14.09         | 129.8                                     | 27.4                                      | 0.21 | 22.3 | 8.14  | 0.13  |
| <i>H. arborea</i>        | 7.27  | 0.135   | 25.84         | 144.6                                     | 25.2                                      | 0.18 | 68.4 | 6.69  | 0.10  |
| <i>K. excelsa</i>        | 1.20  | 0.025   | 18.48         | 108.8                                     | 47.6                                      | 0.44 | 63.8 | 5.77  | 0.18  |
| Cool-temperate           |   |   |               |   |   |      |      |   |   |
| <i>G. littoralis</i>     | 2.06  | 0.041   | 16.09         | 90.0                                      | 25.4                                      | 0.34 | 57.9 | 10.65   | 0.15  |
| <i>F. cliffortioides</i> | 1.30  | 0.092   | 15.39         | 94.4                                      | 16.9                                      | 0.18 | 15.1 | 15.15   | 0.21  |
| <i>L. bidwillii</i>      | 0.01  | 3x10 <sup>-4</sup>  | 7.34          | 44.0                                      | 18.7                                      | 0.41 | 25.2 | 5.15  | 0.10  |
| <i>P. alpinus</i>        | 0.004   | 3x10 <sup>-4</sup>  | 8.07          | 44.2                                      | 7.8                                       | 0.18 | 25.6 | 5.43  | 0.06  |
| <i>P. cunninghamii</i>   | 0.01  | 5x10 <sup>-4</sup>  | 8.24          | 56.1                                      | 16.7                                      | 0.30 | 22.3 | 5.47  | 0.08  |

Warm-temperate species had significantly higher  $D_h$  (t-test,  $p=0.01$ ),  $K_s$  ( $p=0.05$ ), LAR ( $p=0.01$ ) and SLA ( $p=0.003$ ) than the cool-temperate species. Minor differences in  $K_l$  were also found between the warm- and cool-temperate groups ( $p=0.06$ ). However, no significant differences were found between the warm- and cool-temperate groups in terms of LMF ( $p=0.96$ ), LSR ( $p=0.18$ ),  $A_{max}$  ( $p=0.31$ ) or  $g_s$  ( $p=0.57$ ).  $D_h$  values were between 14.1 and 25.8  $\mu\text{m}$  for the warm-temperate species and between 7.3 and 16.1  $\mu\text{m}$  for the cool-temperate species while the  $K_s$  values were between 0.74 and 7.28  $\text{kg s}^{-1}\text{MPa}^{-1}$  for the warm-temperate species and between 0.004 and 2.06  $\text{kg s}^{-1}\text{MPa}^{-1}$  for the cool-temperate species. The other two variables with significant t-test results were LAR and SLA where the warm-temperate species had LAR values of 25-47  $\text{cm}^2 \text{g}^{-1}$  for the warm-temperate species and 7-25  $\text{cm}^2 \text{g}^{-1}$  for the cool-temperate species, and SLA values of 108-154  $\text{cm}^2 \text{g}^{-1}$  for the warm-temperate species and 44-90  $\text{cm}^2 \text{g}^{-1}$  for the cool-temperate species.

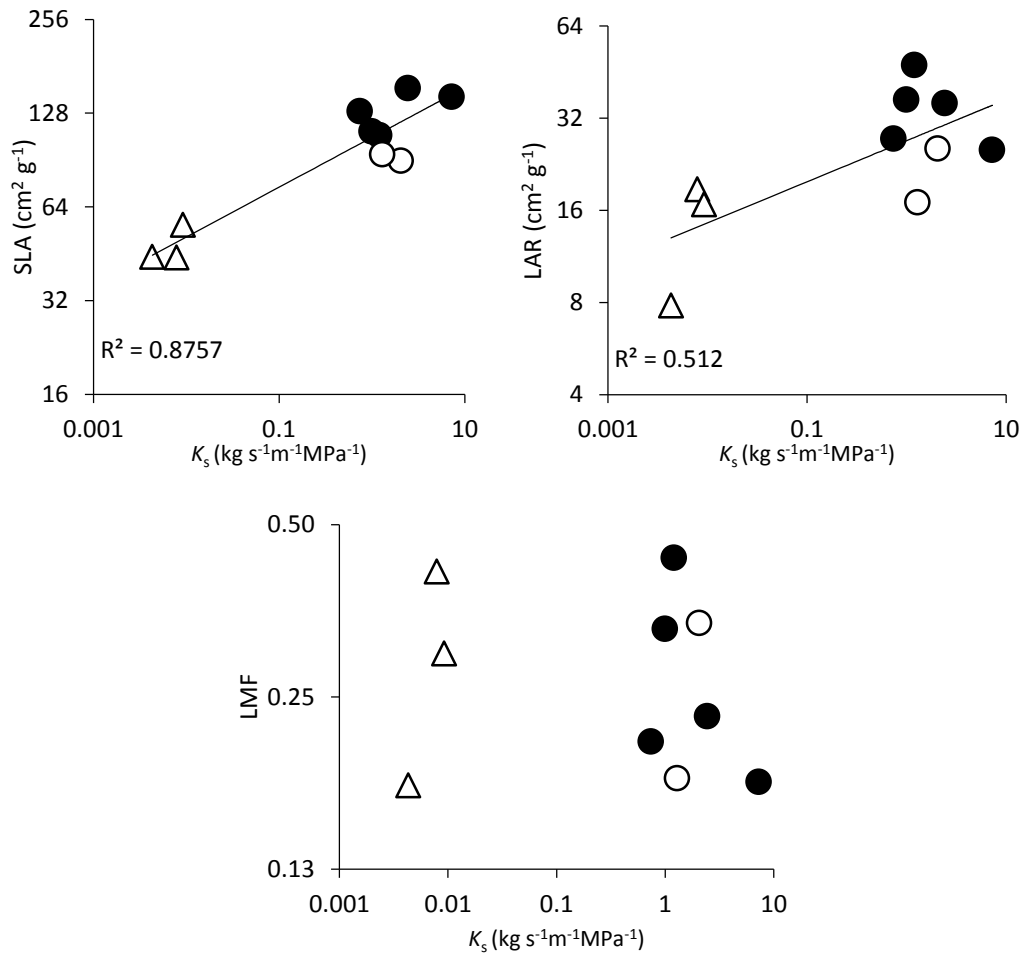
### 3.4.2 Conifer and angiosperm variation

Several variables differed significantly between angiosperms and conifers, with the angiosperms having distinctly higher  $D_h$  ( $p<0.001$ ),  $K_s$  ( $p<0.001$ ),  $K_l$  ( $p<0.001$ ), LAR ( $p=0.02$ ) and SLA ( $p<0.001$ ). However there were no significant differences in LMF ( $p=0.77$ ), LSR ( $p=0.25$ ),  $A_{max}$  ( $p=0.32$ ) or  $g_s$  ( $p=0.42$ ) between the angiosperm and conifer species. It is interesting to note that there were differences in  $K_l$  between the conifer s and angiosperms but not the warm-temperate and cool-temperate groups, a result that is likely driven by the differences in SLA. These results are similar to the results for the warm- and cool-temperate comparisons, clearly influenced by the identity of the species used in this study; three of the five cool-temperate species used were conifers whereas none of the warm-temperate species were conifers.

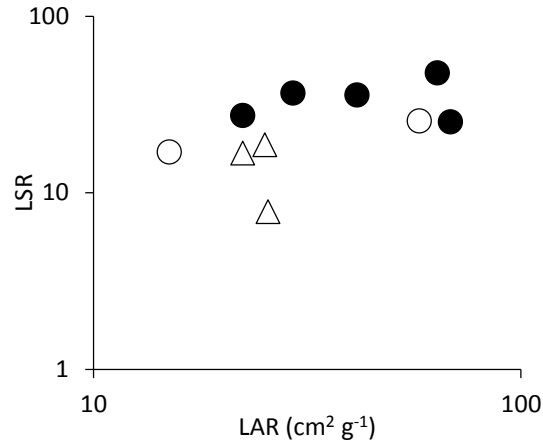
### 3.4.3 Hydraulic relationships

LAR and SLA, two measurements of investment in leaf area, were significantly correlated with  $K_s$  ( $p=0.02$  and  $<0.001$ ) (Figure 6). The  $R^2$  value of 0.51 for LAR indicates that there is a linear relationship between LAR and  $K_s$  but there is an even stronger correlation between SLA and  $K_s$  ( $R^2=0.88$ ). Conversely, LMF

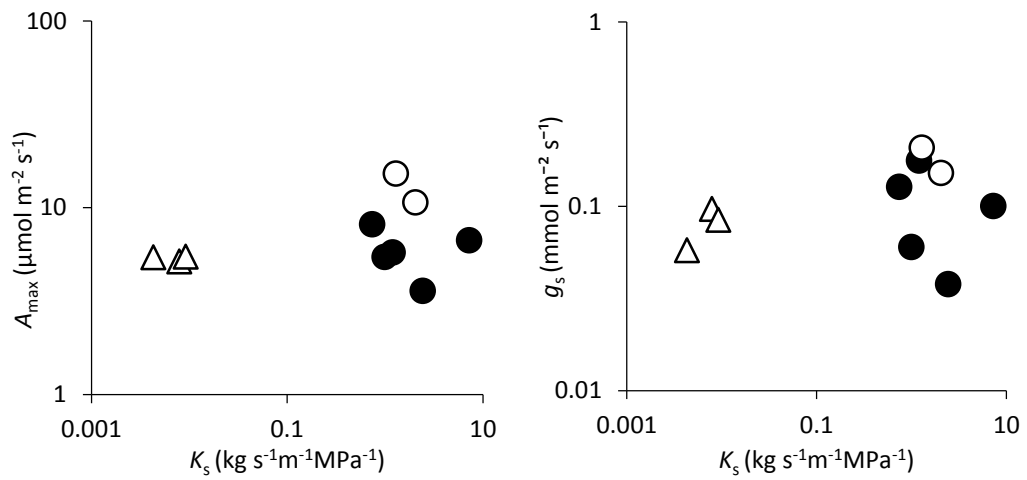
showed no correlation with  $K_s$  ( $p=0.71$ ) with an  $R^2$  value of 0.02. LAR values also showed some correlation with LSR (Figure 7). However, the two measurements of leaf-level gas exchange  $A_{\max}$  and  $g_s$  showed no clear relationships with hydraulic variables (Figure 8), with poor  $R^2$  (0.09 and 0.06) and  $p$ -values (0.41 and 0.49). A similar lack of relationships was found between leaf-specific conductivity and  $A_{\max}$  ( $p=0.46$ ) and  $g_s$  ( $p=0.87$ ) (Figure 9). Accordingly, species with a high  $K_s$  also had a high LAR and SLA. These results indicate that greater  $K_s$  values support a greater investment in ‘leafiness’, rather than higher leaf-level performance.



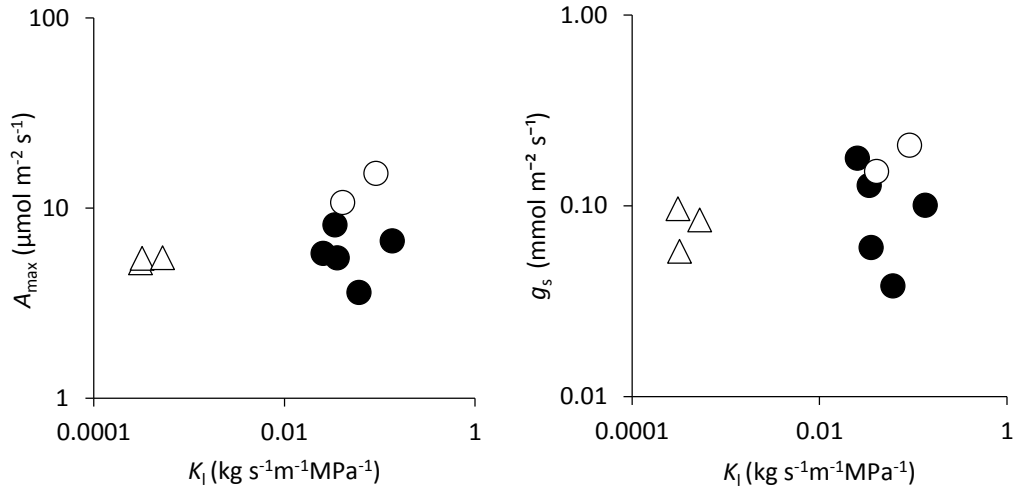
**Figure 6: Relationships of stem conductivity with LAR (upper left), SLA (upper right) and LMF (bottom centre) for angiosperms (circle), conifers (triangle), warm-temperate (black) and cool-temperate (white) species.**



**Figure 7: Relationship between LAR and LSR for angiosperms (circle), conifers (triangle), warm-temperate (black) and cool-temperate (white) species.**



**Figure 8: Relationships of stem-specific conductivity with photosynthetic capacity (left) and stomatal conductance (right) for angiosperms (circle), conifers (triangle), warm-temperate (black) and cool-temperate (white) species.**



**Figure 9: Relationships of leaf-specific conductivity with photosynthetic capacity (left) and stomatal conductance (right) for angiosperms (circle), conifers (triangle), warm-temperate (black) and cool-temperate (white) species.**

### 3.5 Discussion

Of the two mechanisms that could translate higher hydraulic conductivities into increased competitive ability, increased leafiness appeared to play a significant role. The  $K_s$  of the species examined correlated well with measurements of LAR and SLA (Figure 6), indicating that stem hydraulic conductivity is a significant determinant of leaf area deployment at both leaf-level and whole plant-levels.  $K_s$  accounted for 51% of the variation in LAR, an important aspect of growth and tolerance of shade (Poorter, 1999). The high LAR of the warm-temperate species was associated with a high SLA, rather than a high LMF. SLA is closely tied to relative growth rate, with plants with a higher SLA having correspondingly higher growth rate (Walters & Reich, 1999; Poorter *et al.*, 2005). As growth is a primary factor in competitive ability (Loehle, 1998) it would indicate that the link between hydraulic conductivity and ‘leafiness’ is a mechanism that reduces the competitive ability of cold-resistant species in warmer environments. An extensive study of competitive hierarchies in European forests found high SLA values to be associated with the ability to suppress neighbouring trees’ growth (Kunstler *et al.*, 2012). These findings that warm-temperate species have a higher LAR but not



photosynthetic capacity suggests that the higher productivity of warm-temperate species is driven by larger leaf areas rather than higher rates of photosynthesis per unit area.

While it was conceivable that increases in hydraulic conductivity could facilitate a more productive leaf area with higher gas exchange rates, this was not found to be the case (Figure 8). Furthermore there were no significant differences in gas exchange between the warm- and cool-temperate groups, indicating that photosynthetic capacity and stomatal conductance were not influenced by cold resistance. Brodribb and Feild (2000) originally found a relationship between leaf-specific hydraulic conductivity and quantum yield in New Caledonian and Tasmanian rainforest communities. Similarly, there has been some compelling evidence found to suggest a relationship between hydraulic conductivity and stomatal conductance as stomatal conductance plays such an integral role in balancing transpiration with the hydraulic resistance of the soil-leaf pathway (Meinzer, 2002). These findings were later supported by other findings that  $A_{\max}$  and  $g_s$  were correlated with leaf-specific hydraulic conductivity in a variety of tropical and temperate environments (Brodribb, *et al.*, 2002; Zhu, *et al.*, 2013). Neither  $K_s$  nor  $K_l$  were correlated with leaf level measures of photosynthetic capacity in this study meaning that hydraulic constraints may not have been an important determinant of leaf photosynthetic rates under the growth conditions used. Alternatively, stem potential hydraulic conductance may not have accurately reflected actual whole plant hydraulic conductance, because it did not include the effect of conduit end-wall, root, or leaf resistance, or the differences in end-wall frequency and resistance between conifers and angiosperms. A better although technically more challenging approach may be to directly measure whole plant hydraulic conductance using a flow meter.

The warm-temperate species had more conductive xylem with wider conduits than the cool-temperate species, indicating that conduit diameter and, by extension, hydraulic conductivity is limited by a need to tolerate frost events. Plants with wider xylem are more likely to cavitate after a freeze-thaw cycle because they produce larger bubbles that are more likely to form embolisms (Sperry, *et al.*,

1994; Davis, *et al.*, 1999; Feild & Brodribb, 2001). The close tie between conduit diameter and hydraulic conductivity (Tyree, *et al.*, 1994) means that in order to reduce the incidence of embolism formation during frost events a species must reduce its ability to efficiently transport water from the roots to the leaves.

An important consideration when interpreting the differences between the warm- and cool- temperate groups studied is that the warm- and cool-temperate distinction was intrinsically linked with phylogeny. Out of the 10 species used in this study 7 were angiosperms and 3 were conifers, with all of the conifers belonging to the cool-temperate group. This ratio is partially due to the natural prominence of conifers in cool-temperate forests as their physiology lends itself to cold resistance (Sperry, *et al.*, 1994; Davis, *et al.*, 1999). This study of New Zealand trees found that the conduit diameter and hydraulic conductivity of the conifer species were significantly lower than that of the angiosperms, regardless of whether they are warm- or cool-temperate, likely due to the naturally limited diameter of tracheids (Tyree & Ewers, 1991; Becker *et al.*, 1999). Some degree of hydraulic convergence between conifers and angiosperms has been seen in other forests (Brodribb & Feild, 2000), but does not appear to be the case with the species used in this study. This distinction was also true for the other traits, with conifers having significantly different SLA and LAR, but not LMF,  $A_{\max}$  or  $g_s$ . This indicates that differences in these traits are predominantly driven by the conifer-angiosperm differences as well. SLA in particular has been shown to be significantly lower in conifer species than angiosperm species (Reich *et al.*, 1995). Expanding the scope of this study to include more species, particularly warm-temperate conifers, would help determine just how important this distinction is as currently it is difficult to separate the effects of differences between warm- and cool-temperate species from the phylogeny of conifers and angiosperms.

This study broadly supports the idea of a trade-off between cold resistance and competitive ability, and serves to elucidate the mechanisms behind it. It was found that warm-temperate species had more conductive xylem, which was then found to correlate well with differences in LAR and SLA. It appears that the warm-temperate species used this conductive advantage to deploy a greater leaf area,

rather than higher gas exchange rates. This indicates that cool-temperate species will be less competitive in warmer environments as the necessity of cold resistance requires less conductive xylem that in turn restricts the plants' ability to deploy leaf area and assimilate carbon. A relevant avenue of further research following this study would be to use a larger species pool to more thoroughly test the relationships of LAR, SLA, LMF,  $A_{\max}$  and  $g_s$  with hydraulic conductivity, and the role that conifer and angiosperm species play. A wider array of growth forms such as shrubs or understory trees would also provide important insights as the relationships found in this study may shift when they are included.

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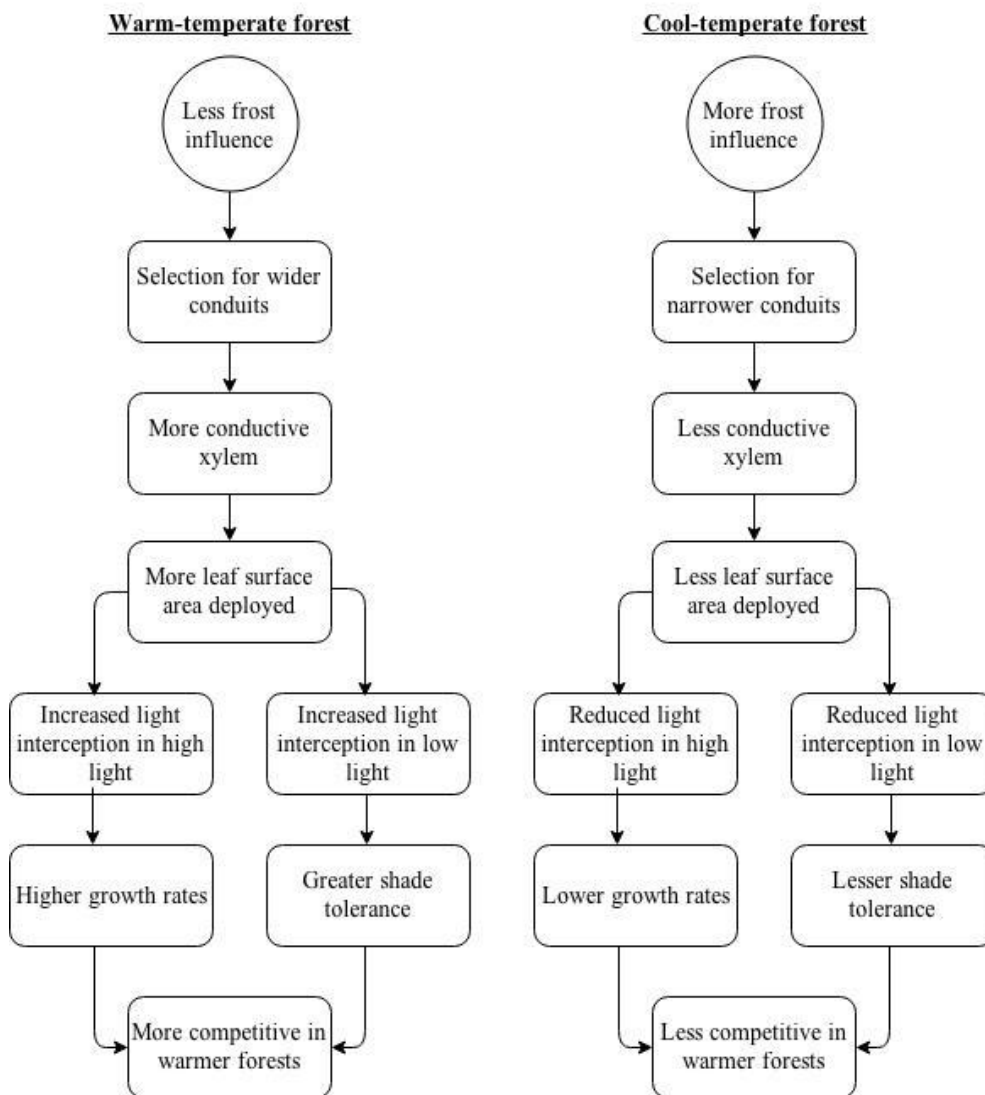
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## 4 Synthesis

This thesis aimed to expand our understanding of the role temperature gradients play in determining the ability of tree species to pass the physiological and biotic filters of a temperate rainforest. The first part of this thesis attempted to determine how the shade tolerance vs. growth rate trade-off changes from warm- to cool-temperate environments (Chapter 2), citing a study by Lusk, *et al.* (2013) that hypothesised a shift in this relationship rather than a single universal trade-off. This hypothesis was supported with evidence that warm-temperate tree species were both faster-growing and more shade-tolerant than their cool-temperate counterparts. The second study conducted aimed to examine the effects of climate-related variation in xylem anatomy on morphological and physiological traits related to competitive ability (Chapter 3). Two hypotheses were proposed: the first being that the conductive ability of a plant's xylem supports the deployment of a greater leaf area (Tyree & Ewers, 1991), and the second being that a higher hydraulic conductivity supports a greater photosynthetic capacity (Brodribb & Feild, 2000). The study in Chapter 3 found evidence that supported the first hypothesis as the hydraulic conductivity of the species examined was found to correlate highly with units of the species' 'leafiness', as well as showing significant differences in hydraulic conductivity, LAR and SLA between the warm- and cool-temperate species.

Taken together the results of this thesis present a sequence of effects that show how the selection for narrower vessels in cool-temperate environments can indirectly influence their competitive ability (Figure 10). The study in Chapter 3 found that cool-temperate species had narrower vessels than their warm-temperate counterparts, a result that has been shown before in other studies (Sperry, *et al.*, 1994). The narrower vessels of the cool-temperate species translated into a lower hydraulic conductivity which also showed significant differences between the two assemblages. Hydraulic conductivity was found to correlate well with measures of 'leafiness' (LAR and SLA), indicating that selection for frost-resistance could indirectly influence leaf deployment. LAR and SLA have been shown to play important roles in determining a species' growth rate and shade tolerance

(Poorter, 1999; Walters & Reich, 1999). This was supported by the evidence in Chapter 3 that warm-temperate species have a higher LAR and SLA than cool-temperate species, and the results of Chapter 2 that show the warm-temperate species having both a higher growth rate and a greater shade tolerance than the cool-temperate species. This then influences the species ability to pass the biotic filters of the forest environment (Lambers & Poorter, 1992) as growth rate and shade tolerance have been proposed as important competitive traits (Keddy & Maclellan, 1990; Loehle, 1998).



**Figure 10: The effect of frost influence on competitive ability in temperate forest environments**

The results presented in this thesis are relevant to several studies and ideas that explain ecological processes. Evidence from that cool-temperate species have narrower vessels supports the findings of other studies that propose vessel diameter as an important frost-resistant trait (Sperry, *et al.*, 1994; Davis, *et al.*, 1999). Significant correlations between LAR and stem-specific hydraulic conductivity support other studies that propose hydraulic conductivity as a limiting factor for the amount of leaf area that can be deployed (Tyree & Ewers, 1991). More generally these studies support the hypothesis of Loehle (1998) that tree species distribution along temperature gradients was driven by a trade-off between growth rate and frost resistance, finding that the warm-temperate species had more conductive xylem, a greater deployment of leaf area, faster growth rates and higher shade tolerance than the cool-temperate species. The higher growth rates and shade tolerance of the warm-temperate species compared to the cool-temperate species also supports the hypothesis of Lusk, *et al.* (2013) which proposed that species sorting along temperature gradients reflects a shift in the growth rate vs. shade tolerance trade-off. This thesis joins other ecophysiological studies that have supported the idea of a trade-off between resistance to environmental stressors and a species' ability intercept light and acquire carbon (Lambers & Poorter, 1992; Reich, *et al.*, 2003; Baltzer & Thomas, 2007) and adds evidence to the idea that the equatorial limit of a species' distribution is determined by biotic factors while the poleward limit is determined by abiotic factors (Dobzhansky, 1950; MacArthur, 1972).

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