Interactions between soil fertility and climate drive variation in functional traits in New Zealand forests

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Abstract

Plant functional traits provide a mechanistic approach to understanding the processes of environmental filtering and community assembly. Variation along environmental gradients results in changes in the adaptive values of traits. Climate and soil fertility are two dominant factors that drive these patterns of trait variation. These two factors simultaneously select for traits during environmental filtering. However, we do not understand how interactions between climate and soil fertility influence the variation in community-level traits of multiple plant organs. The roles of traits in New Zealand forests are also yet to be studied at a national scale.

This thesis aimed to determine the adaptive values of multiple functional traits across broad climate and soil fertility gradients in New Zealand forests. This was achieved by the following methods. Data were collected for leaf, stem, root, seed, flowering, and whole-plant traits from the 64 most common native trees in forests nationwide. Community composition and soil properties were measured at 324 plots across the country. For each plot, long-term average climate data were extracted from a model. A variable representing variation in soil fertility in the plots was derived by principal components analysis (PCA). Community-weighted mean (CWM) functional traits, i.e. average trait values weighted by the abundance of species, were calculated for each plot. Dimensionality of the specie-trait matrix was determined by PCA. Multiple linear regression was used to model the variation of each of the CWM traits as functions of mean annual temperature (MAT), vapour pressure deficit (VPD), soil fertility, soil fertility × MAT interaction, soil fertility × VPD interaction, total basal area and topography.

Five dimensions of trait variation were identified among New Zealand trees. Soil fertility was a more significant predictor of CWM traits than either of the climate variables. However, both of the interaction effects were significant for most traits and overrode the importance of the main effects. For example, in sites with high fertility soil, leaf economics traits varied from ‘slow’ in cool and dry conditions to ‘fast’ in warm and moist conditions, but in sites with low fertility, these traits were ‘slow’ in all climates. Therefore, the adaptive values of multiple functional traits of New Zealand forests varied depending on both soil fertility and climate.

This thesis provides the first recognition of the significant roles of the interaction effects between soil fertility and climate in driving variation in CWM traits from multiple plant organs. Climate and soil fertility interact in a way that influences CWM trait values independently from the influence of each environmental variable. These interactions are suspected to be important globally and should be tested for worldwide to confirm the generality of their effects. In conclusion, this thesis demonstrates that studying the relationships between CWM traits and soil fertility or climate independently is insufficient, when attempting to understand the process of environmental filtering. It is critical that the interaction effects between climate and soil fertility are included in future studies to enhance our understanding and ability to predict community-level responses to processes such as climate change.

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Thesis outline

Chapter One: Literature review

This chapter provides background information as a foundation for the following research chapter. The review begins with a description of functional trait-based ecology and its applications in restoration. Variation in climate and soil fertility both worldwide and in New Zealand is described, followed by a description of some of the main plant functional traits. Previously observed relationships between these traits and both climate and soil fertility are described. The importance of trade-offs and economic spectra in plant traits are described, as is the importance of recognising the intrinsic dimensionality of multi-trait datasets. The interaction effects between climate and soil fertility are recognised as a potentially critical but currently uninvestigated driver of variation in community-weighted mean plant traits.

Chapter Two: The adaptive value of functional traits across broad soil fertility and climate gradients in New Zealand forests

This chapter presents the introduction, aims, methods, results and discussion for the research. The overall aim was to determine the adaptive values of multiple functional traits across broad climate and soil fertility gradients in New Zealand forests.

Chapter Three: Synthesis

This chapter summarises the main findings of Chapter Two and presents some limitations of the study. Applications of these observations and recommendations for further research to build on these conclusions are also discussed.

1 Chapter One: Literature review

1.1 Overview

This literature review provides background information to lay the foundations for the research presented in Chapter Two. First, this review will provide a description of what functional trait-based ecology is, how it differs from more traditional species-focused ecology and will describe its applications for restoration ecology. Second, the important roles of climate and soil fertility in driving variations in functional traits will be discussed. Third, the importance of recognising dimensionality, economic spectra and trade-offs in studies of trait-based ecology will be explained. Fourth, the traits used in the following research and previously observed relationships between these traits and both climate and soil fertility will be described. Finally, the knowledge gap in the role of the interactions between soil fertility and climate in driving variation in functional traits will be identified which will lead on to the research presented in the following chapter.

1.2 What is functional trait-based ecology?

Traditional ecological studies have assessed how the distributions of species vary across landscapes (Grime 1993). Some of these, such as Clarkson (1985a), Druitt *et al.* (1990), Wardle (1964), and Leathwick (1995), assessed how environmental gradients such as temperature or moisture availability relate to these distributions. Concurrently, plant physiology has looked at the influence of changing environmental conditions on species' functional responses (Taiz & Zeiger 2002). Functional trait-based ecology serves to bridge these two subjects, in order to generate a deeper understanding of why the distribution patterns of species vary across environmental gradients (Williams & Eamus 1997). Trait-based ecology has a range of applications from community ecology as in this thesis, to evolutionary studies, conservation biology and invasion biogeography (Kattge *et al.* 2011).

A trait is defined as "any morphological, physiological or phenological character that impacts fitness indirectly via its effects on growth, reproduction and survival" (Violle *et al.* 2007). Plant functional traits therefore provide an indication of how the attributes of an individual influence its overall function and success. There are many traits that can be measured on any plant organ. For example, leaf nitrogen concentration is an example of a leaf trait. The value of a trait of an individual reflects how well that individual can perform the function represented by the trait. For example, leaves with higher leaf N concentration are able to photosynthesise faster than leaves with low N concentration. Trait-based ecology studies how the values of traits vary across environmental gradients (Violle, *et al.* 2007).

When assessing how traits influence species- or community-level patterns, it is important to study appropriate traits. The target is to choose traits with standard measurement protocols, that strongly reflect aspects of plant function and have significant relationships with environmental gradients (Cornelissen *et al.* 2003a). A large number of traits relating to core plant functions are recognised as appropriate (Grime *et al.* 1997). These include leaf traits (such as leaf N concentration), wood traits (such as wood density), root traits (such as root diameter) and seed traits (such as seed mass) (Westoby *et al.* 2002; Westoby & Wright 2006; Perez-Harguindeguy *et al.* 2013; Laughlin 2014a).

Ecologists have recognised for centuries that functional traits influence the distribution of species across landscapes. For instance, Darwin (1859) recognised that “the advantages of diversification of structure, with the accompanying differences of habit and constitution, determine the inhabitants of a site.” Despite this, ecologists continue to be faced with the challenge of predicting community composition and corresponding function across changing time periods, geographic regions and environmental conditions (Webb *et al.* 2010). Trait-based approaches to modelling community assembly have been rapidly developed and tested on many scales in the past decade (Kraft *et al.* 2008). In trait-based ecology, traits provide a mechanistic link between changes in plant communities across environmental gradients and the driving factors for these distributions (Shipley *et al.* 2006). This link enables ecologists to better understand the mechanisms by which and the reasons why a particular assemblage of species grows in certain geographic areas. The use of traits enables scientists to make generalizable conclusions, which are more useful in predictions than conclusions from traditional ecological approaches that tend to be species-specific (McGill *et al.* 2006). Functional trait-based ecology thus is a step forward by providing a deterministic relationship between plant physiology and the environment that promises more predictive and quantitative power for ecology (McGill, *et al.* 2006; Westoby & Wright 2006; Kattge, *et al.* 2011; Laughlin *et al.* 2011; Reich 2014).

1.2.1 The use of functional traits at the community-level

Community assembly is “the process by which species are selected from a regional species pool to inhabit a community in differing abundances” (HilleRisLambers *et al.* 2012). Community assembly is governed by a set of assembly rules which can be considered as a community-level analogue of natural selection (Keddy 1992; HilleRisLambers, *et al.* 2012). Natural selection is the gradual evolutionary process whereby key characteristics of individuals become more or less common in a population depending on the relative contribution of these characteristics to the reproductive fitness of the ancestors of the population (Darwin 1859). Similarly, assembly rules specify which subset of species in the total pool of available species will tolerate the conditions of a given site (Keddy 1992). The main assembly rule acting on a broad scale is environmental filtering (Messier *et al.* 2010; Laughlin *et al.* 2012).

Community assembly involves a number of processes acting at a variety of spatiotemporal scales. Species comprising a regional species pool are constrained by processes such as evolution, long-term disturbances, chance, and dispersal ability (Vellend 2010). Environmental filtering then occurs, whereby species from the regional pool that have functional trait values which confer the highest fitness and performance in the presence of the given environmental factors (such as climate, soil and disturbances) will be most abundant in the community, while species with less suitable trait values in the given conditions will be absent or occur in low abundance (Keddy 1992). For example, in dry conditions, species with resource-conserving traits (eg. higher wood density) have a selective advantage and are expected to be more abundant than species with productive traits (lower wood density) (Hacke & Sperry 2001). Environmental filtering results in species with similar trait values occurring together in a community more often than would be expected by chance (Keddy 1992; HilleRisLambers, *et al.* 2012; Laughlin, *et al.* 2012).

Functional traits can be used to understand the environmental filtering process of community assembly. This requires two datasets; a list of all species in the wider area and a database of the trait values of those species (Keddy 1992). A database of environmental conditions for the given area can then be used to generate environmental filters that govern which traits will be suitable in the given conditions (HilleRisLambers, *et al.* 2012). The species with traits that meet the conditions of the environmental filters will be the species in the resulting community (Grime, *et al.* 1997). The relative abundance of a species in the community will also reflect the suitability of the traits of that species to the given conditions (Keddy 1992). Species that have more organs with traits suited to the given conditions will be more successful and thus attain a greater relative abundance than species with fewer suitable traits.

Community-weighted mean (CWM) traits are often used in community-level trait studies. CWM traits are determined from the average value of a trait within a community, weighted by the relative abundance of each species (Laughlin 2011; Lavorel *et al.* 2011). Trait values that promote fitness in a given environment will be more abundant in that environment and will therefore have a stronger influence on the value of the CWM trait (Shipley *et al.* 2011). For example, high CWM specific leaf area is favourable in moist environments, but low CWM specific leaf area is favoured in dry sites across Australia (Schulze *et al.* 2006). Therefore, the use of CWM traits enables researchers to assess which trait values promote fitness in differing environmental conditions (Keddy 1992).

A trait-based approach to community assembly simultaneously provides predictive and explanatory power because it specifies how environmental filters alter trait distributions (Keddy 1992; Webb, *et al.* 2010). Based on knowledge of relationships between CWM traits and environmental gradients, trait-based ecology at the community-level is to be able to predict which trait values (and thus species) are favoured in particular environmental conditions. This is potentially the key to unlocking a method to predict community and species distributions, which has been considered a ‘Holy Grail’ of ecology (Lavorel & Garnier 2002; Suding & Goldstein 2008).

1.2.2 Applications of functional trait-based ecology in restoration

Ecological restoration is one field in which trait-based ecology can be exceptionally beneficial (Sandel *et al.* 2011; Laughlin 2014b). Traditional restoration of degraded ecosystems relies on the availability of suitable reference sites (Society for Ecological Restoration International Science & Policy Working Group 2004). These are sites in a similar location and with similar conditions to what would be expected to occur in a degraded site prior to degradation. Historic records for the pre-disturbance ecosystems can also be used in addition to or instead of reference sites (Society for Ecological Restoration International Science & Policy Working Group 2004). Reference sites are used to guide the restoration of a degraded site by gradually reverting the degraded site towards the conditions existing in the reference site (White & Walker 1997).

However, because the degradation of natural, ‘pristine’ ecosystems is so severe worldwide, it is increasingly difficult to find suitable reference sites (Society for Ecological Restoration International Science & Policy Working Group 2004). There is a lack of confidence in reference sites is compounded in several ways. The use of historic reference conditions is debated because it is difficult to decide which time frame is suitable to use. Many regions have had centuries of human modification, which tends to make the use of historic conditions unrealistic or unattainable (Palmer *et al.* 1997; Thorpe & Stanley 2011). For example, in New Zealand, it must be decided if the goals of restoration are to revert a site to conditions similar to those of pre-human arrival, pre-Polynesian arrival or pre-European arrival, each of which resembled quite different ecosystems (White & Walker 1997). In addition, climate change, species extinctions and invasions are making it less achievable and realistic to revert a site to a state that reflects traditional reference conditions (Harris *et al.* 2006; Hobbs *et al.* 2009).

Consequently, ecologists are suggesting that the aims of restoration projects should focus on returning degraded systems to a self-sustaining and functioning state, rather than to a ‘fantasised’ historic state (Suding 2011; Thorpe & Stanley 2011). As the world faces environmental changes, it is more meaningful to prepare a site for what conditions it may have to face in the future. In some cases it may not be possible to return a site to within its historic range of condition, so the best target for restoration may be a non-historical state, which offers the most resilient, self-sustaining and functioning ecosystem (Seastedt *et al.* 2008; Jackson & Hobbs 2009; Suding 2011).

Models using functional traits can be used to help facilitate this modern type of restoration planning (Sandel, *et al.* 2011). Knowledge of which trait values are likely to be favoured in given environmental conditions is important preliminary information for these models. From this, ecologists can predict which species and in what relative abundance species are likely to occur in given conditions (Shipley, *et al.* 2011). Such functional trait-based models can be used for predictions of species assemblages and distributions in current as well as future predicted climatic conditions (Laughlin, *et al.* 2011; Frenette-Dussault *et al.* 2013). These models can also be used to predict how ecosystem functions are likely to change when a community is restored (Laughlin 2014b), or whether a certain weed species is likely to become invasive (Moles *et al.* 2008; Godoy *et al.* 2011). Two of the most important environmental factors that drive variation in functional traits are climate and soil fertility (Maire *et al.* 2015).

1.3 Climate

Climatic factors influence the growth rates, timing of reproductive events and survival of plants (Grace 1987). Vegetation distributions depend on climate because the ability of plant species to tolerate temperature and moisture levels and consequently be successful in a given site determines the likelihood of its survival in those conditions (Woodward & McKee 1991). For example, in hot, dry climates species that can tolerate drought are likely to be favoured (McDowell *et al.* 2008).

Two climatic parameters that will be used throughout the research in Chapter Two are mean annual temperature (MAT) and vapour pressure deficit (VPD). MAT is defined as the mean of the 12 monthly averages for daily average temperature (Leathwick *et al.* 2002). VPD is defined as the difference between the pressure exerted by the moisture in the air and the pressure exerted by the moisture that the air can hold when saturated, both measured at the same temperature (Leathwick, *et al.* 2002). High VPD reflects dry conditions and low VPD reflects moist conditions (Howell & Dusek 1995).

New Zealand's climate is described as temperate oceanic. The three main islands span 1500 km and 13° of latitude (34 ° to 47 °S), resulting in many regional climatic variations from warm temperate in the North Island and the Nelson and Marlborough regions in the South Island, to cool temperate throughout the rest of the South Island and Stewart Island (Wardle 1984). Mountain ranges and volcanoes have strong influences on the climatic patterns in New Zealand.

In the North Island, an axis of greywacke mountain ranges extends from the Raukumara Ranges in East Cape, through the Huiarau, Kaimanawa, Kaweka, Ruahine, Tararua, Rimutaka and Aorangi Ranges to Cape Palliser. These ranges have summits of 1,500 – 1,730 m and cover 20 % of the land area (Mackintosh 2001). The three mountains above 2,000 m in the North Island are the volcanoes of Mt Ruapehu (2,797 m) and Mt Ngauruhoe (2,287 m) in the centre, and Mt Taranaki (2,518 m) in the west. In the South Island, the Southern Alps extend from Nelson Lakes in the north-east to Milford Sound in the south-west. The Southern Alps are longer than the ranges in the North Island and contain all the mountains over 3,000 m in New Zealand (Mackintosh 2001).

Most areas in New Zealand receive between 600 mm and 1,600 mm of rainfall per year (Figure 1.1). The Southern Alps create a rain shadow effect with a pronounced moisture gradient from wet in the west to drier on the eastern lee side of the Alps (Sinclair *et al.* 1997). The West Coast of the South Island is the wettest area in New Zealand, with up to 5,000 mm of rainfall a year. In contrast, the east coast of the South Island is the driest region in the country, with rainfall as low as 210 mm per year (Sinclair, *et al.* 1997). The North Island also has higher rainfall on the western side than the eastern side, although the difference is not as pronounced as that in the South Island (Mackintosh 2001).

MAT at sea level spans from 18 °C in the northern most regions of New Zealand, to 10 °C in southern most regions of the South Island (Figure 1.2). MAT also varies with altitude, decreasing about 0.7 °C for every 100 m increase in altitude (Mackintosh 2001). Therefore the lowest MAT of 4 °C occurs on mountain tops. Permanent snow cover is restricted to the mountainous areas and seasonal snowfall occurs in low-lying, eastern and southern parts of the South Island (Molloy 1998).

Frosts can occur throughout New Zealand (Mackintosh 2001). July is usually the coldest month and January or February are the warmest months. Inland and to the east of the ranges, the temperature can vary up to 14 °C between summer and winter, while elsewhere this variation is much lower (Mackintosh 2001).

Climatic effects on trait and species distributions are important because the climate is changing on a global scale. Climate change is a major concern globally, affecting social, economic and environmental wellbeing (Long & Ort 2010; Harrington *et al.* 2014). The IPCC has confirmed that climate warming is unambiguous (IPCC 2007) and there is concern because the current rate of climate change exceeds the bounds of natural climatic variation (Karl & Trenberth 2003). Models predict an average increase in temperatures globally, combined with decreased precipitation in dry regions and increased precipitation in wet regions (Ministry for the Environment 2001; IPCC 2007).

The impacts of climate change worldwide are apparent from observations of biotic and abiotic changes. These include retreating glaciers (Thompson *et al.* 2011) and mean advancement of spring events by 2.3 days per decade (Parmesan & Yohe 2003). Natural communities are currently showing shifts of species ranges averaging up to 6.1 km towards the poles per decade (Parmesan & Yohe 2003; Lenoir *et al.* 2008) and an increasing the occurrence of pollinator mismatch (Petanidou *et al.* 2014). Climate change is expected to increase the extinction rate of species, and to threaten up to one in six species, with the risks being highest for endemic species in regions with no analogous climates (Urban 2015). To avoid extinction, species may respond through 'plastic' changes in physiology, alteration of community structure, or migration to more suitable habitats (Vitt *et al.* 2010).

Climate change is a global phenomenon, however the changes in climate are not uniform across the planet (Ministry for the Environment 2001; IPCC 2007). In New Zealand, global change scenarios predict a relatively even increase in MAT of 0.7-0.9 °C by 2040, and 1.3 - 2.6 °C by 2090 (Kirschbaum *et al.* 2012). When combined with temperature predictions, mean annual rainfall is predicted to change by between -31 % and +44 % by 2090. Rainfall patterns will have more spatial variation than temperature patterns. Regions which currently receive adequate or high rainfall are expected to receive more rain, while regions that currently have low rainfall are expected to experience a decrease in rainfall (Ministry for the Environment 2001). The large area of ocean surrounding New Zealand is expected to buffer against the effects of climate change (Kirschbaum, *et al.* 2012). As a consequence, large changes in species distributions are less likely in New Zealand than in continental countries (McGlone *et al.* 2010a).

The serious potential for major biome shifts triggered by anthropogenic climate change has led researchers in ecology to consider drastic options, such as assisting migration of species to areas where the climate will be more suitable for them in the future (Vitt *et al.* 2009). This is particularly useful in cases where the organism is incapable of moving to the more suitable area itself, or in doing so in a sufficiently timely manner (Vitt, *et al.* 2010). However, there is controversial opposition to these actions by some who claim that such interference with species distributions is not always ethically justified (Albrecht *et al.* 2013; Ahteensuu & Lehvavirta 2014). Human-assisted movements of species rely on our ability to make sound predictions of species range shifts. Trait-based ecology aims to provide this ability.

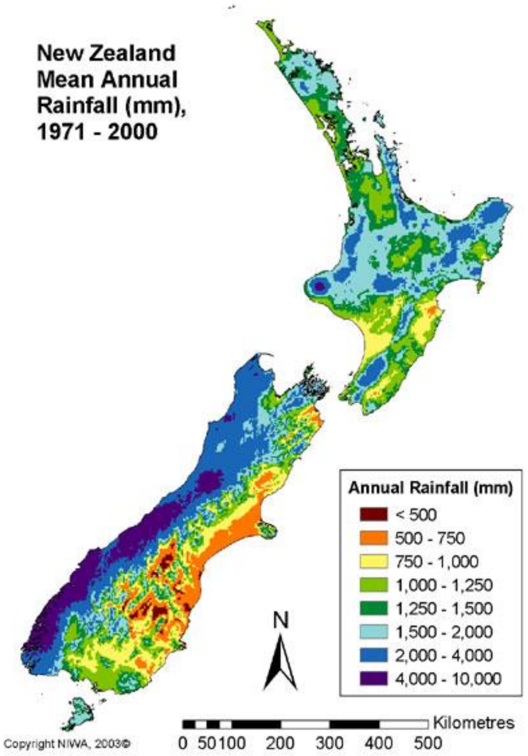


Figure 1.1: Map of mean annual rainfall in New Zealand between 1971 and 2000. Source: Mackintosh (2001).

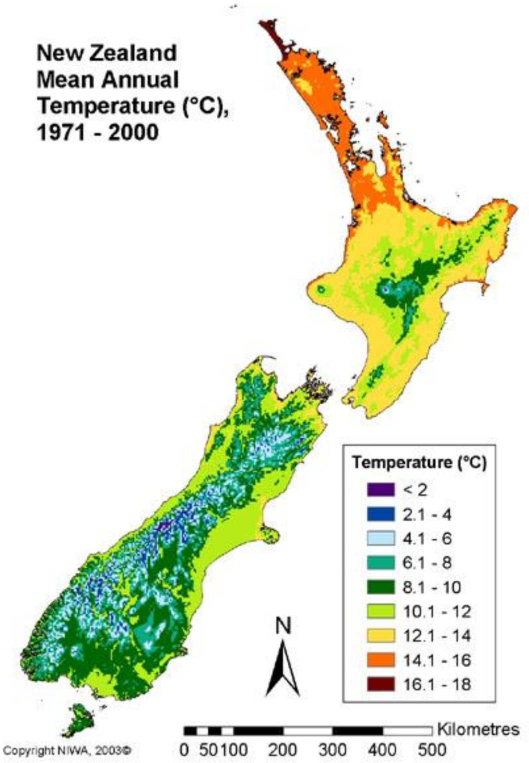


Figure 1.2: Map of mean annual average temperature in New Zealand between 1971 and 2000. Source: Mackintosh (2001).

1.4 Soil fertility

Soil fertility is an important factor influencing species distributions because soil fertility influences nutrient acquisition of plants (Clarkson 1985b; Prentice *et al.* 1992). If sufficient nutrients cannot be acquired, overall plant health can be negatively affected and consequently community composition and species distributions may be altered (Ordonez *et al.* 2009). Three important measures of soil fertility that will be referred to throughout the research in Chapter Two are soil pH, soil carbon to nitrogen ratio and soil organic phosphorus content.

Soil pH is a measure of the alkalinity or acidity of a soil (McLaren & Cameron 1996). Soil pH is defined as the negative logarithm of the concentration of hydrogen ions in soil solution, i.e. –log[H+]. Soil pH below 7 is defined as acidic and above 7 as alkaline. Only a small proportion of the total H+ ions in soil are present in soil solution. The rest of the H+ are attracted to and adsorbed to negatively charged soil colloids at cation exchange sites. These exchangeable cations balance the negative charge of soil colloids and are held in a dynamic equilibrium with H+ in soil solution. Both basic and other acidic cations can be attracted to cation exchange sites, in exchange for the release of H+ into soil solution to balance equilibrium. As the proportion of cation exchange sites occupied by bases increases soil pH decreases because H+ are driven into soil solution in order to maintain the equilibrium. As the proportion of cation exchange sites occupied by bases decreases, soil pH increases because H+ are attracted from solution to the colloids.

The availability of essential plant nutrients depends on soil pH. In acidic soils, the availability of basic cations (eg. Ca, and Mg) is low because they are largely displaced from cation exchange sites by H+ and leach from soil. The availability of nitrogen is also low in acidic soils due to reduced nitrification and nitrogen fixation. The availability of phosphorous is highest between pH 6 and 7 because in more acidic or basic conditions it precipitates with Al, Mn or Ca. Micronutrients are poorly available at high and low pH leading to reduced plant growth or toxicity in these soil conditions. The optimum pH range for plant growth is thus the pH range at which most essential nutrients will be available. Depending on the species, optimum soil pH is typically between 5.5 and 7.5. Hence, soil pH does not determine fertility but is important because it affects the availability of nutrients to plants and soil microorganisms (McLaren & Cameron 1996).

The ratio of carbon to nitrogen in soil (soil C: N ratio) is a measure of the relative availability of nitrogen in soil to plants. Soil C:N varies from 9:1 to 4:1, while C:N of plants varies from 20:1 to 100:1 (McLaren & Cameron 1996). In general plant residues entering the soil have insufficient N to satisfy the N requirements of soil microbes. To compensate, soil microbes often immobilize mineral nitrogen, a process which may lead to nitrogen deficiency of the plants growing in the soil. However, as decomposition continues and the soil C:N ratio falls below 25:1, further decomposition results in mineralisation of N no longer required by the microbes and an increase in total N as a result of the mineralisation of some of the added plant N. Whether microbial activity results in net mineralisation or net immobilization depends on the C:N ratio of the original plant matter and other soil conditions (McLaren & Cameron 1996). In soils with high C:N ratios, N tends to be bound in the microbes and poorly available to plants. The optimum soil C: N for plant growth is when soil C: N is similar to plant C: N because there is then an appropriate supply of carbon relative to nitrogen for plant growth (Heal *et al.* 1997).

The total phosphorus (P) content in soils is generally low (0.02 – 0.15 %) and varies depending on soil parent material and the extent of weathering and leaching that has occurred (McLaren & Cameron 1996). Between 20 and 80 % of the total P in mineral soils exists in organic forms (McLaren & Cameron 1996). Organic soil P originates from compounds formed following the decomposition of plant and animal material. Plants uptake P from soil solution. Concentrations of P in soil solution are extremely low, below 0.3 µg P ml^{-1} (McLaren & Cameron 1996). This is because the rates of mineralisation of P are low and depend on factors governing the rate of decomposition. Soil organic P content is an important measure of soil fertility because soil organic P content is strongly correlated with the concentration of P in soil solution, from which plants uptake P (McLaren & Cameron 1996). The variables of soil pH, soil C:N and soil organic P are commonly used to assess relationships between vegetation composition and soil fertility (Ordonez, *et al.* 2009; Jager *et al.* 2015; Maire, *et al.* 2015)

Soil fertility differs among soil types. The main factors that influence soil types include: soil parent materials; topographic position; climate; biological factors, duration of soil development; and human influences (Jenny 1941; McLaren & Cameron 1996). Across the 270,000 km^2 of land area in New Zealand there are an extensive variety of soil types that result from differing combinations of soil-forming factors (Molloy 1998). New Zealand is a geologically active country, positioned on the boundary of the Australian and Pacific plates, with mountains, volcanoes and frequent earthquakes. This range of landforms provides an equally vast array of soil parent materials. Distinctive biota influence the soil properties, such as native earthworms and kauri (*Agathis australis*) trees (Lee 1959; Verkaik & Braakhekke 2007). The climate has undergone glacial and interglacial periods, subjecting the soil to repeated cycles of development, erosion, rejuvenation and re-vegetation. The arrival of humans lead to expansive burning of vegetation which is evident in the charcoal layers in many soils across New Zealand (Molloy 1998).

Soil types in New Zealand include Spodosols, Ultisols, Inceptisols and Alfisols (Van Rees 2006). These soils support the mixed conifer-broadleaved and beech forests of New Zealand. Weathered volcanic tephra forms the basis of the mature (well-developed) soils throughout the North Island and northern South Island. In the North Island these are is intermixed with recent (poorly-developed) peat and alluvium soils in the low-lying plains. In the South Island soils are mainly derived from glacial deposits of greywacke or schist. In the eastern and southern regions of the South Island there are a mixture of recent and older soils, while in the West Coast recent soils predominate. In the mountain ranges, soils are derived from parent materials of greywacke, schist, granite and gneiss. Soils are poorly developed in the ranges because of slow weathering of parent material, cold, wet climates, and steep slopes Molloy (1998). Soil fertility differs among these soils and is an important factor in determining the adaptive value of traits in differing environments and the consequent distributions of plant species (Maire, *et al.* 2015).

1.5 Plant functional traits used in the following research

The next sections provide background information about dimensionality, spectra and trade-offs in traits, the functions of the main plant organs, the traits included in the research in Chapter Two, and some trends previously observed between traits and environmental gradients.

1.5.1 Dimensionality, economic spectra and trade-offs in traits

When using trait-based ecology there is a seemingly endless number and variety of possible functional traits to study. Community assembly acts on the whole-organism level, rather than on independent traits. Therefore, in order to capture the overall influence of environmental factors on plant communities it is recommended to include traits from multiple organs, as well as whole-plant properties (Perez-Harguindeguy, *et al.* 2013). However, if many different traits are measured some traits are likely to be correlated with others (Laughlin 2014a). Trait-trait correlations may result from shared physiological functions (eg. leaf N and P concentrations are both important determinants of photosynthetic capacity (Chapin 1980; Wright *et al.* 2007)) or phylogenetic restrictions on trait variation between species (Cavender-Bares *et al.* 2009). Correlations between traits are useful when determining intrinsic dimensionality.

Intrinsic dimensionality is the minimum number of independent, orthogonal axes of variation needed to describe a dataset (Lee & Verleyson 2007). It is useful to determine the intrinsic dimensionality of large multi-trait datasets. As more axes are needed to describe a dataset it becomes easier for a model to detect functional differences between species. However, if there are too many dimensions in a dataset, the benefits of using them to analyse functional differences between species decline relative to using the traits themselves (Laughlin 2014a). Traits that are correlated, such as specific leaf area, leaf dry matter content, leaf nitrogen concentration and leaf lifespan tend to form a single trait dimension (Laughlin 2014a). Identification of intrinsic dimensions reduces the complexity of an interpretation of a multi-trait dataset because the correlated traits within a dimension respond in similar ways to variation in environmental gradients.

Similar dimensions in multi-trait datasets often tend be well recognised across different sites. This is because resources are allocated to different plant organs and functions in order to optimise long-term fitness, relative to the environmental selection pressures acting in the site (Kleiman & Aarssen 2007) and similar patterns of resource allocation across environmental gradients occur in different sites. Repeated observations of the same trait dimensions across sites has led to recognition of trait economic spectra.

Dimensions in trait datasets that are widely recognised have been described as economic spectra. Analogous to economic budgets, plants must obtain, store and spend resources in a way that will optimise fitness (Bloom *et al.* 1985). Economic spectra characterise the range of variations in these allocation processes from one extreme to the other. A position along an economic spectrum is described as a trait strategy. For example, there is a leaf economics spectrum and possibly a wood economics spectrum (Chave *et al.* 2009; Reich 2014). The leaf economics spectrum ranges from leaves that have a 'slow' strategy (high leaf mass per unit leaf area, low nutrient concentrations and long leaf lifespans), to leaves that have a 'fast' strategy (low leaf mass per unit area, high leaf nutrient concentrations and short leaf lifespan) (Wright *et al.* 2004). The 'slow' leaf strategy tends to be favoured in harsh conditions such as in cool, dry sites, where conservative growth is needed to achieve overall plant success. Alternatively, the 'fast' leaf strategy is favoured where conditions are more favourable for productive growth and the benefits of investing in leaf structures can quickly be replaced (Wright *et al.* 2005a). Recognition of such spectra in multiple traits provides a way of interpreting the functions of several traits simultaneously.

Another type of pattern in traits that is often recognised across environmental gradients is that of trait trade-offs. Trade-offs in trait function occur when a trait value is adaptive in one environment, but maladaptive in another (Reich 2014). For example, water transport rates are higher in wide xylem conduits than narrow conduits, but at the same time increased conduit diameter decreases the likelihood of maintaining effective water transport during freezing or drought conditions (Baas *et al.* 2004; Chave, *et al.* 2009). Consequently, in environments with risks of freezing or drought, narrower conduits tend to be favoured for their greater safety, despite having lower rates of water transport than wider conduits (Sperry & Sullivan 1992; McDowell, *et al.* 2008). Ecological trade-offs such as this, have been observed in multiple plant functional traits.

1.5.2 Leaf functional traits

Leaves are the site of carbon assimilation and water loss through stomata (Hacke & Sperry 2001). Leaves are important for maintaining atmospheric cycles and decomposition of leaves is a primary aspect of biogeochemical cycles (Cornwell *et al.* 2008). Leaf nutrient concentration is an important determinant of leaf photosynthetic capacity (Chapin 1980). Leaves therefore have many roles including influencing leaf lifespan, tolerance to harsh or variable conditions, plant metabolism and the provision of shelter and food to other organisms (Salisbury 1949; Wright, *et al.* 2004).

1.5.2.1 Specific leaf area

Specific leaf area (SLA) is defined as the one-sided area of a fresh leaf divided by the oven-dry mass of that leaf, reported in $mm^2 mg^{-1}$ (Perez-Harguindeguy, *et al.* 2013). SLA is positively related to potential relative plant growth rate and leaf carbon assimilation rate (Ordonez & Olff 2013). Leaves with low SLA tend to be small, thick and often sclerophyllous, such as leaves of *Knightia excelsa* (Perez-Harguindeguy, *et al.* 2013). Low SLA is also correlated with long leaf lifespan, high tannin concentration, low leaf N concentration and low maximum photosynthetic rates (Perez-Harguindeguy, *et al.* 2013). Leaves with high SLA tend to be larger and thinner, such as leaves of *Schefflera digitata* (Wright, *et al.* 2004). Leaves with high SLA tend to exhibit contrasting traits to leaves with low SLA, including short leaf lifespans, low tannin concentration, high leaf N concentration and high maximum photosynthetic rates (Perez-Harguindeguy, *et al.* 2013).

Several studies have assessed the influence of water limitations on SLA. Leaves with low SLA are typically more adapted to water stress than leaves with high SLA (Reich 2003). Across a rainfall gradient in Australia, Schulze, *et al.* (2006) showed that low SLA is more common in arid environments than high SLA. This trend was supported by several other studies in Australia (Cunningham *et al.* 1999; Fonseca 2000) and across latitudinal ranges from Scandinavia to the Mediterranean (Sanchez-Gomez *et al.* 2013). Low SLA in arid environments provides the benefit of reduced transpirational water loss by reducing boundary layer thickness and thereby ensuring that leaf temperatures remain near to surrounding temperatures (Godoy, *et al.* 2011). Leaves with low SLA have thick cuticles and thick-walled cells that are also beneficial for reducing water loss in water-limited environments (Reich 2003).

Many studies have assessed how SLA varies with temperature. SLA tends to increase with increasing temperature (Craufurd *et al.* 1999; Anacker *et al.* 2011; Laughlin, *et al.* 2012). Individuals with low SLA also tend to be preferentially selected in cold environments (Laughlin, *et al.* 2012). Low SLA promotes fitness in cold environments because the long-lived, dense leaves are capable of fixing carbon despite low temperatures. High SLA is preferentially selected in warm environments because conditions are suitable for optimum growth and the thin short-lived leaves are capable of high carbon gain and supporting rapid growth (Reich 2003).

In general, species in sites with high fertility soil, tend to have higher SLA on average than do species in sites with low fertility soil (Vitousek *et al.* 1992; Grubb 1998; Ordonez, *et al.* 2009; Perez-Harguindeguy, *et al.* 2013; Jager, *et al.* 2015). This is because nutrient-rich environments favour growth of species with high rates of growth. In sites with low soil fertility, low SLA is favoured because it supports a conservative growth strategy with lower resource requirements (Richardson *et al.* 2004).

1.5.2.2 Leaf dry matter content

Leaf dry matter content (LDMC) is calculated by leaf oven-dry mass divided by leaf fresh mass, reported in mg g^{-1} (Niinemets 2001; Perez-Harguindeguy, *et al.* 2013). LDMC is inversely related to SLA and leaf thickness (Perez-Harguindeguy, *et al.* 2013). Leaves with high LDMC tend to be tougher, and more resistant to physical damage and decomposition than leaves with low LDMC (Perez-Harguindeguy, *et al.* 2013). Leaves with high LDMC therefore tend to be favoured in less productive and less disturbed environments because they are more tolerant of harsh conditions than leaves with low LDMC (Perez-Harguindeguy, *et al.* 2013).

High LDMC has several advantages in water-limited and hot environments. Firstly, leaves with high LDMC have higher bulk elasticity than plants with low LDMC. The high bulk elasticity of leaves with high LDMC enables greater storage of water within the leaves for use during water-stressful periods (Niinemets 2001). Bulk elasticity is a measure of the change in leaf cell turgor pressure that occurs per unit change in water content of the cells (Niinemets 2001). A decrease in bulk elasticity occurs with increasing water stress which enables the plant cells to maintain turgor (Saito & Terashima 2004). High bulk elasticity results in large changes in leaf water potential relative to the change in leaf water content in plants in arid conditions (Saito & Terashima 2004). This results in large gradients in water potential between the plant and soil with only small amounts of water loss from the leaf. Hence leaves with higher LDMC have greater rates of water uptake from increasingly dry soil, and greater capacity for water storage than leaves with lower LDMC (Saito & Terashima 2004).

1.5.2.3 Leaf nitrogen and phosphorus concentrations

Leaf nitrogen (N) and phosphorus (P) concentrations are calculated by the total concentration in a leaf sample as a percentage of leaf dry mass (Perez-Harguindeguy, *et al.* 2013). Nitrogen and phosphorus are the two essential nutrients required in the highest amounts for plant survival. Nitrogen is mainly derived from atmospheric fixation, while phosphorus is derived from soil weathering (Wright, *et al.* 2004). Nitrogen is integral to photosynthetic proteins, including Rubisco, the enzyme involved in carbon fixation (Wright, *et al.* 2004). Phosphorus is necessary for nucleic acids, lipid membranes and bioenergetics molecules such as ATP (Wright, *et al.* 2004). Nitrogen and phosphorus are the two nutrients most closely related with the leaf economics spectrum (Wright *et al.* 2005b).

Leaf N: P is positively related to leaf lifespan and inversely to SLA and carbon assimilation rate (Wright, *et al.* 2005b). However, this relationship is weak, possibly because woody species allocate a large amount of biomass to non-reproductive tissue or species-specific differences (such as N-fixing ability) may cloud relationships (Wright, *et al.* 2005b).

Leaf N: P increases from the poles towards the equator in relation to trends in temperature and soil substrate (Wright, *et al.* 2005a). The amount of P available in soil decreases towards the equator because the rate of soil weathering increases with temperature (McLaren & Cameron 1996). This causes P to decrease in relation to N towards the equator. Schulze, *et al.* (2006) reported decreases in leaf N (irrespective of P) in *Eucalyptus* spp. with decreasing rainfall across Western

Australia. Stomatal conductance, number of leaves per plant and photosynthetic area per leaf also decrease in response to declining water availability (Farquhar *et al.* 2002). These combinations of trait variations “spread the responsibility” for surviving water stress (Farquhar, *et al.* 2002) and illustrate how important it is to assess the responses of multiple traits to environmental gradients.

1.5.2.1 The leaf economics spectrum

The leaf economics spectrum, described by Wright, *et al.* (2004), reflects how the main leaf traits are correlated and is largely universal. The traits included in this spectrum are leaf mass per unit area (LMA, the inverse of SLA), leaf lifespan (LL), leaf N and P concentration, leaf dark respiration rate and photosynthetic capacity. The leaf economics spectrum runs from quick to slow return on investment of nutrients and dry mass in leaves (Wright, *et al.* 2004). Species with quick rates of return have ‘fast’ leaves with high maximum rates of photosynthesis, fast growth rates, high SLA, high leaf N and P concentrations, short leaf lifespans, and low LDMC. Species with slower rates of return have ‘slow’ leaves with lower maximum rates of photosynthesis, slow growth rates, low SLA, low leaf N and P concentrations, long leaf lifespans and high LDMC (Wright, *et al.* 2004; Funk & Cornwell 2013; Reich 2014). The advantages and disadvantages of the leaf traits at each end of the spectrum result in a performance trade-off at high versus low resource supply (Reich 2014).

The ‘productive’ strategy of having ‘fast’ traits involves the use of high amounts of resources to acquire carbon. ‘Fast’ traits are advantageous in nutrient rich environments because the supply of resources is able to meet the high demand from the leaves. However, fast traits are maladaptive in resource-limited and harsh environments, because the costs of investing in expensive structures designed for rapid resource acquisition cannot be met in resource-limited and harsh conditions. In contrast, ‘slow’ and conservative traits are advantageous in resource-limited, harsh conditions because the rate of demand for resources by leaves is reduced to a level that is more attainable in the given environment. Considerable savings can be made by conservative strategies, such as reduced water loss in arid conditions and reduced costs of nutrient foraging in infertile conditions or harsh climates (Craine 2009; Reich 2014). It is unfeasible to be equally successful in all environments and the leaf economics spectrum exemplifies how variation in traits can make an individual more or less adaptive in different conditions.

1.5.2.2 Leaf phenolic concentration

The trait of leaf phenolic concentration is not included in the leaf economics spectrum. Phenolics are a group of structurally diverse plant secondary metabolites that include phenols, tannins, lignans, flavonoids and quinines (Bennett & Wallsgrove 1994). Phenolics are substances which contain one or more hydroxyl (OH) substituent bonded onto an aromatic ring. They are the most studied group of secondary metabolites because of their significant concentrations and roles in plants (Sumbele *et al.* 2012).

At least four different functions of leaf phenolics have been recognised. Firstly, leaf phenolics have a role in defending plants against herbivory by insects, animals and damage by pathogens (Bennett & Wallsgrove 1994; Roberts & Paul 2006). Deterrence of herbivores can occur either by the direct toxic effects of phenolics, or by the formation of barriers such as lignin (Sumbele, *et al.* 2012). Secondly, phenolics act as protective filters that reduce the penetration of UV and visible light to sensitive leaf tissues (Middleton & Teramura 1993). Thirdly, phenolics have roles in plant-plant and plant-litter-soil interactions (Kraus *et al.* 2003). Fourthly, leaf phenolics have been shown to act as antioxidants (Close & McArthur 2002).

The trait of leaf phenolic concentration is defined as the total concentration of phenolics in a leaf sample, as a percent of dry leaf mass. The relationships between leaf phenolic concentration and environmental gradients have been studied less often than these relationships have been studied for other leaf traits. Across large spatial scales leaf phenolic concentrations relate to soil nutrient availability. Plants growing in low fertility soils tend to have higher concentrations of leaf phenolics than plants growing in higher fertility soils (Wright *et al.* 2010). Soil N availability is a stronger determinant of leaf phenolic concentration than soil P availability (Wright, *et al.* 2010). Leaves with low nutrient concentrations also tend to have higher phenolic concentrations than leaves with higher nutrient concentrations (Wright, *et al.* 2010). This accumulation of phenolics in leaves of plants occurring on low fertility soils is suggested to increase leaf toughness and longevity, as well as regulate nutrient cycling by reducing rates of decomposition and N mineralisation (Kraus, *et al.* 2003). Thereby increased phenolic production may represent a conservative strategy by which plants reduce nutrient losses to the soil microbial community (Hättenschwiler & Vitousek 2000).

It has long been considered that because tropical climates (warm and moist year-round) are productive for organism growth, species interactions, including herbivory, are more common and intense in the tropics than at higher latitudes (Dobzhansky 1950). This has led to a hypothesis that plant traits that function in defence against herbivores, such as high leaf phenolic concentrations, should be favoured in the tropics (Schemske *et al.* 2009). Some studies have supported for this hypothesis. For example, latitudinal gradients in leaf tannin and total phenolic concentrations have been identified, both within (Siska *et al.* 2002) and across species (Coley & Aide 1991; Hallam & Read 2006). However, many studies, including a meta-analysis of previous studies (Moles *et al.* 2011a) and a large-scale empirical study (Moles *et al.* 2011b) have not supported this hypothesis (Gaston *et al.* 2004; Stark *et al.* 2008; Adams *et al.* 2009; Martz *et al.* 2009; Graça & Cressa 2010; Steinbauer 2010). In fact, traits inferring greater defence against herbivory tend to be more common towards the poles than near the equator (Moles, *et al.* 2011b). The greater defence of leaves (via traits such as high phenolic concentration) at high-latitudes may result from the higher cost of replacing tissue that has been damaged or eaten by herbivores in moist, cool, and low fertility environments, than in warm, wet and highly productive environments in the tropics (Moles, *et al.* 2011b). Alternatively, this trend in traits may be a response to the harsher abiotic conditions near the poles than near the equator. Factors such as UV radiation (Close & McArthur 2002; Stark, *et al.* 2008), soil fertility (Wainhouse *et al.* 1998), moisture availability (Hura *et al.* 2012) and temperature (Laine & Henttonen 1987; Veteli *et al.* 2002) may favour an increasing concentration of phenolics in leaves near the poles because of the increased physical defence these chemicals enable.

It should also be noted that there are a large number of different types of plant defences (including physical defences such as spines and hairs) against herbivory. There is conflicting support for the relationship between higher adaptive values of chemical defence traits in the tropics than near the poles (Moles *et al.* 2013). Perhaps it is more beneficial for species to exhibit different combinations of chemical and physical defences to their neighbours, in order to increase the difficulty for herbivores to recognise and overcome local defences (Moles, *et al.* 2013). Therefore it may be important to consider variation in defence against herbivores by using an index of integrated measures from several types of defence traits rather than considering many individual defence traits independently.

1.5.3 Stem functional traits

The main stems of trees have significant roles in biomechanical support, storage and transport of water and nutrients, and resistance to stresses and disturbances (Kozlowski 1992; Chave, *et al.* 2009). These roles are shared between the wood and bark components of stems.

1.5.3.1 Wood density and wood dry matter content

Wood density is referred to as “the best descriptor of wood” because it integrates many wood properties (Weiher 1995; Enquist 1999; Chave, *et al.* 2009). Wood density is defined as the oven dry mass of a wood sample divided by the fresh volume (Chave, *et al.* 2009). Wood density varies from 0 - 1.5 g cm^{-3}, depending upon the chemical and structural arrangement of cells, proportion of air spaces and moisture content (Chave, *et al.* 2009). Wood dry matter content (WDMC) is calculated as the oven-dry mass of stem divided by stem fresh mass (Mason *et al.* 2011). Wood dry matter content is correlated with and therefore a surrogate for wood density (Jager 2014).

Wood provides a pathway for the transport of water and nutrients around the plant, via vascular tissue (Hacke & Sperry 2001; Tyree & Zimmermann 2002). Wood with high proportions of small-diameter xylem conduits and thick conduit walls relative to the conduit lumen diameters, has high wood density. In contrast, wood with low proportions of conduit tissue and thin conduit walls relative to conduit lumen diameters, have low wood density (Pratt *et al.* 2007; Swenson & Enquist 2007; Chave, *et al.* 2009). Wood density is thus related to hydraulic conductivity.

A significant risk to plant health is hydraulic cavitation. This occurs when there is a blockage (such as an air bubble) in a xylem conduit which reduces the capacity of the plant to transport water effectively and impairs rates of carbon assimilation by inducing stomatal closure (Sperry *et al.* 1994). Hydraulic cavitation can be caused by the high xylem tensions occurring during drought (Sperry, *et al.* 1994), or during cycles of freezing and thawing of sap under tension (Sperry & Sullivan 1992; Sperry, *et al.* 1994). High density wood has a lower risk of hydraulic cavitation than less dense wood (Hacke & Sperry 2001). This is because dense wood has thick conduit cell walls relative to the diameter of conduit lumens, so the tension required to create a cavitation is higher (Hacke & Sperry 2001). Dense wood also has tightly packed conduits that can provide alternate routes for hydraulic conductance whilst the embolised conduits are refilled (Secchi & Zwieniecki 2011). Therefore, wood density is related to transport safety which affects the overall ability of a tree to survive and tolerate stress.

Wood density tends to increase with increasing mean annual temperature (MAT). This was observed in south-western USA (Laughlin, *et al.* 2011). Also, across a gradient from 52 °N to the equator Wiemann (2002) reported a 0.0049 g cm^{-3} increase of angiosperm wood density per °C increase in MAT. This trend was strongest in the temperate zones (Wiemann 2002). The occurrence of high density wood in hot, dry environments (such as the Atlantic forests of Brazil) (Chave 2006) is attributed to drought stress (Hacke & Sperry 2001; Meinzer *et al.* 2001). This is because high wood density provides greater hydraulic resistance to drought-induced cavitation and therefore increases performance in hot, dry environments, beyond that of trees with less dense wood (Hacke & Sperry 2001).

Wood density also increases slightly at colder values of MAT (Laughlin, *et al.* 2011). In these environments, dense wood provide the benefit of reducing the risk of hydraulic cavitation induced by freeze-thaw cycles (Sperry & Sullivan 1992). High wood density may also be adaptive in cold, dry alpine environments, because mechanical reinforcing from densely packed fibres is beneficial in providing support against strong winds (Sperry & Sullivan 1992) and reducing the risk of drought-induced cavitation (Laughlin, *et al.* 2011).

There are a variety of relationships reported between mean annual precipitation (MAP) and wood density. Wiemann (2002) found a weak trend of decreasing wood density with increasing MAP from the temperate regions to the warm tropics. Likewise, in Mexico wood density was negatively related to precipitation (Barajas-

Morales 1987; Chave 2006). In contrast, in tropical America, Chudnoff (1976) found that wood density was strongly positively related to MAP. In Ghana, variation in wood density was not significantly related to MAP (ter Steege 2001). MAP is a better predictor of wood density in the warm tropical zones than other sites (Chave 2006). In temperate sites, mean annual temperature is a stronger predictor and tends to override the effect of MAP (Chudnoff 1976). Therefore a general relationship between wood density and MAP is yet to be recognised.

Wood density is related to mechanical properties, which influence the stability of trees when exposed to disturbance (Poorter 2008). Dense wood has greater stability than less dense wood, when faced with potentially-damaging disturbance forces, such as strong winds (Pratt, *et al.* 2007; Poorter 2008). For example, Curran (2008) found that species with high density wood in Queensland, Australia, withstood tropical cyclones better than species with less dense wood. However, dense wood does not always infer a greater resistance to disturbance (Zimmerman *et al.* 1994; Bellingham *et al.* 1995). Resistance depends on the form of disturbance and type of bending and breaking forces occurring (Webb 2014). In general, high wood density is related to greater biomechanical safety than low wood density (Bier 1999; Osunkoya 2007; Chao 2008; Poorter *et al.* 2010).

Herbivore defence mechanisms may also influence wood density, particularly in tropical regions (Janz 2011; Tanentzap *et al.* 2011). Over 25,000 secondary compounds have a role in plant defence (Agrawal 2006). Dark coloured hardwoods tend to have higher concentrations of these compounds and greater durability than lighter coloured hardwoods (Chave, *et al.* 2009). Additionally, secretory resin canals can provide defence by impairing the entry of wood decay insects. The occurrence of these canals increases with increasing wood density (Farrell 1991). There are higher numbers of insect herbivores in tropical communities compared to temperate communities (Novotny 2006). Higher wood density in wet Neotropical forests, compared to temperate forests, may reflect greater investment in mechanisms to defend against insect herbivores (Ehrlich & Raven 1964; Farrell 1991). Dense wood may therefore have an evolutionary advantage in regions with high populations of herbivores.

Wood density also reflects the position of a species along a continuum of fast to slow growing trees (Weiher 1995; Chave, *et al.* 2009; Reich 2014). Fast growing species have low density wood (Putz *et al.* 1983; ter Steege 2001; Muller-Landau 2004) with high hydraulic conductivity and low construction costs in terms of energy and resource allocation. Conversely, species with high wood density, have lower conductivity, slower growth rates and higher construction costs, but their tissue is more resistant to physical damage, hydraulic cavitation, and predators and pathogens, making it longer lasting (Farrell 1991; Hacke & Sperry 2001; Rowe & Speck 2005; Janz 2011). Here a trade-off exists such that trees either have low density and fast growing wood, or higher density and slower growing wood (Putz, *et al.* 1983; Gourlet-Fleury *et al.* 2011; Richardson *et al.* 2013).

1.5.3.2 Bark functional traits

Bark is important for protecting stem meristems and bud primordia (Rosell 2014). Relative bark thickness is the only bark trait that has been shown to vary across sites (Paine 2010; Lawes 2011). Relative bark thickness is calculated as bark thickness (the part of the stem, including the cambium, which is external to the wood) divided by the diameter of the tree at breast height (135 cm) (Perez-Harguindeguy, *et al.* 2013; Rosell 2014).

Bark consists of several layers of tissue with differing structure and function. The rhytidome layer is the main contributor to bark thickness (Paine 2010). The rhytidome is the dead section of the bark and consists of several layers of periderm (Trockenbrodt 1990; Ghosh 2006). Each layer of periderm consists of three tissues: phellem, phellogen and phelloderm. The phellem (cork cells) are dead when mature and often covered in suberin. The phellogen is the cork cambium comprising tannin-rich cells. The phelloderm are living cells which function in photosynthesis or starch storage (Pfanz 2002). Within the rhytidome are the living tissues of the cortex and secondary phloem from which a new bark layer is produced annually (Ghosh 2006; Rosell 2014). The functions of bark include protection, storage and strength.

Bark provides protection and enhances recovery from fire by buffering the living stem from heat damage (Vines 1968; Lawes 2011, 2013). The rate of temperature increase at the vulnerable vascular cambium depends on bark thickness and thermal diffusivity (Vines 1968; Brando 2012). Species with thin bark (such as *Eucalyptus punctata*) are more fire-sensitive than species with thicker bark (such as *E. obliqua*) (Vines 1968) because thin bark provides less protection from fire than thicker bark. Thicker bark provides a greater buffer against damage from fires (Lawes 2013).

Relative bark thickness and climate are linked via the mediating effects of bark thickness on fire because mean annual temperature and precipitation influence the likelihood of fire (Westerling 2006). Across a 12 °C temperature gradient in south-western USA, community-weighted mean bark thickness increased with increasing mean annual temperature (Laughlin, *et al.* 2011). Across Mexico's xerophytic shrubland and Australia's tropical rainforests, bark thickness decreased with decreasing mean annual temperature and increasing moisture (Rosell 2014). Thick bark is advantageous in warmer, drier regions where fire is frequent and severe (Vines 1968; Westerling 2006; Laughlin, *et al.* 2011; Lawes 2013; Rosell 2014).

Bark acts as a water storage tissue (Meinzer, *et al.* 2001). The dead bark layers are parenchyma cells with elastic cell walls. These can undergo significant changes in volume with relatively small changes in turgor, making them effective at water storage (Meinzer, *et al.* 2001; Scholz 2007). Thin bark is able to store more water than thick bark because the less lignified cell walls of thin bark have higher cell wall elasticity and therefore a greater potential to expand and store water, with a minimal change in turgor (Meinzer, *et al.* 2001; Scholz 2007). This is advantageous in drier environments because stored water can move into the transpiration stream and help to reduce temporal imbalances in water availability (Meinzer, *et al.* 2001). Thin bark is also advantageous in dry regions with infrequent fires because when fires do occur, vaporisation of the large amount of stored water reduces the difference in temperature between the heat source and vascular cambium. This reduces the rate of vascular cambium burning and overall damage to the stem (Brando 2012). In moister regions such as tropical rainforests, thin bark may be more common than thick bark because it has lower respiratory costs than thick bark and the need for defence against fires is low (Lawes 2013; Rosell 2014).

Bark is also important for defence against herbivores and pathogens, and other physical disturbances (Baraloto *et al.* 2010; Rosell 2014). Trees reduce the spread of decay throughout woody tissue by "compartmentalisation" (Shigo 1984). This involves formation of chemical and anatomical boundaries that resist the spread of pathogens (Shigo 1984). Thick bark provides a more efficient seal by compartmentalisation, than thinner bark (Romero & Bolker 2008). Thick bark may thus be advantageous where damage caused by factors other than fire is common.

Bark contributes to stem strength (Rosell 2014). Bark provides an average of 10 % of the flexural rigidity of tropical rainforest tree stems (Paine 2010). Thicker bark enhances mechanical stability more than thin bark (Poorter 2014). Therefore, despite representing a low proportion of stem diameter, the role of bark is significant when assessing the strength of a plant stem subjected to bending forces, such as severe winds (Niklas 1999).

There is a trade-off between bark water storage and strength (Rosell 2014). Thin bark is better at storing water than thick bark (Scholz 2007). However, thick bark with higher lignin content has greater physical strength (Niklas 1999) and protection ability than thin bark with low lignin content (Vines 1968; Farrell 1991).

Bark thickness also relates to soil fertility. In Puketī Forest, New Zealand, Jager, *et al.* (2015) observed that species associated with low-fertility soils had thicker bark than species associated with high-fertility soils. This study supports the idea that thicker bark is often found in species occurring in stressful sites because thick bark provides defence against herbivory and general disturbances, such as resource-limitation (Paine 2010). Thick bark thus increases the longevity of tissues that are sensitive or expensive to build when resources are scarce (Herms & Mattson 1992).

In general, wood density tends to increase with increasing mean annual temperature and decrease with increasing mean annual precipitation. High wood density in hot environments, or cold and dry environments, provides an advantage against the high risk of hydraulic cavitation, induced by drought or freeze-thaw. Bark thickness increases with MAT and decreases with MAP. Thick bark is advantageous in hot, dry, low fertility environments because it provides defence against damage from fires, herbivores and other disturbances. Thin bark is advantageous in moist regions with low fire frequency because it provides greater water storage, protection against infrequent fires and is less energetically expensive to produce than thick bark.

1.5.4 Root functional traits

Fine roots (< 2 mm diameter) are the primary plant organs for the uptake of water and nutrients from the soil to above-ground organs (Perez-Harguindeguy, *et al.* 2013). In order to be successful roots must detect and respond to the varying spatial and temporal availability of resources. Roots are also the anchor of a plant, holding it in the soil against the strength of wind and other physical factors. As the interface with soil, roots must also avoid damage from environmental stressors and organisms that may threaten the life of the plant (Van Noordwijk *et al.* 1998).

Most studies on root traits focus on the fine roots because these have better abilities for resource uptake than larger roots (Fitter *et al.* 1985; McCully 1999). Variation in below-ground traits is poorly quantified compared with that of above-ground traits (Reich 2014). This is largely due to the logistical difficulties of sampling roots in the field compared to sampling above-ground organs. In forests, the soil is often an interwoven matrix of thick and thin roots, gravels and finer soil particles. This makes it very difficult to extract suitable root samples without damaging them. Species identification of roots in the field is also challenging and relies on observations of colour, texture, and smell, or tracing of roots back to the tree for species which lack distinguishing characteristics (Holdaway *et al.* 2011). Studies of root traits from plants grown in glasshouses are therefore more common because the glasshouse provides standardised conditions and enables simpler sampling methods (Cornelissen *et al.* 2003b; Mokany & Ash 2008).

Root dry matter content (RDMC) is the ratio of root dry mass per unit root fresh mass (Perez-Harguindeguy, *et al.* 2013). RDMC is often used as a surrogate for root tissue density because it is reliable and cheap to measure (Birouste *et al.* 2014). Root diameter (mm) is the average diameter of fine roots, measured behind the zone of root elongation (Cornelissen, *et al.* 2003a).

One of the most widely studied root traits is specific root length (SRL). SRL is the ratio of root length to mass (m g^{-1}) (Cornelissen, *et al.* 2003a). SRL is considered as the below-ground analogue of SLA, because it describes the amount of absorptive tissue produced, per unit of root mass invested. Plants with high SRL are able to build longer roots for a given investment of dry mass, by constructing roots of thin diameter or low RDMC. In contrast, plants with low SRL build shorter roots for a given investment of dry mass but their roots have higher RDMC or thicker diameter than high SRL roots. Root diameter and RDMC are therefore correlated with SRL (Reich 2014). If root tissue density is constant, SRL is mainly determined by root diameter, and vice versa (Fitter, *et al.* 1985). However, it is recommended to assess both RDMC and root diameter independently because the relationship of these traits with SRL is not yet fully understood (Perez-Harguindeguy, *et al.* 2013).

Based on the location of roots within soil, it would be logical for root traits to vary with soil fertility. However, some studies have shown that root diameter is highly conserved phylogenetically (Comas & Eissenstat 2004; Comas & Eissenstat 2009; Valverde-Barrantes *et al.* 2014) and therefore not directly related to soil fertility or plant growth strategies (Kembel *et al.* 2008; Alvarez-Uria & Koerner 2011). Other studies have shown variation in root diameter with soil fertility (McCormack *et al.* 2012). Higher root diameter may facilitate tolerance of low fertility soils through an association of thick roots with longer root lifespan and longer nutrient retention than thin roots (McCormack, *et al.* 2012). Larger root diameter also provides more root volume for mycorrhizal symbionts to colonize and thereby enhance the nutrient uptake of large diameter roots (Eissenstat 1992; Newsham *et al.* 1995). However, the type of mycorrhizal symbiont may be just as important as the amount present because the relationship between root diameter and mycorrhizal colonisation may be limited to arbuscular mycorrhizal associations (Valverde-Barrantes, *et al.* 2014). These are the most common type of mycorrhizal symbiont, both globally and in New Zealand (McNabb 1958; Wang & Qiu 2006). In addition, the relationship between root diameter and soil fertility may differ depending on the relative limitation of important nutrients. Decreases in root diameter were reported in P-limited soils (Hill *et al.* 2006; Holdaway, *et al.* 2011), while root diameter remained relatively constant in N-limited soils (Hill, *et al.* 2006). Nevertheless, these trends are not universally consistent responses to soil fertility (Borch *et al.* 1999; Lambers *et al.* 2006) and require further testing.

The relationships between root traits and moisture availability are unclear. Studies have found a positive relationship between root diameter and water availability (Fitter, *et al.* 1985; Cortina *et al.* 2008; Olmo *et al.* 2014). Thin roots may be advantageous in drought conditions because the small xylem vessel (Alameda &

Villar 2012) and root diameters (Fitter 1987) may infer a higher resistance to hydraulic cavitation than thick roots. Thin roots also have lower carbon and nutrient costs for water uptake from soils than thicker roots (Leuschner *et al.* 2004). However, there are also records of thin roots being more vulnerable to hydraulic cavitation than thicker roots (Fitter 1987). Therefore, the relationship between root diameter and moisture availability also requires further testing.

Root growth and development is temperature dependent (Kaspar & Bland 1992). The availability of nutrients in soils also depends on temperature and decreases with decreasing temperature as a result of decreased metabolic activity of soil mineralisation microbes (Geng *et al.* 2014). However, there is disagreement on the effects of temperature on root diameter (Kaspar & Bland 1992). The lower metabolic cost of small diameter roots (Eissenstat 1992) may be favoured in cool environments as a means of conserving resources. While in warmer environments, thicker roots may be selected for because the resulting benefits of greater nutrient foraging ability (Newsham, *et al.* 1995) will outweigh the higher energetic costs (Eissenstat 1992). These root trait-temperature relationships need further testing.

Root dry matter content is inversely correlated with SRL (Reich 2014). Therefore RDMC is also an indicator of the potential uptake per g investment in root tissue. RDMC has been considered to align with a ‘fast-slow’ plant economic spectrum across leaves, stems and roots (Reich 2014). Where conditions are harsh (low fertility, cool, dry or wet), species with a slow strategy and high RDMC have a selective advantage because the ‘slow’ growth rate and longer root lifespan enable persistence despite the harsh conditions. Although roots of high RDMC require a greater investment of resources to produce them than low RDMC roots, they are resistant to disturbances and have a longer lifespan so they do not need to be replaced often. Species with a ‘fast’ strategy and low RDMC are more favourable in conditions more suitable for growth (high fertility, warmer, moist). In these conditions, low RDMC supports rapid growth of highly productive tissue for a small investment cost. Low RDMC roots are short lived so any loss of tissue can be quickly be replaced. Such correlations between environmental factors and ‘fast-slow’ traits was observed in three New Zealand tree species (Freschet *et al.* 2013a). However, in other cases these patterns are weak (Craine & Lee 2003; Craine *et al.* 2005). Further studies are needed to confirm the generality of these trends.

1.5.5 Functional traits of flowers

Flowering is one of the three primary challenges faced by plants, alongside dispersal and establishment (Weiher *et al.* 1999). The reproductive success of plants relies on completing flowering and seed set during favourable growing conditions and ontogenetic stages (Mouradov *et al.* 2002). Therefore many plants have evolved to initiate flowering in response to environmental triggers. The most reliable triggers for predicting a suitable flowering time are those which vary in predictable patterns across the year (Ausín *et al.* 2005). Two such triggers are changes in day length and temperature (Amasino 1996; Bernier & Perilleux 2005). In many winter-flowering species, flowering is triggered following a period of cold, in a process called vernalisation (Mouradov, *et al.* 2002). An added challenge is that environmental triggers vary over short and long time spans. Fortunately, plants are able to adjust their development in response to these temporal changes in environmental conditions (Mouradov, *et al.* 2002).

Plant phenology is the most commonly reported biological indicator of anthropogenic climate change because of the strong link between flowering time and climate (Wolkovich & Ettinger 2014). If summer temperatures occur earlier in the year, then flowering tends to be triggered earlier (Fitter & Fitter 2002). This is important because it can have significant flow on effects for the surrounding ecological networks (Memmott *et al.* 2007). Detrimental phenological mismatches between plants and animals, including plant pollinators, are predicted to become increasingly common as a consequence of climate change (Petanidou, *et al.* 2014). This may lead to failed seed set and an eventual decline in plant populations over time (Hegland *et al.* 2009).

Flowering phenology has not been included in as many trait-based studies of community ecology as leaf and stem traits (Laughlin 2014a; Wolkovich & Ettinger 2014). Despite this, it was recognised as a core trait by Weiher, *et al.* (1999) and Laughlin (2014a). Flowering phenology varies within and between species in a way that functions to avoid stress or disturbance (Weiher, *et al.* 1999). Two flowering traits are included in this research. Flowering onset is measured as the mean date of anthesis. This measure should be based on field observations (Weiher, *et al.* 1999).

Flowering duration is measured as the number of days from anthesis until the flowering end date (Weiher, *et al.* 1999). Julian dates are used to document flowering phenology whereby, dates are recorded as the number of days after January 1 in the Northern Hemisphere and the number of days after July 1 in the Southern Hemisphere.

Flowering onset and duration are controlled by environmental conditions and developmental regulation (Rathcke & Lacey 1985; Mouradov, *et al.* 2002). Starting and continuing flowering during optimal conditions leads to maximal chances of successful pollination and seed set (Aronson *et al.* 1992). Early or delayed flowering onset to times with suboptimal environmental conditions can result in reduced chances of successful seed set. The date of flowering onset is approximately negatively linearly related to temperature, such that with increasing temperature, flowering onset becomes earlier and reaches a lower limit defined by the phenology of the species at its southern distributional limit (Sparks *et al.* 2000; Parmesan & Yohe 2003; Primack *et al.* 2004; Menzel *et al.* 2006; Bock *et al.* 2014). This trend also occurs at the community-level (Cook *et al.* 2012).

There are fewer studies that examine variation of flowering duration with environmental variables than examine flowering onset with environmental variables. Despite this changes in flowering duration could also have significant ecological, economic and agronomic impacts (Rosenzweig & Parry 1994; Sparks *et al.* 2012). The studies conducted tend to have produced contradictory results because of methodological variations (Bock, *et al.* 2014). Bock, *et al.* (2014) showed that negative relationships between temperature and flowering duration are less common than they are with flowering onset. Short flowering duration reduces the period of time for pollination and may therefore decrease pollination success. But if the energetic cost of flowering is reduced in species that flower for shorter periods, and if pollination is successful during this time, then the high costs and short duration of investment are worthwhile. When an advance in flowering date occurs simultaneously with a shortening of flowering duration there is even greater concern for potentially serious impacts on pollinators, biodiversity and agriculture (Bock, *et al.* 2014).

There are also few studies of flowering phenology in relation to moisture availability and soil fertility. Drought stress has been shown to lead to reduced duration of plant lifecycles, and thereby reduced flowering duration and earlier flowering onset (Aronson, *et al.* 1992). Following a decrease in soil fertility in Mediterranean grasslands, Peco *et al.* (2012) reported an increased abundance of later flowering species. Further studies are needed to confirm the influence of environmental factors on flowering.

Previous studies across the world have highlighted important correlations between flowering phenology and other traits (Wolkovich & Cleland 2014). Earlier flowering tends to be associated with traits related to quicker returns on investments (such as faster growth rates, higher SLA, greater heights, shallower roots) while later-flowering tends be associated with traits related to slower returns on investments (for example, slower growth rates, greater heights, deeper roots). A trade-off between competition and colonisation may explain this. The cheap traits of early flowering individuals enable rapid colonisation, growth and reproduction in disturbed sites, before strong competition for flowering and seedling establishment begins. In contrast, individuals flowering later in the season, must survive competition throughout the season. This is achieved by producing more robust tissues that may draw down resources to lower levels and make these species more effective competitors than earlier flowering individuals (Wolkovich & Cleland 2014; Wolkovich & Ettinger 2014).

1.5.6 Seed functional traits

Seed mass is calculated as the oven-dry mass of an average seed of a species (Perez-Harguindeguy, *et al.* 2013). Seed mass is an important trait because it links reproductive ecology and seedling establishment with the stage of vegetative growth (Leishman *et al.* 2000). There is a ten magnitude variation in seed mass from the tiniest seeds of the Orchidaceae (around 10^{-6} g), to the largest seeds of the double coconut (*Lodoicea seychellarum*) (10^4g) (Leishman, *et al.* 2000).

The chance of a seed establishing successfully increases with increasing seed mass, particularly in stressful environments (Westoby, *et al.* 2002). Larger seed mass is commonly associated with a greater tolerance of shade and low fertility. This is because larger seeds contain more stored nutrients than smaller seeds, which enables larger seeds to survive for longer prior to being able to photosynthesise (Reich *et al.* 1998). Larger seeded species also tend to have slower relative growth rates (ter Steege *et al.* 2006).

It is unclear which environmental factors are the strongest drivers of the relationships between seed mass and environmental conditions. Larger seed mass tends to be favourable under conditions of soil nutrient deficiency, however the evidence for such relationships remains equivocal (Leishman, *et al.* 2000). For instance, seed mass decreased with decreasing soil fertility, in native trees in Northland, New Zealand (Jager, *et al.* 2015). Although, this trend was complicated by differing light conditions across the sites. In the fertile gullies, low light favoured shade-tolerant species with high seed mass, while in the well-lit infertile ridges species with lower seed mass were favoured. Large seeds enable greater survival in shaded conditions where competition for light is high, by persistent, slow growth until a canopy gap forms (Coomes *et al.* 2009). Lower seed mass is favoured in well-lit conditions where competition is low and it is adaptive to have a higher growth rate (Westoby *et al.* 1992). Hence, the relationship between seed mass and soil fertility needs further testing.

Seed mass varies across geographical gradients in ways that suggest that climatic factors could play a role in driving these relationships. For example, there is an increase in seed mass from both poles towards the equator (Moles & Westoby 2003), and seed mass increases along a longitudinal gradient in Australia from the temperate east coast to the arid interior (Murray *et al.* 2003). Large seed mass was correlated with high mean annual temperature in Australia (Murray *et al.* 2004). Metabolic costs of respiration for growth and maintenance increase with increasing temperature (Murray, *et al.* 2004). Therefore, the costs of producing a seedling from stored seed reserves are higher in warm climates than cooler climates, such that a larger seed mass would be required to produce a seedling of a given size in warmer climates (Lord *et al.* 1997). These costs may account for the global pattern of larger seed mass at low latitudes and toward the centres of continents (Lord, *et al.* 1997). Large seed mass can also increase seedling establishment under drought (Leishman, *et al.* 2000). Consequently, larger seeds may be favoured in arid regions with low rainfall (Murray & Gill 2001). However, associations between seed mass and moisture availability are somewhat unclear (Leishman, *et al.* 2000). For example Wright and Westoby (1999) found larger seed mass in high-rainfall species than low-rainfall species. The relationships between seed mass and climatic conditions are in need of further research.

There is a trade-off between seed size and the number of seeds produced (Greene & Johnson 1994; Aarssen & Jordan 2001; Henery & Westoby 2001)). Species that produce large seeds cannot economically produce the immense number of seeds that species with smaller seeds are capable of producing (Henery & Westoby 2001). However, small seeds are not physically capable of storing the quantity of reserves that larger seeds are able to. Therefore, small seeds are less resistant to harsh conditions and less likely to successfully establish in harsh environments than larger seeds. Species with small seeds can energetically afford to produce thousands of them, which increases the likelihood that a small number of them will reach a site that is suitable for establishment. This likelihood of safe dispersal to a suitable site decreases with increasing seed mass (Wright, *et al.* 2007). This seed mass-seed size trade-off is consistent across the globe (Moles & Westoby 2004; Moles *et al.* 2007).

1.5.7 Whole-plant functional traits

Traits that represent the overall functioning of a plant can provide unique information to those which reflect the functioning of a single organ. Maximum plant height is a commonly used whole-plant trait, and is defined as the maximum stature a typical mature individual of a species can attain in a given environment (Perez-Harguindeguy, *et al.* 2013). Maximum height ranges across four orders of magnitude, from about 0.01 m to 100 m (Westoby, *et al.* 2002).

Greater maximum plant height is competitively advantageous in survival because taller plants are able to intercept more light than shorter neighbouring plants (Westoby, *et al.* 2002). However, taller plants have greater costs involved in producing and maintaining main stems (Falster & Westoby 2003). Taller stems also suffer from an increased risk of breakage when exposed to strong winds or extreme conditions than shorter stems (King 1990). Taller trees also have disadvantages because transporting water to great heights results in increased risk of hydraulic cavitation (Ryan & Yoder 1997; Koch *et al.* 2004; Niklas 2007). This is known as the hydraulic limitation hypothesis. To avoid cavitation caused by extremely negative water pressures, plants are forced to close their stomata, thereby decreasing the amount of photosynthesis able to provide carbon for further growth in height (Ryan *et al.* 2006). If competition is low, short species may have the advantage by reducing survival costs whilst maximising light interception. This trade-off between the costs and benefits of height ensures that plants continue to exhibit a wide range of maximum heights (Westoby & Wright 2006).

Since maximum height is closely associated with competition for light, it often lacks a strong relationship with soil fertility. However, there have been many attempts to determine this relationship. In tropical forests in Panama and China, Liu *et al.* (2012) reported that maximum height was positively correlated with soil fertility. Similarly, long-term soil age chronosequences in both temperate and tropical forests showed increasing tree height with increasing soil fertility (Richardson, *et al.* 2004; Peltzer *et al.* 2010). A global analysis found that tall plants are common in productive sites, while a wide range of plant heights occur in sites of low productivity (Moles *et al.* 2009). However, tall trees can grow in low fertility soils (Webb 1959). This was demonstrated in Northland, New Zealand, where greater maximum plant height was associated with low fertility sites than high fertility sites (Jager, *et al.* 2015). This negative association may relate to differences in disturbance regimes between the sites in this study. The high fertility gullies favour species with lower allocation to height, that can respond rapidly to frequent, gap-disturbances, while the lower fertility ridgetops favour species able to tolerate less frequent, large-scale disturbances (Ferry *et al.* 2010). Therefore, there are reasons to suspect that the relationship between soil fertility and plant height may depend on other environmental factors.

Climatic variables have not been shown to be strongly associated with maximum height either. Moles, *et al.* (2009) found that out of 22 environmental variables, precipitation of the wettest month had the strongest relationship with plant height. Moisture availability was also recognised as an important factor influencing plant height in mountainous areas (Littell *et al.* 2008). The importance of moisture availability in determining plant height follows the hypothesis of hydraulic limitation to tree height (Ryan & Yoder 1997; Ryan, *et al.* 2006). In very cold places, temperature seems to be of more importance than moisture availability (Körner

1998). This may be because at very low temperatures plants risk embolism by freeze-thaw mechanisms (Sperry & Sullivan 1992). The global study of Moles, *et al.* (2009) assessed the combined influence of climate and soil fertility on maximum height. In low fertility, cool, dry environments a wide range of heights were present, but in more fertile, warm, moist environments there was a lack of very short species. Maximum height may, therefore be an example of a trait for which the adaptive values vary with climate and soil fertility simultaneously.

1.6 Influence of climate and soil fertility on plant functional traits

Both climate and soil properties are known to influence CWM functional traits and species distributions. This is because individuals can only grow and survive to reproduce in an environment in which their traits have adaptive values (Lavorel & Garnier 2002). Climate and soil fertility are two factors that are highly recognised drivers of community assembly (Violle, *et al.* 2007).

It is well recognised that global patterns of vegetation and climate are correlated (Woodward & McKee 1991). For decades, ecologists have defined climatic envelopes for vegetation types based on the correlations between the distribution patterns of vegetation and climatic variables, such as temperature and moisture levels (Holdridge 1947). The development of a physiological understanding of these correlations is leading to improvement of these models. Physiological measures frequently considered useful include thermal tolerance, and temperature and moisture requirements (Prentice, *et al.* 1992). Thermal tolerance influences individual survival and limits the distribution of species to within a range of sites with suitable temperature ranges (Sakai 1979). Chilling is needed as a trigger for some species to initiate budburst in spring (Murray *et al.* 1989). Sufficient periods of suitably warm temperatures (growing degree days) are needed for plant growth (Kauppi & Posch 1985). Moisture is also required for growth, in differing amounts between species. The seasonal distribution of moisture also affects the need for plants to tolerate drought or waterlogging (Prentice, *et al.* 1992). Temperature and moisture availability are therefore two drivers of plant distribution patterns.

Soil fertility has a major effect on plant survival by affecting the concentrations of nutrients available for plants (Lambers *et al.* 2008). If sufficient nutrients are not acquired, overall plant health can be negatively affected and consequent plant community composition and species distributions may be altered (Ordonez, *et al.* 2009). Nitrogen and phosphorus are the main limiting nutrients for plant growth (Lambers, *et al.* 2008) because they are required for the production of proteins and enzymes (Vance 2001). In most terrestrial environments, plant growth is N-limited but P-limitation also occurs frequently (Aerts & Chapin 2000; Lambers *et al.* 2010). Although these two nutrients are quite abundant in many soils, they tend to exist in a chemical form that is unavailable for direct uptake by plants (Lambers, *et al.* 2008).

A significant factor that complicates studies of soil fertility is that of plant feedback effects (Aerts 1999; Van der Putten *et al.* 2013). Plant-feedbacks are changes to soil properties caused by plants, that in turn influence the performance of plants (Van der Putten, *et al.* 2013). An example of a feedback effect occurs in kauri (*Agathis australis*) dominated forest in New Zealand (Verkaik & Braakhekke 2007). Kauri tend to grow in low fertility soil and produce long-lived, tough leaves with low nutrient concentrations. Decomposition of these leaves, returns low concentrations of nutrients to the soil, thereby reinforcing the low fertility of the soil (Burns & Leathwick 1996; Ordonez, *et al.* 2009). In these forests, the effect is so intense that it has a strong effect on the community composition, continuing to promote dominance of kauri, while creating non-favourable conditions for competing species (Verkaik *et al.* 2007; Wyse *et al.* 2014). In this way the properties of dominant plant species may alter soil fertility (Wardle *et al.* 2012; Freschet *et al.* 2013b; Meisner *et al.* 2014).

Many studies have looked at variation in plant traits across either soil fertility (Mason *et al.* 2012; Jager, *et al.* 2015) or climatic gradients (Laughlin, *et al.* 2011; Reich 2014) at both local and worldwide scales. However, climate and soil may interact in a way that influences plant distributions independently from the influence of each predictor variable alone (Fernandez-Going *et al.* 2013). This may result in a statistical interaction effect, whereby the "relation between two variables changes as a function of a third variable" (Fürst & Ghisletta 2009). Interactive effects are multiplicative effects (the product of two independent effects). Interactive effects are also independent from the main effects, such that, the interactive effect may be significant, while the main effects are not (Fürst & Ghisletta 2009). Because of the shared importance of climate and soil fertility, a potentially strong interaction effect may be unaccounted for in previous studies of trait-based community assembly that included only climate or soil fertility.

Despite suggestions of the importance of interaction effects between climate and soil (Hobbie *et al.* 2002; Reich & Oleksyn 2004), few studies have assessed how plant functional traits vary across climate and soil fertility gradients simultaneously. Current models of plant responses to multiple limitations are inadequate (Lynch & St.Clair 2004). Maire, *et al.* (2015) showed that global variation in leaf photosynthetic traits is best explained by soil pH, P availability, and a moisture index, simultaneously. Dwyer *et al.* (2015) found that significant interactions between local soil P and moisture availability were important drivers of CWM trait values. For instance, when soil P and moisture availability were high, CWM height, seed mass and SLA increased (Dwyer, *et al.* 2015). This follows the global observation that components of soil fertility generally decline on older soils and in very wet conditions with low plant productivity (Huston 2012). Soil fertility has been shown to be a stronger predictor of CWM traits than climate (Ordonez, *et al.* 2009; Maire, *et al.* 2015). Most vegetation occurs on weathered soils with some form of mineral stress and each mineral stress has distinct interactions with climate (Lynch & St.Clair 2004). Experimental studies of plant responses to increased temperature have been troubled by the inability to account for soil fertility (Rustad *et al.* 2001). Ordonez, *et al.* (2009) provided evidence that SLA is influenced by the interaction of mean annual precipitation with soil C:N globally. However, there are no studies that have assessed the influence of multiple interaction effects between climate and soil fertility on multiple CWM plant traits.

1.7 Conclusion

This literature review has shown that functional trait-based studies have the potential to provide greater predictive and quantitative power than species-level studies. Trait-based studies enable ecologists to understand the mechanisms by which distributions of species vary and communities assemble. Species with traits that have greater adaptive value in given environmental conditions will occur in higher abundance than species with less favourable traits in those conditions.

Climate and soil fertility are two of the dominant factors that drive environmental filtering of species during community assembly. Previously recognised relationships between these two factors and traits from multiple plant organs were summarised in this review. However, the interaction effects between these two factors were identified as potentially highly important to consider because interaction effects may influence plant distributions and community assembly independently from the influence of each factor alone. For example, SLA may be high in sites with high soil fertility and warm, moist conditions, but low in sites with low soil fertility and the same climatic conditions, because the advantages of having dense, long-lived leaves in resource-limited soils may be so important that SLA is restricted in low fertility soils despite the favourable climate. However, no studies were identified that have assessed the potentially critical role of the interaction effects of climate and soil fertility on multiple CWM plant traits.

In Chapter Two, I will assess the influence of interaction effects between climate and soil fertility on multiple CWM traits in New Zealand forests. New Zealand is an island nation with a unique flora, encompassing large latitudinal and altitudinal gradients (Leathwick 1995). These gradients provide ample opportunity to study climatic tolerances (Jump *et al.* 2009; De Frenne *et al.* 2013). The broad range of variation in climate (Leathwick, *et al.* 2002) and soil fertility (Molloy 1998) in New Zealand make this an ideal system for a much-needed study of the interactive effects between climate and soil fertility on community assembly.

2 Chapter Two: The adaptive values of functional traits across broad soil fertility and climate gradients in New Zealand forests

2.1 Introduction

The search for general rules that govern associations between species attributes, and biotic and abiotic factors has troubled community ecologists for decades (Lavorel & Garnier 2002). Initial studies in ecology were largely descriptions of the environmental associations of plants. These studies have been criticised for being 'soft science' of little use for making accurate predictions across a range of biomes (Lawton 1999). As awareness and understanding of the widespread impacts of global environmental issues grows, the need for predictive ecological methods increases rapidly. Functional trait-based ecology provides an important means of facilitating this transition of ecology into a harder science, with the ability to predict future changes in species responses and distributions, and to guide management and policy (McGill, *et al.* 2006; Suding & Goldstein 2008).

A major driver of community assembly is environmental filtering, a process that sorts species along environmental gradients based on their fitness in that habitat (Lavorel & Garnier 2002). Species grow and reproduce at a site if they have a range of functional traits which are suitably fit to that environment (Keddy 1992). Species which lack combinations of functional traits that have adaptive value in a given site will be unsuccessful, and remain at low abundance or be eliminated from the site. Trait-based ecology can test which trait values promote fitness along climate and soil gradients. A community-weighted mean (CWM) trait value represents the average value of a given trait within a community, weighted by the relative abundance of each species (Laughlin 2011; Lavorel, *et al.* 2011). Community-level functional traits therefore reflect the values of traits that promote maximum fitness in a given environment (Shipley, *et al.* 2011). The importance of trait-based ecology in understanding environmental filtering and community assembly is exemplified by studies that have shown how plant traits vary across climatic (Laughlin, *et al.* 2011), soil (Vitousek *et al.* 1995; ter Steege, *et al.* 2006) and successional gradients (Lohbeck *et al.* 2013).

A large number of different functional traits from all plant organs have been studied on a vast quantity of species globally. The tremendous variation in plant traits is being classified into broad trait spectra which represent the dominant drivers of plant function (Reich 2014). The leaf economics spectrum (Wright*, et al.* 2004) and wood economics spectrum (Chave*, et al.* 2009) are examples of consistent empirical trends that have been recognised across a large number of trait-based studies at multiple spatial and temporal scales. For example, species with "fast" traits (low tissue density, short tissue lifespan and high rates of resource acquisition and flux) tend to occur on fertile soils in environments with productive climates, while species with contrasting "slow" traits tend to occur on resource-poor soils in environments with harsh climates (Reich 2014). Reliable quantification of such spectra across biomes is valuable for creating models of how vegetation boundaries will shift with changes in land-use, climate and nutrient cycles. The recognition and quantification of such widespread trends is necessary if ecology is to take the leap from an observational qualitative field, to a theory-driven quantitative science that is able to make well supported and robust predictions.

The influence of climate on plants is important to study because climate acts across broad scales as one of the primary limiting factors of plant distributions (Díaz *et al.* 1999). Measures of mean annual temperature and moisture availability relate strongly to vegetation distributions (Wardle 1991; Leathwick 1995; Leathwick & Whitehead 2001; Wright*, et al.* 2005a; Shipley*, et al.* 2011; Maire*, et al.* 2015) because these factors strongly influence plant success via impacts on photosynthesis and growth rates, transpiration water loss, and water and nutrient uptake (Jones 1992; Leathwick 1995; Yang *et al.* 2012). Understanding the relative importance of climatic factors that influence plant traits can help us to improve our understanding of how and which factors influence plant ecological strategies and the distribution patterns of different vegetation types (Moles *et al.* 2014; Jager*, et al.* 2015).

Soil fertility is also important to study because plant functional traits and species distributions have been shown to change over soil fertility gradients (Vitousek*, et al.* 1995; ter Steege*, et al.* 2006). Soil properties such as texture, depth and fertility appear to be related to the types of vegetation and species inhabiting them (Molloy

1998; Binkley & Fisher 2013). For example, species with ‘fast’ leaf traits (high SLA, high leaf N and P concentrations) and low stem density are likely to be associated with soils of high nutrient availability (Vitousek, *et al.* 1995; Muller-Landau 2004; ter Steege, *et al.* 2006; Richardson *et al.* 2008; Gourlet-Fleury, *et al.* 2011; Holdaway, *et al.* 2011; Jager, *et al.* 2015). The relationships of other traits with soil fertility are less well studied. In Northland, New Zealand, Jager, *et al.* (2015) found that in low fertility soil, trees had larger maximum heights, thicker bark, and lower seed mass than trees in higher fertility sites. Despite contrasting to previous studies, this showed that tall trees are capable of growing on low fertility soil. Thick bark may be a defensive strategy in low fertility sites and large seeds may provide increased nutrient reserves for species establishing in shaded or low fertility soils (Jager, *et al.* 2015). Further testing is needed to determine if soil fertility is an important driving factor of plant distributions across large scales.

Climate and soil fertility may interact in a way that influences plant distributions independently from the influence of each predictor variable alone (Fernandez-Going, *et al.* 2013). This is because the types of traits and species that are suitably fit for a community in a site with specific climatic conditions may vary depending on soil fertility. For example, in sites with high fertility soil, high SLA may be favoured in warm and moist environments while low SLA is favoured in cool, dry environments. However, in sites with low fertility soil, low SLA may be favoured regardless of climatic conditions because the disadvantages of producing ‘expensive’ leaves with high SLA are severe in resource-poor soils. If such interactions between climate and soil fertility do occur, then it may be crucial to include them in studies of species-environment relationships and models of community assembly. For instance, if a model is developed to predict the occurrence of a species in a site using the relationship between SLA and climatic factors only, the predictions are likely to be inaccurate and unreliable if soil fertility also varies at the site. Following the current example, without considering soil fertility, it could be predicted that SLA would be high in all warm and moist sites, which would be incorrect in environments with low fertility soil. This has serious implications for many applications of trait-based ecology such as modelling species distributions and responses to climate change. It is therefore important to understand how differing combinations of climate and soil fertility impact the adaptive values of functional traits. Many studies have assessed variation in plant traits across either soil fertility (Mason, *et al.* 2012; Jager, *et al.* 2015) or climatic gradients (Laughlin, *et al.* 2011; Reich 2014) at local and worldwide scales. However, few studies have assessed how functional traits vary across climatic and soil fertility gradients simultaneously (Ordonez, *et al.* 2009; Maire, *et al.* 2015) and none have evaluated the potentially critical interaction effects of soil fertility and climate on multiple traits.

Early botanists noted the importance of climate and soil in determining the distribution patterns of New Zealand forests (Cockayne 1928; Zotov 1938). However, there have only been a few attempts to quantify the relationships between native trees and climate or soil gradients at a national scale. Wardle (1991) provided a qualitative description of tree species distributions along gradients of temperature, moisture and soil fertility, but these are yet to be rigorously evaluated with data. Indirect gradients have been used as a surrogate for the underlying factors affecting plant distribution patterns. For example, Wardle (1984) and Allen *et al.* (1991) used altitude as an indirect proxy for temperature. Yet, the use of indirect gradients is less generalizable than use of direct gradients, because the relationships identified are location specific (Austin & Smith 1989). Leathwick (1995) provided one of the first analyses of the relationships between the distributions of tree species and direct environmental factors of: mean annual temperature, winter minimum temperature, solar radiation, moisture availability, and lithography. This research found that: broad-leaved trees occurred in moist, warm, well-lit and fertile environments; beech trees occurred in less optimum sites with cool, poorly-lit and lower fertility conditions, with some small-scale/low intensity disturbances; and conifers occurred in the most limited sites, where soil fertility was low, large-scale/high intensity disturbances occurred and broad-leaved trees were uncompetitive. In contrast to this species-level study, my study will use community-level plant traits to understand the physiological drivers of plant community-environment relationships in New Zealand forests. Trait-based studies provide a more general approach than species-based studies and therefore have more predictive and quantitative power, and enable greater application of the results to other regions.

My overall aim was to determine the adaptive value of multiple functional traits across broad climate and soil fertility gradients in New Zealand forests. Two analyses were conducted to achieve this goal. First, I evaluated the multivariate correlations of 13 traits among 64 tree species to determine the principal axes of functional trait variation in New Zealand trees. Second, I used multiple linear regression to evaluate how community-weighted mean traits relate to mean annual temperature, vapour pressure deficit, soil fertility, and the interaction effects of these three factors among 324 forest plots throughout New Zealand.

2.2 Methods

2.2.1 Study system

This study was conducted in temperate forests throughout the three main islands of New Zealand. New Zealand is located in the Pacific Ocean to the east of Australia, between 35° and 47° S and has a small land mass of 270, 000 km^2 (Leathwick 1998). Diverse climatic variation across the country results from the wide latitudinal range, diverse topography and situation of mountain ranges across the prevailing westerly winds. Climate is warm temperate from the top of the North Island to the Nelson and Marlborough regions of the South Island, and cool temperate throughout the rest of the South Island (Meurk 1984). There is a gradient of precipitation from wet in the west of New Zealand to drier in the east which is particularly pronounced in the South Island due to the rain shadow effect of the Southern Alps (Sinclair, *et al.* 1997). Mean annual precipitation varies from 5,000 mm on the West Coast of the South Island to 210 mm on the eastern side of the South Island (Sinclair, *et al.* 1997). Mean annual temperature at sea level ranges from 18 °C in the northern-most regions to 10 °C in the southern-most regions (Mackintosh 2001).

Soil types in New Zealand include Spodosols, Ultisols, Inceptisols and Alfisols (Van Rees 2006). Weathered volcanic tephra forms the basis of mature soils throughout the North Island and northern South Island. In the North Island, this is intermixed with recent peat and alluvium based soils in the low-lying plains. In the South Island, both old and recent soils occur which are mainly derived from glacial deposits. On the mountain ranges, soils are poorly developed and derived from parent materials of greywacke, schist and gneiss (Molloy 1998).

The indigenous forests of New Zealand are predominantly evergreen and contain a kaleidoscopic variety of communities (Wardle 1991; McGlone *et al.* 2004). However, deforestation has removed 70% of the total forest that once covered the country (Leathwick 1995; Allen *et al.* 2013). Temperate mixed conifer/broadleaf forests cover much of New Zealand with variation in the dominant species with latitude (Wardle 1991). In Northland, kauri (*Agathis australis*) dominates the forest community (Wyse, *et al.* 2014). Evergreen beeches (Nothofagaceae) are the dominant forest type in most dry and high altitude regions with poor soil (Leathwick 1995).

2.2.2 Data assembly

Three datasets were assembled in order to conduct this analysis: plant community data, environmental data and functional trait data.

Plant community data

The community data was obtained from previous measurements made for carbon analysis under the Kyoto Protocol called the Land Use Carbon Analysis System (LUCAS) (Stephens *et al.* 2007). This System has a database of tree species distributions and basal area measurements from every forest type in New Zealand. The LUCAS has surveyed the vegetation at 1,177 plots (the LUCAS plots) of 20×20 m size, (Payton *et al.* 2004) located at the intersections of an 8 x 8 km grid across New Zealand's forests (Wiser *et al.* 2011). The 324 plots which had associated soil information were selected. These plots were located across a range of climatic and altitudinal ranges in native forest (Figure 2.1). Forest tree community composition was measured on each plot. Diameters were measured on all individual stems ≥ 2.5 cm diameter at breast height (dbh; 135 cm) and were identified to species. Basal area (ba) was calculated for each species in each plot. The relative abundance of species *i* in plot *k* was calculated as $ra_{ik} = ba_{ik} / \Sigma\, ba_k$.

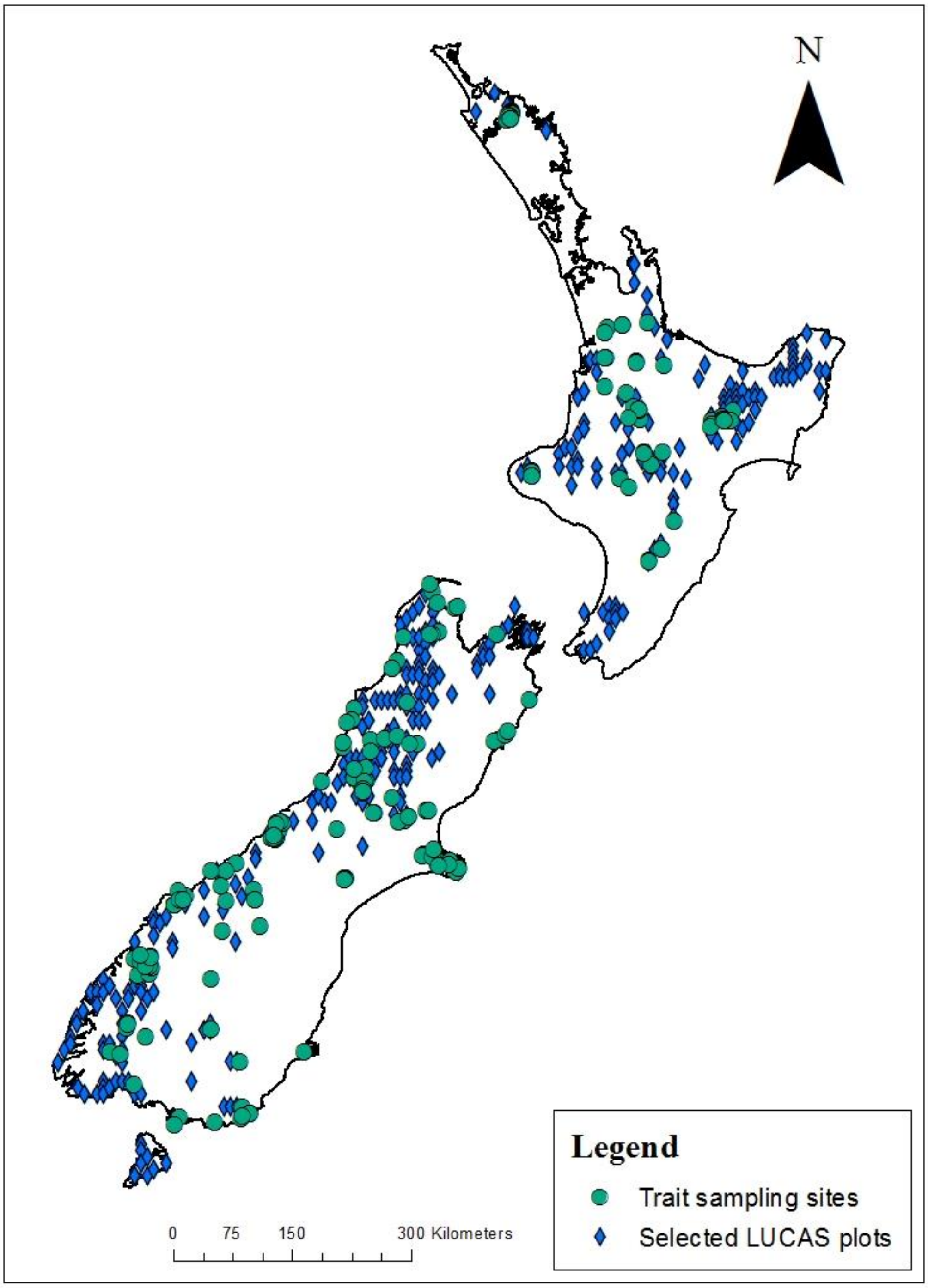


Figure 2.1: Map of sites where plant functional traits were sampled and the LUCAS plots which were selected for use.

Environmental data

Climate and soil data was obtained from two sources (Table 2.1). These were publically available datasets from Land Environments of New Zealand (LENZ) (Leathwick 2003) and the LUCAS database (Wiser, *et al.* 2011). Environmental variables were chosen based on previously observed relationships with species distributions by Leathwick (1995). Climate data for mean annual temperature

(MAT) and October vapour pressure deficit (VPD) at the locations of the 324 LUCAS plots (Figure 2.1) were extracted from the LENZ climate surfaces using the “add surface information” tool in ArcGIS Desktop 10 (Environmental Systems Research Institute 2011) . VPD is measured in October because during this month persistent westerly winds result in strong geographic variation in VPD across New Zealand (Leathwick, *et al.* 2002). Solar radiation was initially included but was removed when it was not found to be an important factor in the multiple linear regression models developed in this study.

A variety of soil properties were analysed from samples taken in each LUCAS plot, at the Landcare Research Plant and Soil Laboratory in Palmerston North, New Zealand. Soil organic carbon (C) % and total N % were measured using a Leco CNS 2000 Analyser (Leco Corporation, St. Joseph, Michigan, USA) which utilises the Dumas dry combustion principal (Metson *et al.* 1979). Total phosphorus (P) and organic P concentrations were determined using flow injection analysis on a Lachat QuikChem 8000 (Lachet Instruments, Loveland, Colorado, USA) following ignition at 550 °C for 60 min and extraction with 0.5M H_2SO_4 at a soil-to-extractant ratio of 1:200 for 16 hrs (Blakemore *et al.* 1987). Soil pH was measured in solution with a 1:2.5 soil-to-distilled water ratio using a Radiometer PHM210 pH meter equipped with a Radiometer pHC2401-8 electrode. We used these three variables to represent variation in soil fertility. Soil pH is considered a ‘master variable’ of soil chemistry (Binkley *et al.* 2011). Soil C:N ratio is indicative of quality of the soil organic matter (Heal, *et al.* 1997) and the relative availability of nitrogen, because N in soils with high C:N ratios will likely be bound up in the microbial biomass and will be less available to plants. We used organic P because it comprises the majority of total P across most of these forests: the average ratio of organic P:total P is 0.80 and the median ratio is 0.85 (Laughlin *et al.* 2015). These variables are widely used to assess relationships among vegetation structure and soil properties (Ordonez, *et al.* 2009; Jager, *et al.* 2015; Maire, *et al.* 2015).

Table 2.1: Environmental variables, units, sources and the range of values for each variable occurring in the 324 selected LUCAS plots.

Environmental variable	Unit	Source	Range
Mean annual temperature	°C	Leathwick, 2003	5.3 – 15.7
October vapour pressure deficit	kPa	Leathwick, 2003	0.01 – 0.54
Soil pH	Dimensionless (-log[H+])	Stephens et al., 2007	3.04 – 6.25
Soil C:N	ratio	Stephens et al., 2007	10.24 – 49.29
Soil organic P	mg P kg^{-1} soil	Stephens et al., 2007	30.51 – 2040

Rather than selecting a single variable to reflect soil fertility, principal component analysis (PCA) using the *princomp* function in the vegan library of R (Oksanen *et al.* 2011) was used to reduce the three highly correlated soil properties (soil pH, soil C : N ratio and soil organic P) down to a single dimension for use as a predictor in the regression analyses. The first principal component was the only axis with an eigenvalue greater than one and explained most of the variation (65%) in these collinear soil properties (Table 2.2). This dominant soil fertility gradient varies from soils with high C:N ratio, low pH, and low organic P, to soils with low C:N ratio, high pH, and high organic P. This gradient is used in later analyses, referred to as “soil fertility”.

Table 2.2: Results of the PCA of the correlation matrix derived from three soil properties measured on 324 plots. For each component, the eigenvalues and proportions of variance explained are provided. Eigenvectors for each of the components are listed below.

	PC1	PC2	PC3
Eigenvalues	1.948	0.795	0.257
Proportion of variance	0.649	0.265	0.086
Cumulative proportion	0.649	0.914	1.00
Eigenvectors:			
pH	0.631	-0.361	0.687
C:N	-0.649	0.240	0.722
Soil organic P	0.426	0.901	0.083

A topographical index was calculated for each LUCAS plot to capture the continuous variation in landforms and terrain across New Zealand (McNab 1993).

The index was calculated as the mean of eight slope gradients from the plot centre to skyline. Low values of the topographical index indicate ridges and high values indicate gullies.

A successional index was calculated for each LUCAS plot to represent the stage of succession of each site. This was done to account for the fact that community-weighted mean traits of forests may change with succession (Lohbeck, *et al.* 2013). An interspecific trade-off between shade-tolerance and growth rates in high light is a major driver of secondary succession (Bazzaz & Pickett 1980; Smith & Huston 1989; Lusk *et al.* 2015). Basal area ($\log(\mathrm{m}^2\ \mathrm{ha}^{-1})$) of the forest was used as a surrogate for successional stage because stand basal area is a structural variable of succession and is related to the age of a forest stand (Lohbeck, *et al.* 2013).

Species selection

Species were selected from the New Zealand indigenous arborescent flora depending on their relative abundance and frequency across the country. Based on the LUCAS plot data (Wiser, *et al.* 2011), species were selected according to the following criteria: (*i*) the species must attain a diameter at breast height of at least 10 cm; (*ii*) the species must contribute at least 10 % to the total basal area of at least one plot; and (*iii*) the species must occur on at least 1 % of all the plots. These criteria resulted in a list of 64 species (Table 2.3). None of the 64 species are listed as threatened or endangered (de Lange *et al.* 2009).

Table 2.3: Table of the names and species codes of the 64 New Zealand tree species sampled.

Species code	Scientific name	Common name
ARISER	*Aristotelia serrata*	Wineberry
BEITAR	*Beilschmiedia tarairi*	Tarairi
BEITAW	*Beilschmiedia tawa*	Tawa
CARSER	*Carpodetus serratus*	Marbleleaf
COPLIN	*Coprosma linariifolia*	Mikimiki
CYACUN	*Cyathea cunninghamii*	Gully tree fern
CYADEA	*Cyathea dealbata*	Silver fern
CYAMED	*Cyathea medullaris*	Black tree fern
CYASMI	*Cyathea smithii*	Soft tree fern
DACCUP	*Dacrydium cupressinum*	Rimu
DACDAC	*Dacrycarpus dacrydioides*	Kahikatea
DICFIB	*Dicksonia fibrosa*	Wheki-ponga
DICSQU	*Dicksonia squarrosa*	Wheki
DRALON	*Dracophyllum longifolium*	Inaka
DRATRA	*Dracophyllum traversii*	Mountain neinei
DYSSPE	*Dysoxylum spectabile*	Kohekohe
ELADEN	*Elaeocarpus dentatus*	Hinau
ELAHOO	*Elaeocarpus hookerianus*	Pokaka
FUCEXC	*Fuchsia excorticata*	Tree fuchsia
FUSCLI	*Fuscospora cliffortioides*	Mountain beech
FUSFUS	*Fuscospora fusca*	Red beech
FUSSOL	*Fuscospora solandri*	Black beech
FUSTRU	*Fuscospora truncata*	Hard beech
GRILIT	*Griselinia littoralis*	Broadleaf
HALBIF	*Halocarpus biformis*	Pink pine
HEDARB	*Hedycarya arborea*	Pigeonwood
HOHGLA	*Hoheria glabrata*	Mountain ribbonwood
IXEBRE	*Ixerba brexioides*	Tawari
KNIEXC	*Knightia excelsa*	Rewarewa
KUNERI	*Kunzea ericoides*	Kanuka
LAUNOV	*Laurelia zelandiae*	Pukatea
LEPINT	*Lepidothamnus intermedius*	Yellow-silver pine
LEPSCO	*Leptospermum scoparium*	Manuka
LIBBID	*Libocedrus bidwillii*	Mountain cedar
LOPMEN	*Lophozonia menziesii*	Silver beech
MELRAM	*Melicytus ramiflorus*	Mahoe
METROB	*Metrosideros robusta*	Northern rata
METUMB	*Metrosideros umbellata*	Southern rata
MYRAUS	*Myrsine australis*	Red matipo
MYRDIV	*Myrsine divaricata*	Weeping matipo
MYRSAL	*Myrsine salicina*	Toro
NEOCOL	*Pseudopanax colensoi*	Mountain five-finger
NESCUN	*Nestegis cunninghamii*	Black maire

NESLAN	*Nestegis lanceolata*	White maire
OLECOL	*Olearia colensoi*	Leatherwood
OLERAN	*Olearia rani*	Heketara
PENCOR	*Pennantia corymbosa*	Kaikomako
PHYALP	*Phyllocladus alpinus*	Mountain toatoa
PHYTRI	*Phyllocladus trichomanoides*	Tanekaha
PITEUG	*Pittosporum eugenioides*	Lemonwood
PITTEN	*Pittosporum tenuifolium*	Kohuhu
PODHAL	*Podocarpus hallii*	Mountain totara
PODTOT	*Podocarpus totara*	Lowland totara
PRUFER	*Prumnopitys ferruginea*	Miro
PRUTAX	*Prumnopitys taxifolia*	Matai
PSEARB	*Pseudopanax arboreus*	Five-finger
PSECOL	*Pseudowintera colorata*	Mountain horopito
PSECRA	*Pseudopanax crassifolius*	Lancewood
QUIACU	*Quintinia acutifolia*	Tawheowheo
QUISER	*Quintinia serrata*	Tawheowheo
RHOSAP	*Rhopalostylis sapida*	Nikau
SCHDIG	*Schefflera digitata*	Pate
WEIRAC	*Weinmannia racemosa*	Kamahi
WEISIL	*Weinmannia silvicola*	Towai

Functional trait data collection

Thirteen functional traits (Table 2.4) were measured on each of the 64 species. Standard protocols for measuring leaf, stem, root, flowering, seed and whole-plant functional traits were used (Perez-Harguindeguy, *et al.* 2013). For each species, an average of 54 replicates (minimum of 3 replicates for *Nestegis lanceolata* and maximum of 120 replicates for *Carpodetus serratus*) were obtained for the traits of SLA, LDMC, WDMC and RBT to ensure sufficient representation in the analyses.

Table 2.4: Functional traits, their associated abbreviations, units and range of values in this study.

Functional Trait	Abbreviation	Unit	Range
Leaf traits			
Specific leaf area	SLA	$mm^2\ mg^{-1}$	1.76 to 25.59
Leaf dry matter content	LDMC	$g\ g^{-1}$	0.211 to 0.53
Leaf nitrogen concentration	LNC	%	0.62 to 3.32
Leaf phosphorus concentration	LPC	%	0.04 to 0.40
Leaf total phenol concentration	Phenolic	%	0.81 to 26.19
Stem traits			
Wood dry matter content	WDMC	$g\ g^{-1}$	0.18 to 0.66
Relative bark thickness	RBT	%	0 to 6.19
Root traits			
Root dry matter content	RDMC	$mg\ g^{-1}$	0.07 to 0.26
Root diameter	Rootdiam	mm	0.22 to 1.25
Flowering traits			
Flowering onset	Flronset	Julian date	31 to 278
Flowering duration	Flrduration	Julian date	30 to 222
Seed traits			
Seed mass (dry)	Sm	mg	0.0008 to 1868
Whole-plant traits			
Maximum height	Htmax	m	6 to 50

In order to maximise functional trait sampling efficiency, sites were selected across the latitudinal range of New Zealand that include extensive altitudinal variation (Figure 2.1). This ensured that many species had the potential to be sampled at each site and intraspecific variation in traits was captured. North Island sampling sites in the Waikato included Pukemokemoke Bush Reserve, Pirongia Forest Park, Hakarimata Scenic Reserve, and the Kaimai Mamaku Forest Park. Other North Island sites included the Whirinaki Te Pua-a-Tāne Conservation Park, Ruahine Forest Park, Egmont National Park, Pureora Ecological District and Puketi Forest. South Island sites included Fiordland National Park, Westland Tai Poutini National

Park, the Catlins, Banks Peninsula, Abel Tasman National Park and Kahurangi National Park. Sampling was conducted during summer months (Nov-Feb).

An opportunistic sampling strategy was used. At each site, the field team searched for individual trees. Upon finding a desired species, the team collected leaf and wood material from individuals > 10 cm dbh of each species at that location. The number of trees of each species, sampled at each site, varied from 1 to 10, depending on the diversity of the location and accessibility of the trees. Sampling locations were recorded using geographic coordinates. In total, trait data was collected from 3411 individual trees during this field work. Additional leaf and stem trait data on these species was obtained from previous research by Dr Daniel Laughlin and Dr Sarah Richardson (Landcare Research) at 40 sites across the country.

2.2.2.1 Leaf functional traits

Where possible the leaves sampled were mature, fully expanded, well-lit and from healthy canopies. A 4 m and 8 m telescopic pruner were used to cut leaves off branches up to 10 m high. The number of leaves, leaflets or photosynthetic units (hereafter, collectively termed 'leaves') varied depending on the size and area of the leaves. For medium to large, compound- leaved species, one leaflet from three different leaves on each individual was collected. *Rhopalostylis sapida* is a large palm, so five sections, approximately 15 cm long, of five different fronds were collected. For simple, medium to large leaves, three leaves were collected from each individual tree. Five leaves were collected from *Nothofagus* spp. because they have small leaves. Ten pinnae were collected from tree fern species. Phylloclades (i.e. photosynthetic structures on Phyllocladaceae) were treated as operational photosynthetic units and are hereafter referred to as 'leaves'. Ten leaves were collected from *Phyllocladus* spp., *Podocarpus* spp., *Prumnopitys* spp., *Coprosma linariifolia, Myrsine divaricata* and *Dracophyllum longifolium*, because they have small leaves. Thirty leaves were collected from *Kunzea ericoides* and *Leptospermum scoparium* because they have very small leaves. Five small (approximately 5 cm x 5 cm) branchlets were collected from *Dacrycarpus dacrydioides*, *Lepidothamnus intermedius*, *Dacrydium cuppressinum*, *Libocedrus bidwillii*, *Halocarpus biformis*, because these needled species were too difficult to collect individual needles from. Leaves were stored in air-tight plastic bags to minimise water loss.

Once the field crew returned from the field back to the accommodation, leaf area and mass measurements were made. This was typically completed within seven hours from the time of sample collection. Leaf area and leaf fresh mass of the combined leaves of each sample were measured using a CI-202 Portable Leaf Area Meter (CID Bio-Sciences, Inc., Camas, WA, USA) and a Mettler-Toledo PB3002-S DeltaRange portable analytical balance. Leaf area of the very small and needled leaves could not be measured accurately using the portable leaf area meter. So these leaves were transported inside wet paper towels within air-tight plastic bags back to the laboratory in Hamilton within one week. Leaf area was then measured on a LICOR LI-3100C Area Meter (LICOR Biosciences, Lincoln, NE, USA). All leaves were oven-dried in a Contherm Thermotec 2000 Series oven at 60 °C for a minimum of one week and then cooled to room temperature in a Lab Companion vacuum desiccator before being re-weighed using a Mettler-Toledo MS304S analytical balance to obtain oven-dry mass. SLA was calculated by dividing the one-sided area of the fresh leaves by their dry mass. LDMC was calculated as dry mass per unit fresh mass of the leaves.

Extra leaves were collected from one tree of each species sampled at each location. These leaves were also oven dried in the Contherm Thermotec 2000 Series oven at 60 °C for a minimum of one week and then ground into a fine powder using a Retsch MM 2000 grinder. Approximately 20 g of fresh leaf sample was ground to provide the desired 1 g of dry ground leaf material for each sample. Ground leaf samples were then sent to the Landcare Research Environmental Chemistry Laboratory in Palmerston North for flow injection analysis using a Lachat QuikChem 8000 series. This test provided measurements of total leaf N, P and phenolic concentrations. A total of 173 leaf samples were analysed.

2.2.2.2 Stem functional traits

Tree diameter at breast height was measured using a diameter tape measure. For species, which were not above 10 cm dbh, the diameter of the main stem was measured as high up the stem as possible. Three equivalent methods were used for measuring stem tissue traits. For angiosperms and conifers with a dbh greater than 10 cm and the only palm tree (*Rhopalostylis sapida*), tree cores were extracted from the tree trunk using a Suunto increment borer with hardened steel bits. The cores were 5.15 mm diameter. The length of the core varied depending on the diameter of the tree but was taken until the pith of the tree was reached or, in the case of large trees, until the total length of the 30 cm borer was used. Because wood density varies across the diameter of a tree it was intended to collect a core sample representative of the entire radius (Muller-Landau 2004). One core per tree was taken at breast height. The cores samples included both the outer bark and wood. To minimise the chances of infection after coring, the borer was used at a slightly downward angle to allow any moisture in the hole to drain from the trunk and was cleaned between samples (Norton 1998). For trees where wood could not be extracted with a borer (such as *Dracophyllum* spp.), a twig of approximately 15 cm length was collected from a healthy lower branch using secateurs. The length of the wood core or twig was measured and it was stored in an appropriately labelled paper bag. Wood fresh mass measurements were made using a Mettler-Toledo PB3002-S DeltaRange portable analytical balance. This was completed within seven hours from the time of sample collection. The mean wood fresh mass for each species was used in the calculation of wood dry matter content. Wood samples were oven dried at 100 °C in a Contherm Thermotec 2000 Series oven (Williamson & Wiemann 2010) for a minimum of one week and then cooled to room temperature in a Lab Companion vacuum desiccator before being re-weighed using a Mettler-Toledo MS304S analytical balance to obtain oven-dry mass. Wood dry matter content was calculated as the oven dry mass divided by the fresh wood mass.

Increment borers were not effective at extracting stem tissue from tree ferns, so data from another study was used to calculate stem traits of the tree ferns (Jager, *et al.* 2015). Six individuals of tree ferns of *Cyathea medullaris*, *C. dealbata* and *Dicksonia squarrossa* in the Waikato region, were cut down. Whole disks were cut from three heights in the tree ferns, at the base, midstem and top. After removing the adventitious roots and non-vascular tissue from the outside of the disks, wood dry matter content was calculated by dividing dry mass (oven dried at 100 C for a minimum of 1 week) of the disk by fresh mass of the disk. The mean across the three measured tree fern species was used as the value for wood dry matter content of *C. smithii*, *C. cunninghamii*, and *D. fibrosa*.

Bark thickness, including the cambium, was measured from the bark on the core or twig, using digital callipers. Where bark was fissured we measured thickness from the thickest point (Lawes *et al.* 2014). Relative bark thickness was calculated as the thickness of the bark divided by dbh. Relative bark thickness is useful for determining the amount of external bark a tree has per mm of internal wood (Lawes, 2013; Laughlin, 2012). Bark thickness of tree ferns was recorded as zero.

2.2.2.3 Root functional traits

Root trait data was sourced from measurements on nursery-grown seedlings by Kramer-Walter (2015). Trait measurements were made according to standardised protocols (Cornelissen, *et al.* 2003a; Perez-Harguindeguy, *et al.* 2013). Root balls were washed by gently massaging them under water. Subsections of fine roots were removed from the root ball and washed more thoroughly. Once clean, roots were transferred into a clear acrylic tray on an Epson Expression 10000XL scanner (Tokyo, Japan). Fine paintbrushes were used to spread the roots out and minimise overlap. Average root diameter was calculated using WinRhizo Pro software (Version 2012b, Regent Instruments Inc., Quebec City, Canada). Fresh root mass of each sample was obtained after removing the surface water from the roots using paper towels. The root sections were then dried at 60 °C for at least 48 hours before obtaining dry mass. Root dry matter content was calculated as root dry mass divided by root fresh mass.

2.2.2.4 Flowering functional traits

A literature search was completed for information on flowering phenology of the 65 species in this project (Allan 1961; Davies 1961; Esler 1969; Leathwick 1984; Salmon 1985; Best & Bellingham 1991; Wilson 1994; Dijkgraaf 2002; Farjon 2005). Dates of flowering onset, peak flowering and flowering end, were extracted from these reports of flowering time at different locations across the country. The flowering dates were converted to Southern hemisphere Julian dates, using July 1 as the first day of the Southern Hemisphere Julian calendar (Weiher, *et al.* 1999). For example, Allan (1961) report that *Laurelia novae-zelandiae* flowers from October through December, which corresponds to the Southern hemisphere Julian dates 92 through 183. Flowering peak was taken as the median date between these two dates.

2.2.2.5 Seed traits

Seed mass was measured by Sarah Richardson from Landcare Research. Seed dry mass was measured on each of the 65 species from seeds stored in the Allan

Herbarium (CHR, Lincoln, New Zealand). Seeds were oven-dried to a constant mass before weighing. An average weight of fern spore mass (0.0008 mg) was used as mean 'seed mass' for the six tree ferns in this study.

2.2.2.6 Whole-plant functional traits

Maximum height estimates for each species were derived from regional floras (McGlone *et al.* 2010b). Maximum plant height is the distance between the upper heights of the main photosynthetic tissues and the ground level (Perez-Harguindeguy, *et al.* 2013).

2.2.3 Data analysis

For species-trait combinations where quantitative data was not obtained, data was imputed using the *mice* function in the 'mice' library in R (Van Buuren & Groothuis-Oudshoorn 2011; R Development Core Team 2014) prior to further analysis.

Determining the intrinsic dimensions

Given that many functional traits are correlated, it is important to determine which traits or combinations of traits represent independent axes of functional specialization (Laughlin 2014a). Principal component analysis was conducted using the *princomp* function in R, to determine the intrinsic dimensionality of the species-trait matrix (R Development Core Team 2014). The Kaiser-Guttman criterion (if an axis is significant then the eigenvalue of that axis should be greater than one (McCune & Grace 2002)) was used to determine which principal components were important. Interpretation of the principal components was based on identifying which traits were most strongly correlated with each component.

Determining the relationships between CWM traits and environmental factors

Community-weighted mean (CWM) traits were calculated for each trait j in each of the 324 LUCAS plots k as $CWM_{jk} = \sum_{i=1}^{S} t_i p_{ik}$, where t_i is the mean trait of species i across all trait measurements of that trait, p_{ik} is the relative abundance of species i in plot k, and S is the number of species in the plot (Shipley, *et al.* 2011). All CWM traits were log transformed prior to use in the following analyses.

Multiple linear regression was used to model each CWM trait as a function of five main effect environmental variables using the *lm* function in R (R Development Core Team 2014). The main effects included in each model were soil fertility, mean annual temperature, vapour pressure deficit, basal area, and the topographic index. Scatterplots with lines of best fit and correlation coefficients were made to illustrate the correlations between these main effects and the CWM traits. Two interaction effects were included in each model: soil fertility × MAT, and soil fertility × VPD. All predictors were continuous variables so they were centred and scaled to unit variance in order to estimate interaction effects. This was done using the formula, centred variable = (variable – mean of the variable) / (standard deviation of the variable). The values of the centred variables ranged from -2 to +2.

To facilitate interpretation of the complex models, two types of plot were created. First, colourful interaction plots were created using the 'fields' library of R (Nychka *et al.* 2015). A prediction matrix was generated for use in predicting CWM trait values based on the centred variables. This matrix was also used to categorise the predicted CWM trait values depending on whether they were generated in low fertility or high fertility soils. 'Low fertility soils' were classed as -2 and 'high fertility soils' were classed as +2, i.e. ± 2 standard deviations from the average soil fertility. 'High' and 'low' fertility soils are simplified concepts because in reality soils are highly dynamic and nutrients can be distributed heterogeneously in both space and time (Campbell & Grime 1992; McLaren & Cameron 1996). The *smooth.2d* function was used to predict CWM trait values for each trait and soil fertility category. The model-predicted CWM trait values were plotted on a colour-scale using the *image.plot* function, to illustrate the modelled variation of trait values with MAT and VPD within both soil fertility levels. Second, line interaction plots were created to improve visualisation of the variations in interactions across soil fertility. To achieve this effects of the interactions of soil fertility × MAT, and soil fertility × VPD were plotted for the linear model of each CWM trait, using the 'effects' library in R (Fox 2003; R Development Core Team 2014).

2.3 Results

2.3.1 Dimensions of trait variation among New Zealand trees

The principal component analysis (Table 2.5) illustrates how leaf, stem, root, flowering, seed, and whole-plant traits are correlated with each other and how these traits vary between species. The Kaiser criterion suggested that this species- trait matrix was at least five dimensional because the first five eigenvalues were greater than one (Table 2.5). These five dimensions accounted for 76% of the total variation and correlation structure of the 13 traits measured in this study.

The five dimensions relate to traits from all of the plant organs (Table 2.5). The first axis represents variation along the leaf economics spectrum (Figure 2.2). This axis spans from species with high specific leaf area, low leaf dry matter content, high leaf N concentration and high leaf P concentration to species with low SLA, high LDMC, low leaf P concentration and low leaf N concentration. The second axis represents variation in root diameter, flowering duration, seed mass and leaf phenolic concentration (Figure 2.2). This axis varies from species with large root diameters, large seeds, short flowering duration and low leaf phenolic concentration to species with small root diameters small seeds, long flowering duration and high leaf phenolic concentration. The third axis represents variation in stem traits of relative bark thickness and wood dry matter content. This axis spans from species with high RBT and high WDMC to species with low RBT and WDMC. The fourth axis ranges from species with high maximum plant height to species with low maximum plant height. The fifth axis represents variation in root dry matter content and flowering onset. This axis ranges from species with high RDMC and early flowering onset to species with low RDMC and late flowering onset.

Table 2.5: Results of the PCA analysis of the correlation matrix derived from the thirteen traits measured on 64 tree species. For each axis, the eigenvalues and proportion of variance explained are provided. Eigenvectors for each of the axes are listed below and variables most strongly correlated with each component are in bold.

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalues	**4.41**	**1.74**	**1.45**	**1.21**	**1.02**	0.83
Proportion of variance	0.34	0.13	0.11	0.09	0.08	0.06
Cumulative proportion	0.34	0.47	0.58	0.68	0.76	0.82
Eigenvectors:						
Specific leaf area	**0.405**	-0.123	0.253	0.130	-0.110	-0.028
Leaf dry matter content	**-0.402**	-0.022	-0.257	0.145	-0.031	0.007
Leaf nitrogen concentration	**0.407**	-0.018	0.255	0.267	-0.107	0.032
Leaf phosphorus concentration	**0.391**	0.062	0.189	0.294	0.067	-0.164
Root diameter	0.072	**0.588**	-0.107	-0.255	-0.032	0.197
Flowering duration	-0.069	**-0.495**	0.294	-0.238	-0.271	0.482
Seed mass	-0.060	**0.449**	0.161	0.226	-0.394	0.559
Leaf phenolic concentration	-0.275	**-0.298**	0.219	0.293	0.182	0.137
Relative bark thickness	-0.197	0.157	**0.542**	-0.329	-0.065	-0.324
Wood dry matter content	-0.266	0.208	**0.358**	0.031	-0.254	-0.419
Max height	-0.219	0.207	0.097	**0.587**	0.322	0.033
Root dry matter content	-0.242	-0.144	-0.105	0.290	**-0.597**	-0.173
Flowering onset	0.223	-0.037	-0.393	0.092	**-0.424**	-0.241

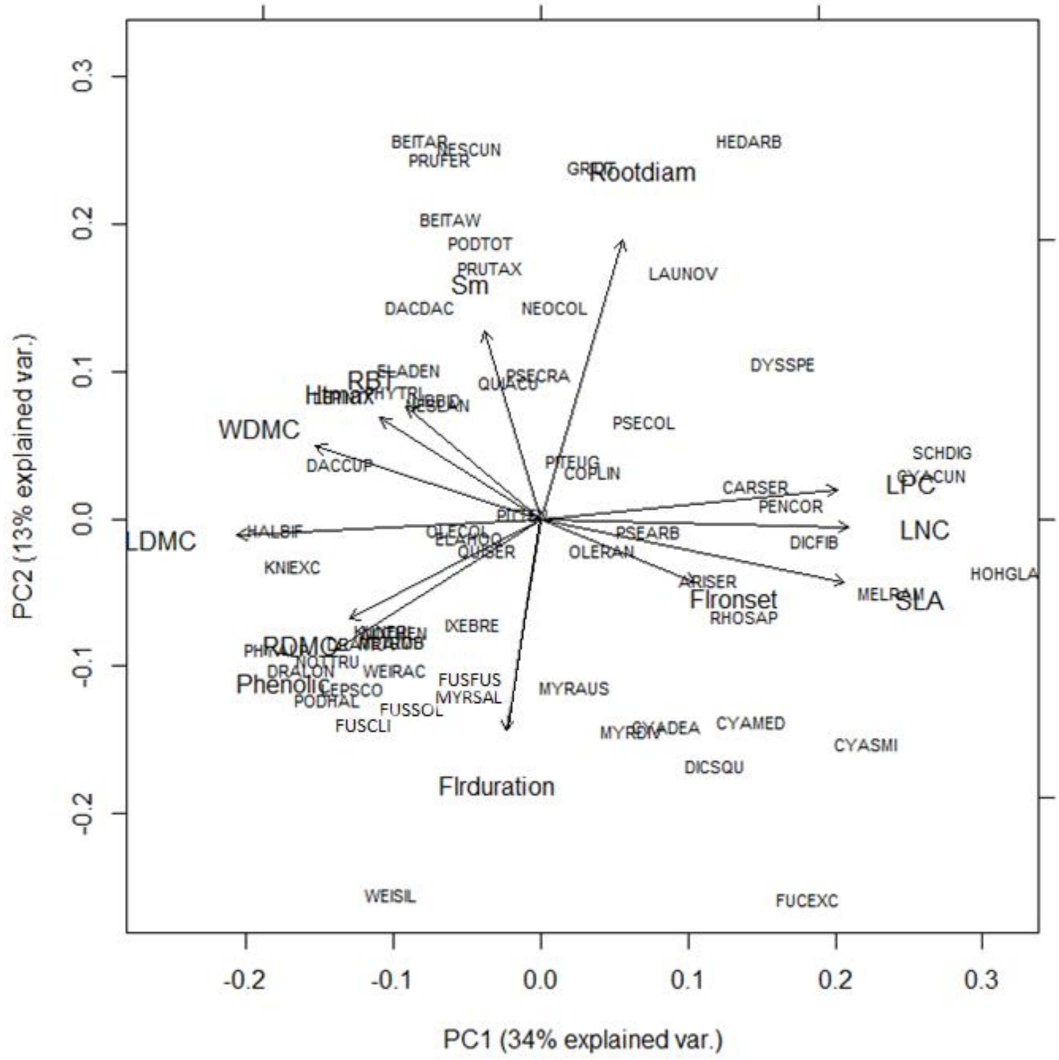


Figure 2.2: Ordination of PCA results showing the relationships between species and leaf, stem, root, flowering, seed, and whole-plant traits. Refer to Table 2.3 for species codes and Table 2.4 for trait abbreviations.

2.3.2 Relationships between CWM traits and environmental factors

Soil fertility consistently had stronger relationships with all community-weighted mean (CWM) traits than climate variables (Table 2.6). The main effect variables were significant for most CWM traits (Table 2.6, Figure 2.3, 2.6, 2.9, 2.12, 2.15). Soil fertility and mean annual temperature were significant predictors for all traits. Vapour pressure deficit was a significant predictor of all traits except flowering duration, maximum height, and seed mass. Total basal area was a significant predictor for only four traits: leaf dry matter content, flowering duration, maximum height, and seed mass. Topography was a significant predictor for only six traits: specific leaf area, leaf N concentration, leaf P concentration, root dry matter content root diameter and maximum height. However, because the interaction effects were significant for all traits except seed mass and root dry matter content, it is not straightforward to interpret the relationships between CWM traits and the main effects of soil fertility and climate. The interaction effects varied in strength and direction between traits. The interaction effect of soil fertility × MAT was significant for all traits except root dry matter content and seed mass. The interaction effect of soil fertility × VPD was significant for all traits except leaf phenolic concentration, root dry matter content, root diameter and seed mass. In the following section, the relationships of CWM traits with soil fertility, MAT, VPD, and the interaction effects of these three factors will be explained, in an order based on the loadings on the principal component axes.

Table 2.6: Results of multiple linear regression models where CWM traits were fitted as functions of environmental variables (using centred predictor variables scaled to unit variance). Significance codes: p < 0 '*', p< 0.001 '**', p< 0.01 '*'. Refer to Table 2.4 for trait abbreviations.**

	Predictor estimates						Interaction predictor estimates		Overall model		
Trait	Intercept	Soil fertility	MAT	VPD	Log(ba)	Topo	Soil fertility × MAT	Soil fertility × VPD	p <	$F_{7,316}$	R^2_{adj}
SLA	2.11***	0.11***	0.05**	0.03*	0.01	0.05***	0.05**	-0.05***	2.2^{e-16}	27.03	0.36
LDMC	-0.83***	-0.05***	-0.04***	0.03***	-0.01*	-0.005	-0.02**	0.01*	2.2^{e-16}	38.49	0.45
LNC	0.16***	0.08***	-0.02	0.04***	0.00	0.04***	0.07***	-0.03**	2.2^{e-16}	22.34	0.32
LPC	-2.36***	0.10***	-0.06***	0.03*	0.01	0.05***	0.07***	-0.03*	2.2^{e-16}	20.11	0.29
Rootdiam	-0.86***	0.13***	0.11***	-0.08***	0.00	-0.03**	0.03*	-0.001	2.2^{e-16}	43.94	0.48
Flrduration	4.60***	0.05***	0.04***	0.004	-0.05***	-0.005	0.05***	-0.03**	2.2^{e-16}	18.53	0.28
Sm	2.43***	0.37***	0.65***	-0.06	0.35***	-0.10	0.11	-0.17	9.4^{e-15}	13.04	0.21
Phenolic	2.24***	-0.26***	-0.11***	0.08**	0.01	0.02	-0.20***	0.07	2.2^{e-16}	36.3	0.43
RBT	0.87***	-0.09***	-0.13***	0.08***	-0.01	-0.009	-0.09***	0.05**	2.2^{e-16}	32.21	0.40
WDMC	-0.63***	-0.04***	-0.04***	0.02**	0.00	-0.006	-0.02**	0.02***	2.2^{e-16}	28.04	0.37
Htmax	3.11***	-0.14***	0.05**	0.03	0.09***	0.04*	-0.10***	0.07***	2.2^{e-16}	20.32	0.30
RDMC	-1.74***	-0.06***	-0.06***	0.02*	-0.002	0.01*	-0.004	-0.003	2.2^{e-16}	31.41	0.40
Flronset	4.72***	0.08***	0.03*	-0.09***	0.02	-0.02	0.08***	-0.05***	2.2^{e-16}	17.68	0.27

Principal component one: leaf economic traits

The multiple regression models explained significant variation in community-weighted mean SLA ($R^2_{adj} = 0.36$), LDMC ($R^2_{adj} = 0.45$), LNC ($R^2_{adj} = 0.32$), and LPC ($R^2_{adj} = 0.29$) (Table 2.6). Soil fertility exhibited stronger relationships with leaf traits than the climatic variables did (Figure 2.3). SLA, LNC and LPC were positively related to soil fertility, while LDMC was negatively related to soil fertility (Table 2.6, Figure 2.3). Most leaf traits were positively related to VPD. LDMC was negatively related to MAT, while SLA and LNC were positively related to MAT (Figure 2.3). The only leaf trait that was related to total basal area was LDMC which was negatively related to total basal area (Table 2.6). SLA, LNC and LPC were positively associated with gully environments (Table 2.6).

Significant interactions between soil fertility and both climatic variables influenced all of the CWM leaf traits (Table 2.6). In environments with low fertility soils, SLA, LNC and LPC were generally low, across all climatic conditions (Figure 2.4). However, with increases in soil fertility, SLA, LNC and LPC increased rapidly in warm and moist environments but stayed approximately unchanged in cool, dry environments (Figure 2.5). In high soil fertility, low SLA, LNC and LPC values in cool and dry environments changed to high values in warm and moist environments (Figure 2.4). LDMC showed an inverse pattern to SLA, LNC and LPC. LDMC was high in low fertility soils across all climatic conditions (Figure 2.4). However, with increasing soil fertility, LDMC decreased rapidly in warm and moist environments (Figure 2.5). In high fertility soils, high LDMC in cool and dry environments changed to low LDMC in warm and moist environments (Figure 2.4).

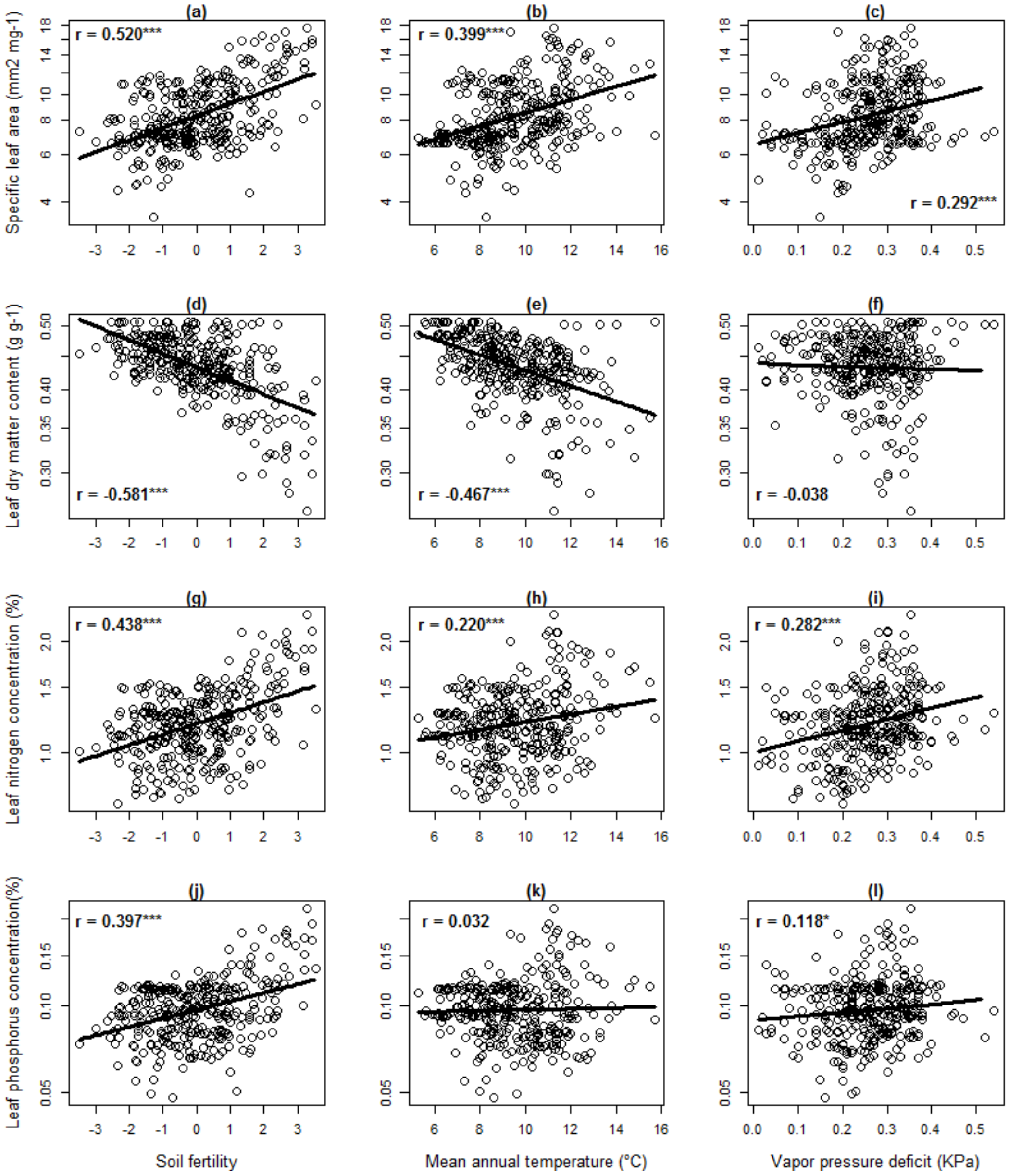


Figure 2.3: Scatterplots of CWM from principal component one against the environmental predictor variables. Soil fertility increases from left to right along the x-axis. Onto each plot are overlaid the modelled fit and correlation coefficients for the bivariate relationships.

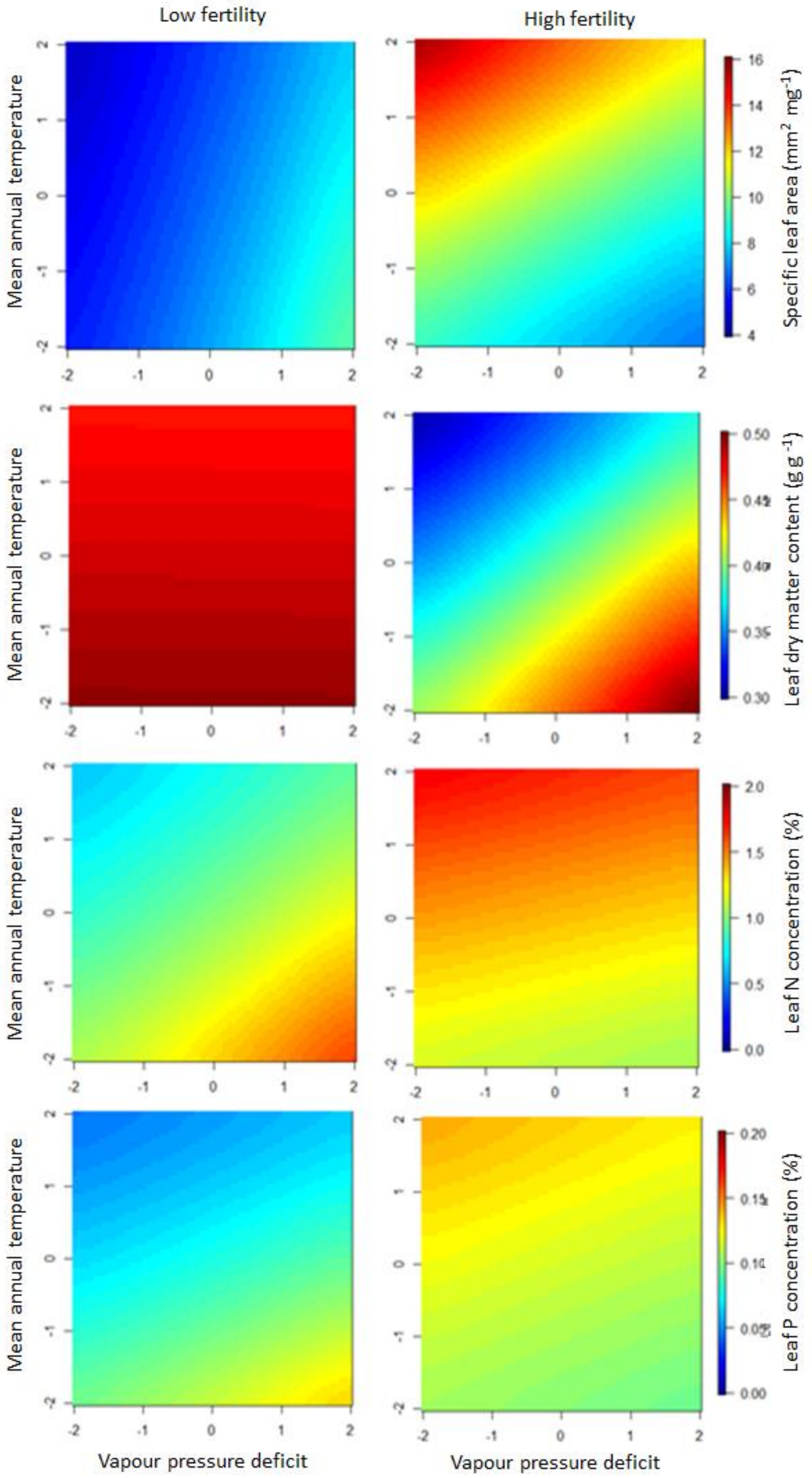


Figure 2.4: Interaction plots of the CWM traits from principal component one ((specific leaf area (mm^2 mg^{-1}), leaf dry matter content (g g^{-1}), leaf nitrogen concentration (%) and leaf phosphorus concentration (%)) with mean annual temperature (°C) and vapour pressure deficit (kPa) at two levels of soil fertility (using centred predictor variables scaled to unit variance).

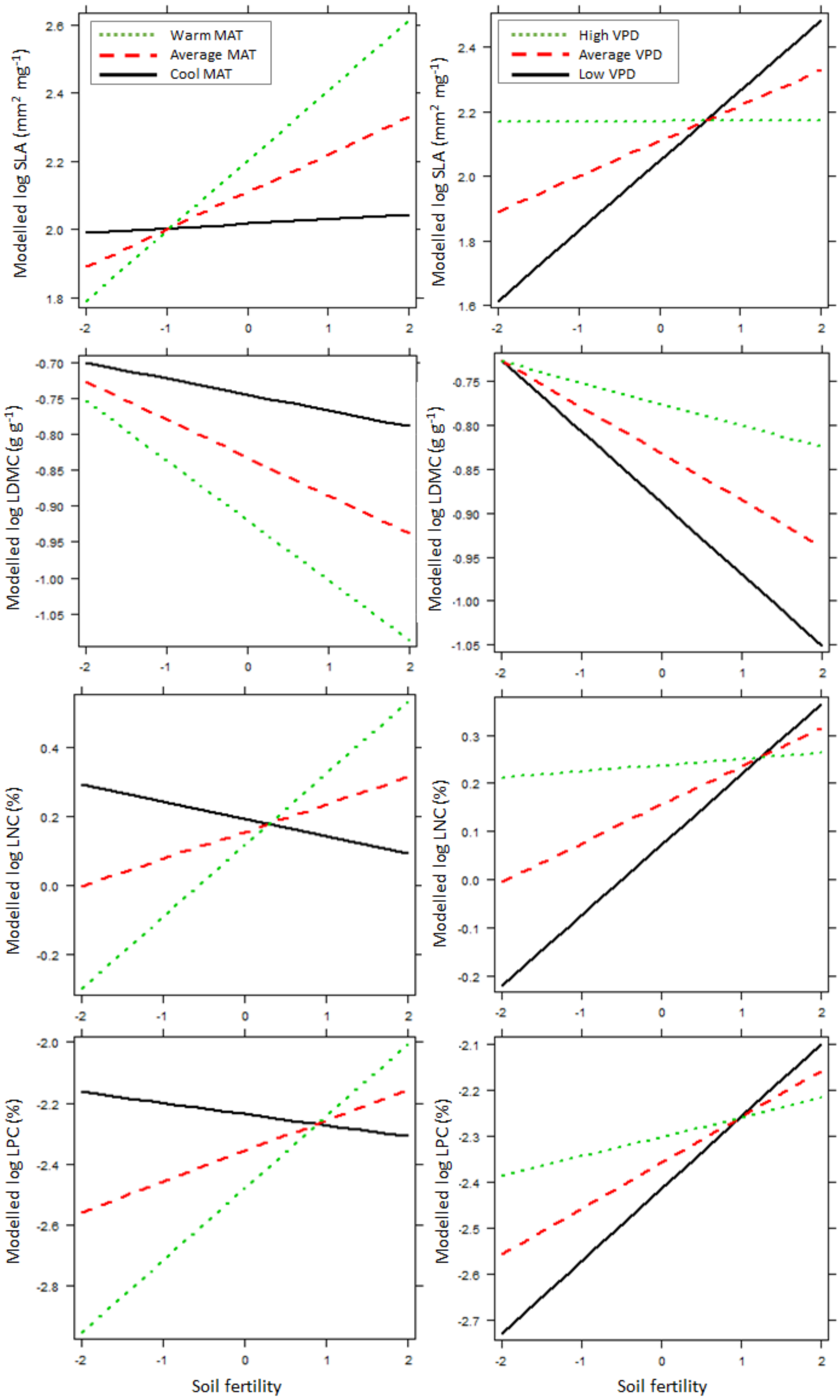


Figure 2.5: Line interaction plots of the CWM traits from principal component one ((specific leaf area (mm^2 mg^{-1}), leaf dry matter content (g g^{-1}), leaf nitrogen concentration (%) and leaf phosphorus concentration (%)) with mean annual temperature (°C), vapour pressure deficit (kPa) and soil fertility (using centred predictor variables scaled to unit variance). Soil fertility increases from left to right along the x-axis.

Principal component two: root diameter flowering duration, seed mass and leaf phenolic concentration

The multiple regression models explained significant variation in community-weighted mean root diameter ($R^2_{adj} = 0.48$), flowering duration ($R^2_{adj} = 0.28$), seed mass ($R^2_{adj} = 0.21$) and leaf phenolic concentration ($R^2_{adj} = 0.43$) (Table 2.6). Root diameter, flowering duration and seed mass were positively related to soil fertility and MAT (Table 2.6, Figure 2.6). Leaf phenolic concentration was negatively related to soil fertility and MAT (Figure 2.6). Root diameter was negatively related to VPD, but flowering duration and seed mass were not related to VPD (Table 2.6, Figure 2.6). Leaf phenolic concentrations were positively related to VPD. Root diameter was unrelated to total basal area, but flowering duration was negatively related to total basal area. Seed mass was positively associated with total basal area but not related to topography. Root diameter was positively associated with ridge environments and flowering duration was not associated with topography (Table 2.6). Leaf phenolic concentrations were not significantly related to either total basal area or topography (Table 2.6).

Significant interactions between soil fertility and climatic variables influenced root diameter, flowering duration and leaf phenolic concentration but neither interaction influenced seed mass (Table 2.6). Root diameter and leaf phenolic concentration were influenced by the interaction of soil fertility × MAT only, while flowering duration was influenced by both the interactions of soil fertility × MAT, and soil fertility × VPD (Table 2.6). Root diameter and flowering duration were low in low fertility soil across all climatic conditions (Figure 2.7). However, as soil fertility increased, root diameter increased rapidly in warm environments and flowering duration increased rapidly in warm and moist environments (Figure 2.7, Figure 2.8). In high fertility soils, moderate root diameter and short flowering duration in cool and dry climates, changed to high root diameter and long flowering duration in warm and moist climates (Figure 2.7).

Seed mass was low in low soil fertility across all climates (Figure 2.7). In high fertility soils, seed mass was also generally low, but increased rapidly to high seed mass in warm and moist environments (Figure 2.7).

When soil fertility was high, leaf phenolic concentration was generally low across all climates (Figure 2.7). However, as soil fertility decreased, leaf phenolic concentration increased rapidly in warm and moist environments (Figure 2.7, Figure 2.8). In low fertility soil, leaf phenolic concentration was low in cool conditions and changed to high values in warmt conditions (Figure 2.7).

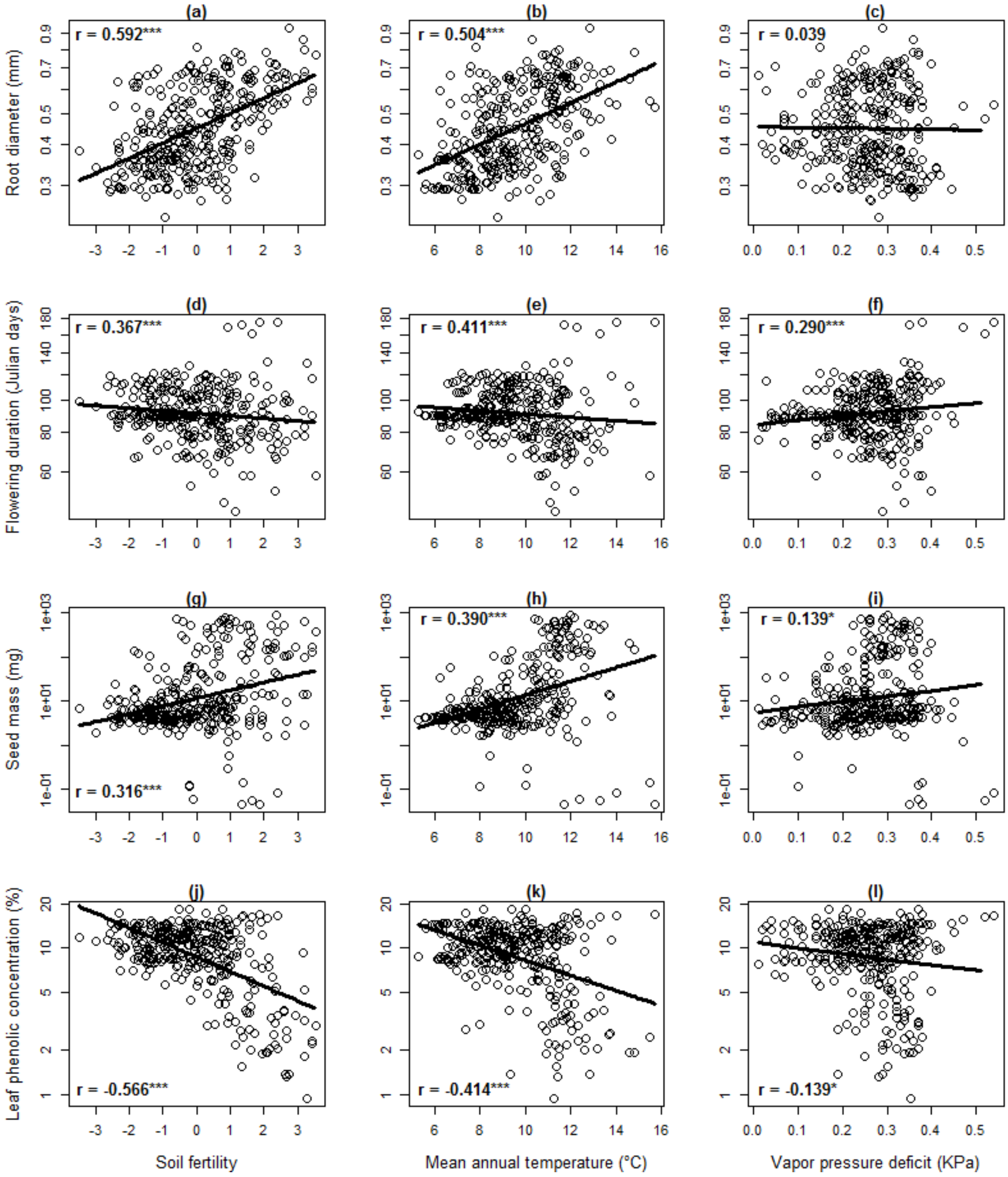


Figure 2.6: Scatterplots of CWM from principal component two against the environmental predictor variables. Soil fertility increases from left to right along the x-axis. Onto each plot are overlaid the modelled fit and correlation coefficients for the bivariate relationships.

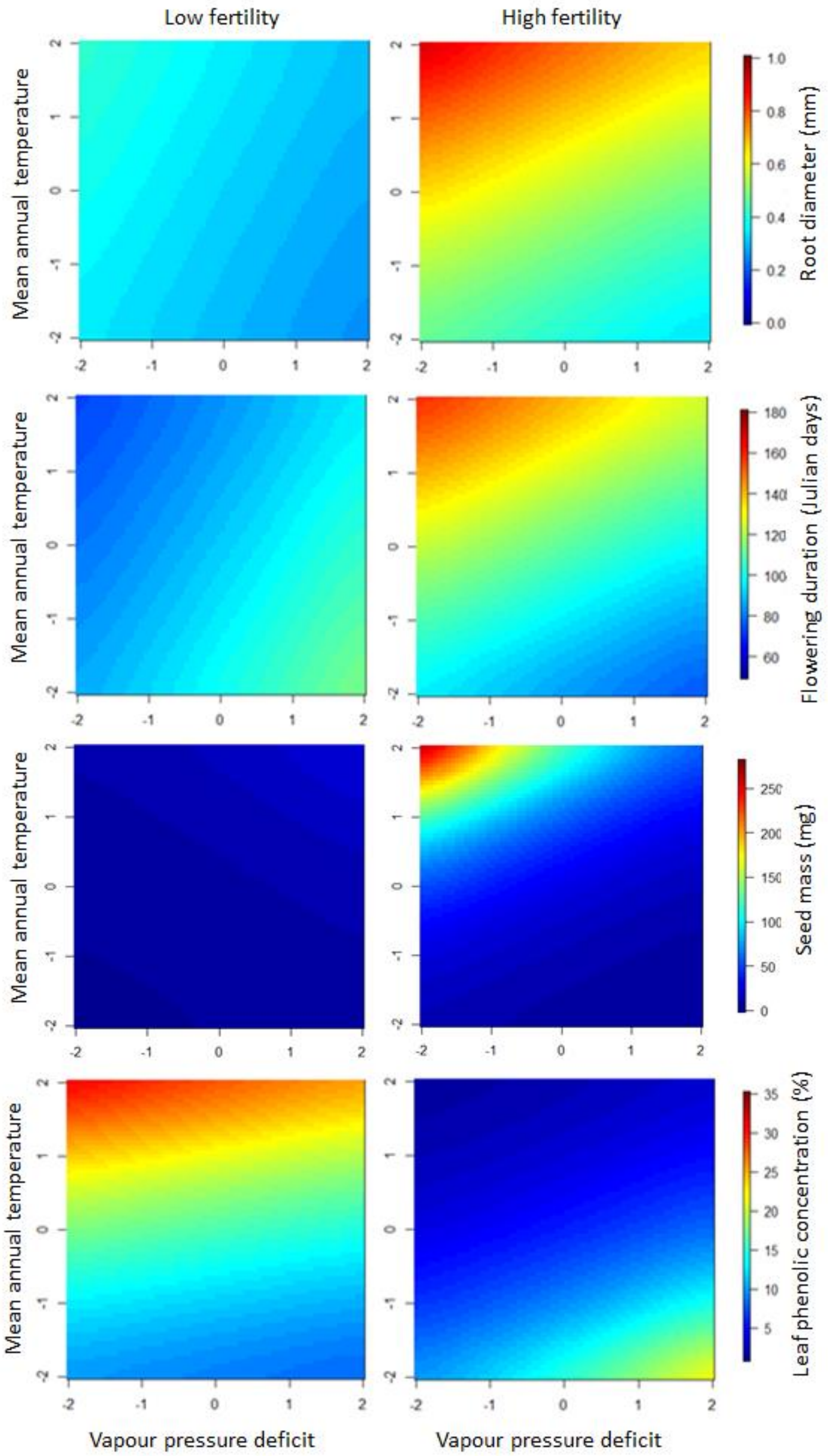


Figure 2.7: Interaction plots of the CWM traits from principal component two (root diameter (mm) and flowering duration (Julian days)) with mean annual temperature (°C) and vapour pressure deficit (kPa) at two levels of soil fertility (using centred predictor variables scaled to unit variance).

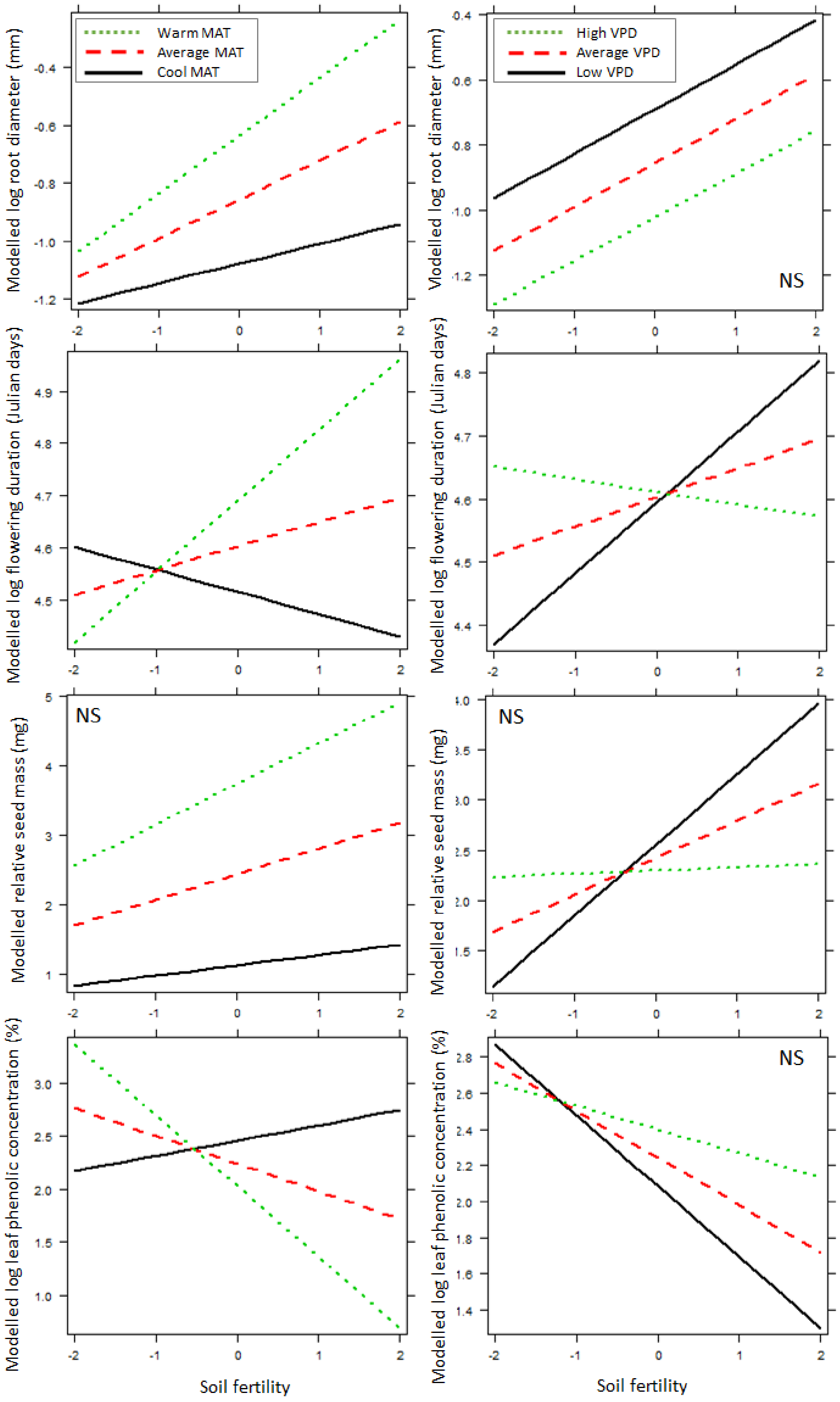


Figure 2.8: Line interaction plots of the CWM traits from principal component two (root diameter (mm) and flowering duration (Julian days)) with mean annual temperature (°C), vapour pressure deficit (kPa) and soil fertility (using centred predictor variables scaled to unit variance). Soil fertility increases from left to right along the x-axis.

Principal component three: relative bark thickness and wood dry matter content

The multiple regression models explained significant variation in community-weighted mean relative bark thickness ($R^2_{adj} = 0.40$) and wood dry matter content ($R^2_{adj} = 0.37$) (Table 2.6). Relative bark thickness and wood dry matter content were negatively related to soil fertility and MAT (Table 2.6, Figure 2.9). Relative bark thickness and wood dry matter content were weakly related to VPD (Table 2.6, Figure 2.9). None of the traits from principal component five were associated with total basal area or topography (Table 2.6).

Interactions between soil fertility and both climatic variables had a significant influence on relative bark thickness and wood dry matter content (Table 2.6). Relative bark thickness was moderate in low fertility soil across all climatic conditions, but increased slightly in warm and moist climates (Figure 2.10). However, relative bark thickness decreased rapidly with increasing soil fertility in warm and moist climates (Figure 2.10, Figure 2.11) and increased with increasing soil fertility in cool and dry climates (Figure 2.10). Wood dry matter content in low fertility soils, ranged from high in moist environments to moderate in dry environments. Wood dry matter content decreased rapidly with increasing soil fertility in warm and moist environments (Figure 2.10, Figure 2.11) and varied little with increasing soil fertility in cool and dry environments. In high soil fertility, low wood dry matter contents in warm and moist environments changed to high values in cool and dry environments (Figure 2.10).

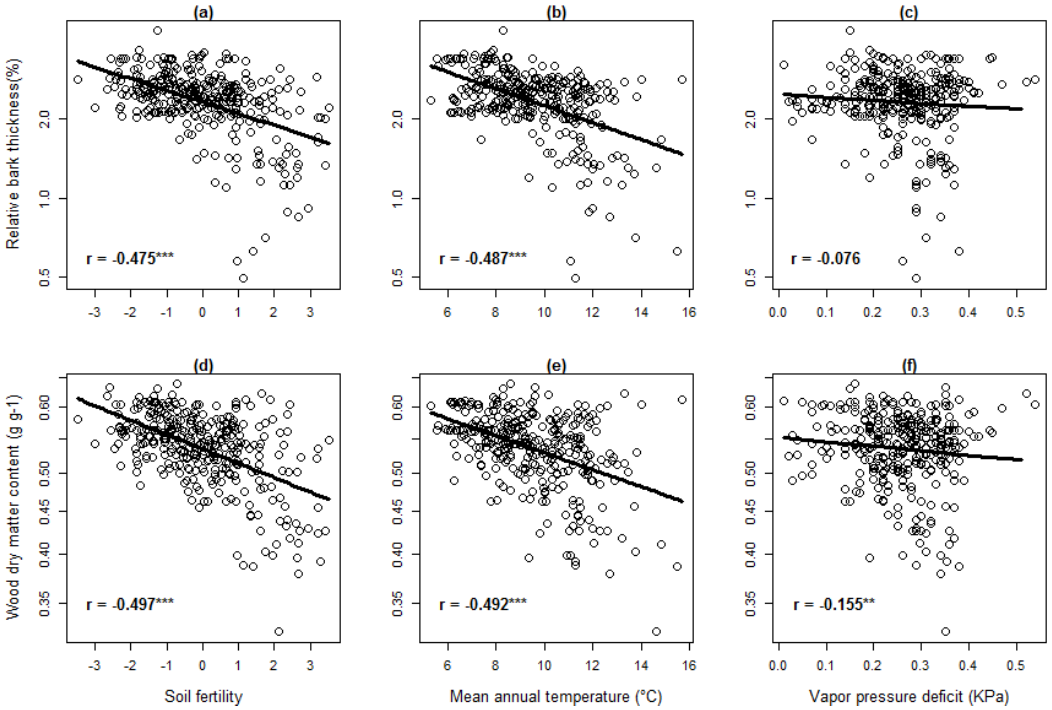


Figure 2.9: Scatterplots of CWM from principal component three against the environmental predictor variables. Soil fertility increases from left to right along the x-axis. Onto each plot are overlaid the modelled fit and correlation coefficients for the bivariate relationships.

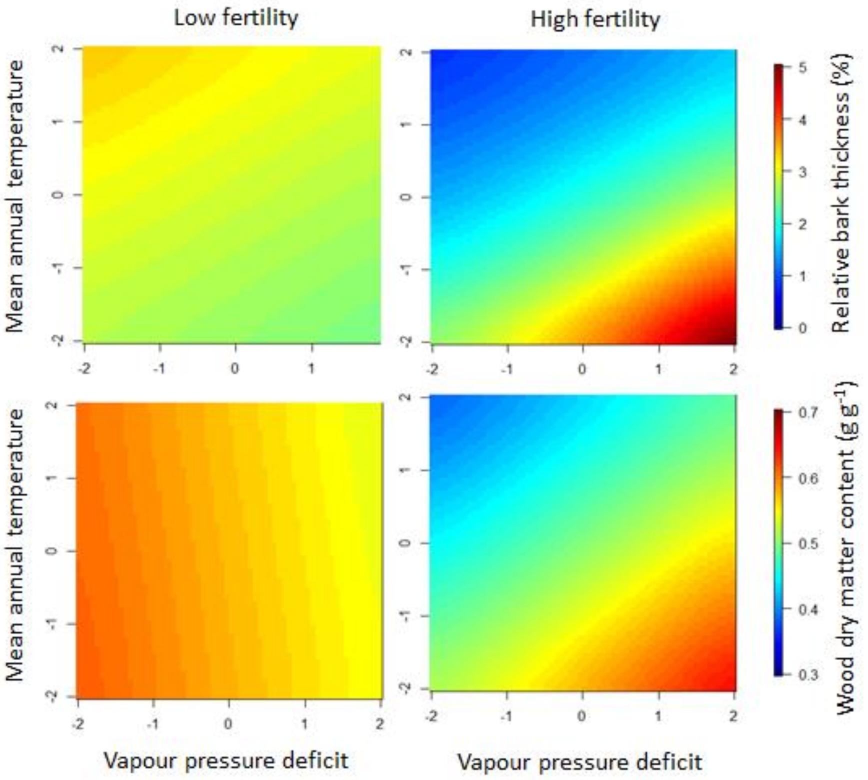


Figure 2.10: Interaction plots of the CWM traits from principal component three (relative bark thickness (%) and wood dry matter content (g g^{-1})) with mean annual temperature (°C) and vapour pressure deficit (kPa) at two levels of soil fertility (using centred predictor variables scaled to unit variance).

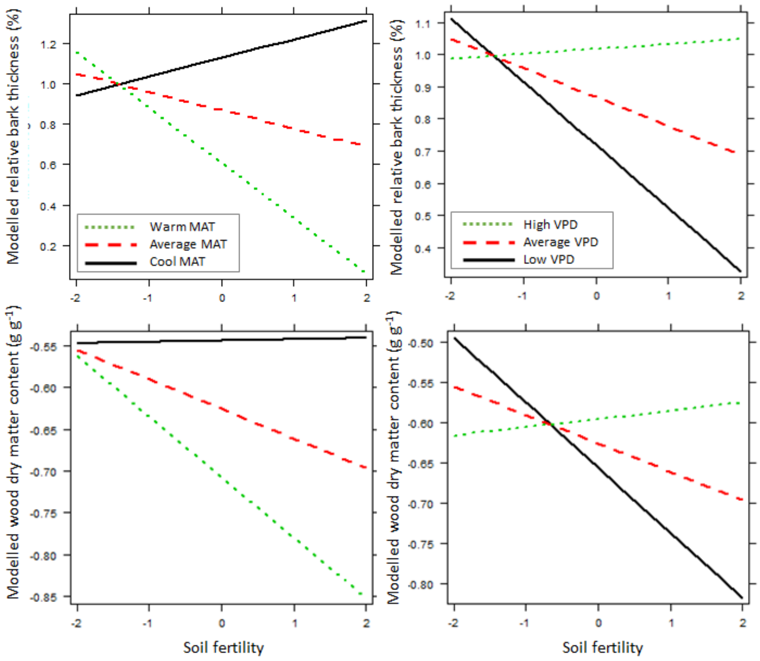


Figure 2.11: Line interaction plots of the CWM traits from principal component three (relative bark thickness (%) and wood dry matter content (g g^{-1})) with mean annual temperature, vapour pressure deficit and soil fertility (using centred predictor variables scaled to unit variance). Soil fertility increases from left to right along the x-axis.

Principal component four: maximum plant height

The multiple regression models explained significant variation in community-weighted mean maximum height ($R^2_{adj} = 0.30$) (Table 2.6). Maximum height was negatively related to soil fertility (Figure 2.12). Maximum height was positively related to MAT, but was not related to VPD (Table 2.6, Figure 2.12). Maximum height was positively associated with total basal area and gully environments (Table 2.6).

Maximum plant height was influenced by both the interaction effects of soil fertility × MAT, and soil fertility × VPD (Table 2.6). When soil fertility was high, maximum height was generally low across all climates (Figure 2.13). However, as soil fertility decreased, maximum height increased rapidly in warm and moist environments (Figure 2.13, Figure 2.14). In low soil fertility, short maximum plant heights in cool and dry environments changed to taller values in warm and moist environments (Figure 2.13).

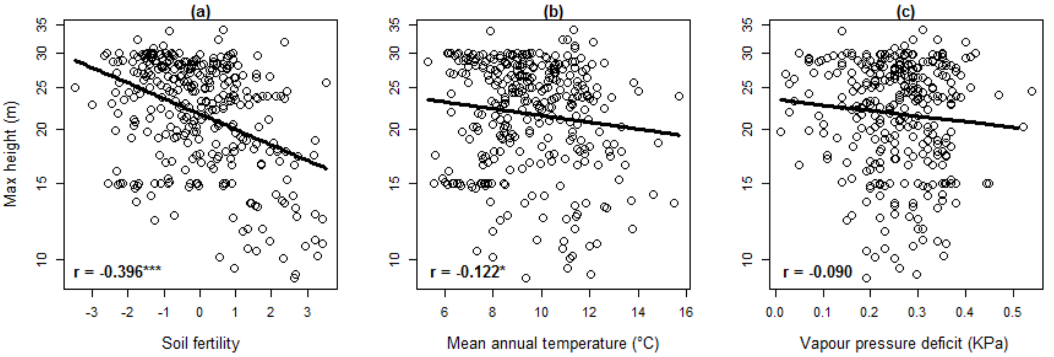


Figure 2.12: Scatterplots of CWM from principal component four against the environmental predictor variables. Soil fertility increases from left to right along the x-axis. Onto each plot are overlaid the modelled fit and correlation coefficients for the bivariate relationships.

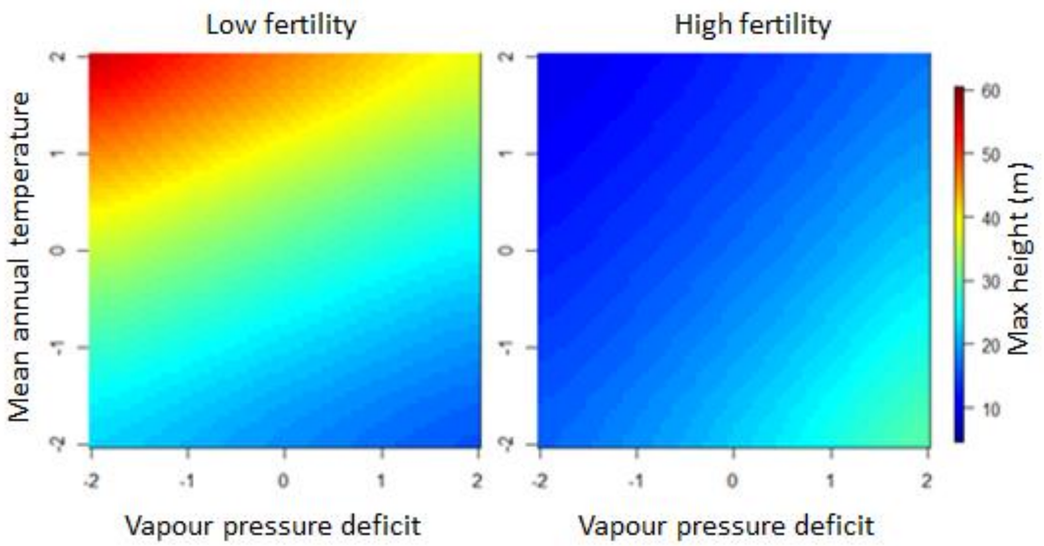


Figure 2.13: Interaction plots of the CWM traits from principal component four (maximum plant height (m)) with mean annual temperature (°C) and vapour pressure deficit (kPa) at two levels of soil fertility (using centred predictor variables scaled to unit variance).

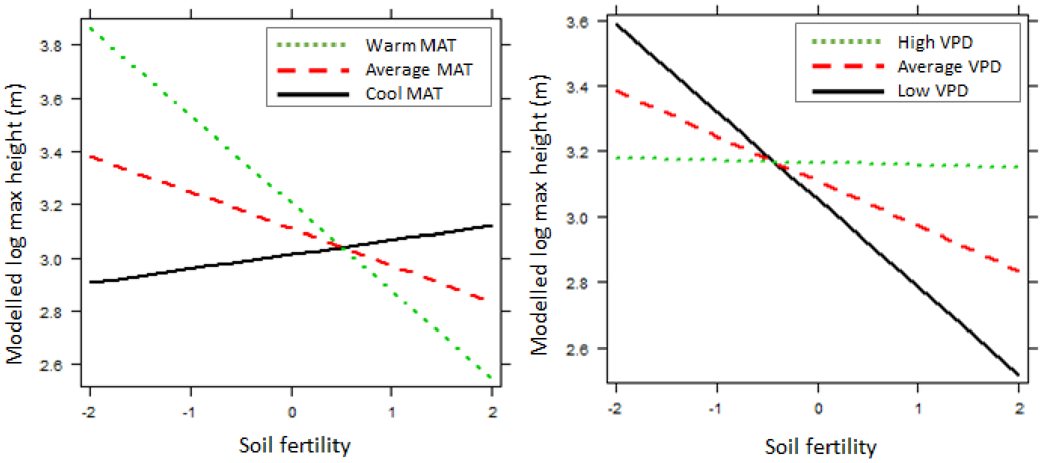


Figure 2.14: Line interaction plots of the CWM traits from principal component four (maximum plant height (m)) with mean annual temperature (°C), vapour pressure deficit (kPa) and soil fertility (using centred predictor variables scaled to unit variance). Soil fertility increases from left to right along the x-axis.

Principal component five: root dry matter content and flowering onset

The multiple regression models explained significant variation in community-weighted mean root dry matter content (R^2_{adj} = 0.40) and flowering onset (R^2_{adj} = 0.27) (Table 2.6). Root dry matter content was negatively related to the main effects of soil fertility and MAT, and positively related to VPD (Table 2.6, Figure 2.15). In contrast, flowering onset was positively related to soil fertility and MAT, and negatively related to VPD (Table 2.6, Figure 2.15). Root dry matter content was not associated with total basal area but was positively associated with gully environments (Table 2.6). There were no significant associations between flowering onset and total basal area or topography (Table 2.6).

Interactions between soil fertility and both climatic variables had a significant influence on flowering onset but neither interaction had a significant influence on root dry matter content (Table 2.6). In low fertility soils, root dry matter content varied from moderate in warm and moist conditions to high in cool and dry conditions (Figure 2.16). However, in high fertility soils, root dry matter content varied from low in warm conditions to moderate in cooler conditions (Figure 2.16). In low fertility soils, flowering onset was generally early in all climates (Figure 2.16). Flowering onset increased rapidly with increasing soil fertility in warm and moist conditions (Figure 2.16, Figure 2.17). In high soil fertility, flowering onset varied from early in cool and dry environments to a later date in warm and moist environments (Figure 2.16).

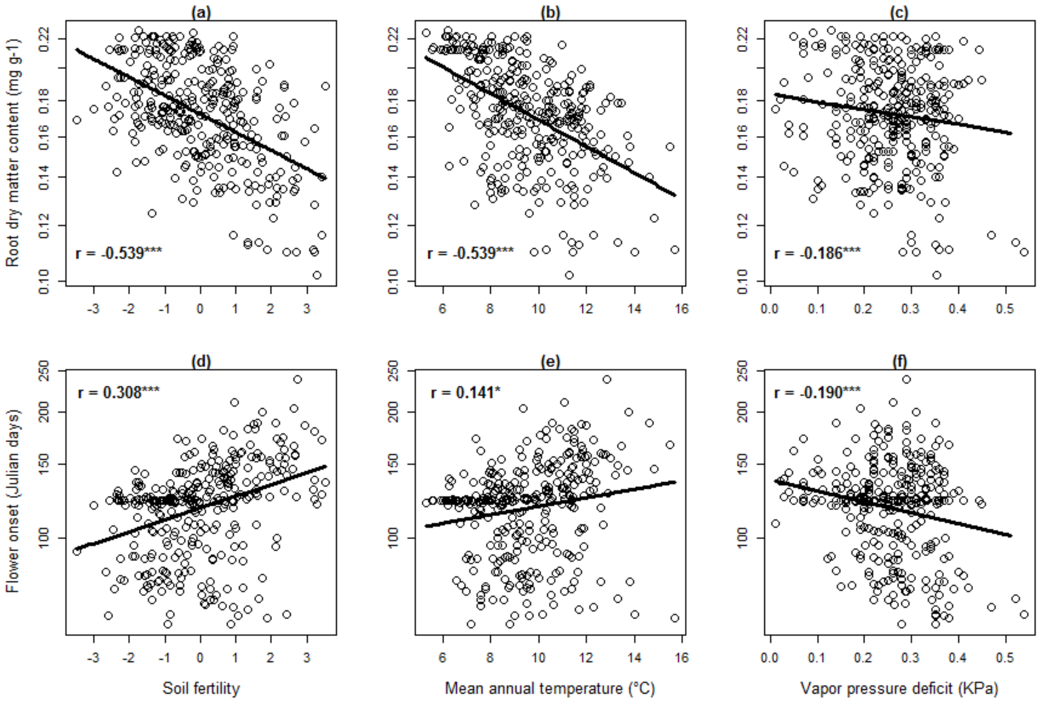


Figure 2.15: Scatterplots of CWM from principal component five against the environmental predictor variables. Soil fertility increases from left to right along the x-axis. Onto each plot are overlaid the modelled fit and correlation coefficients for the bivariate relationships.

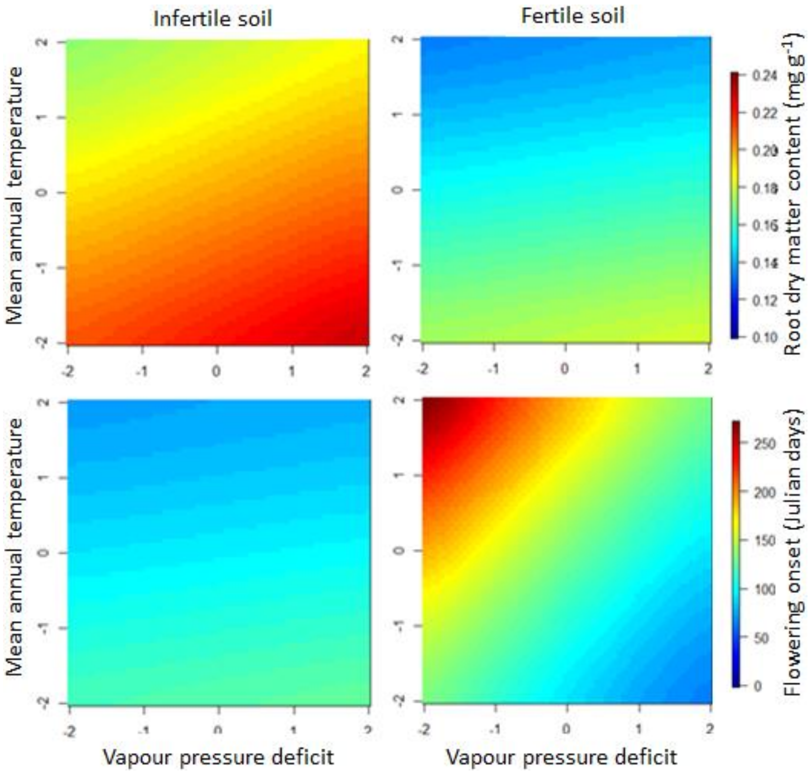


Figure 2.16: Interaction plots of the CWM traits from principal component four (root dry matter content (mg g^{-1}) and flowering onset (Julian days)) with mean annual temperature (°C) and vapour pressure deficit (kPa) at two levels of soil fertility (using centred predictor variables scaled to unit variance.

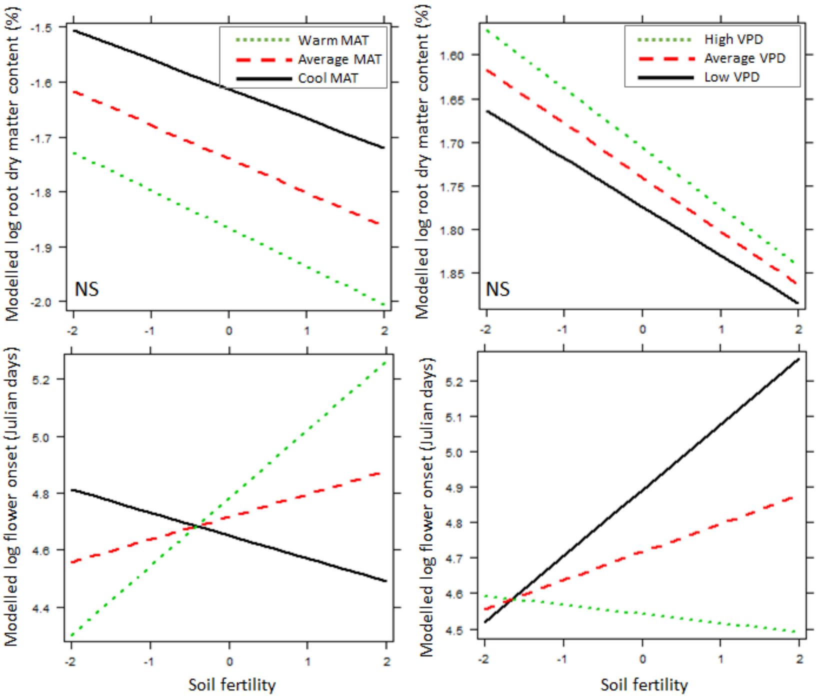


Figure 2.17: Line interaction plots of the CWM traits from principal component four (root dry matter content (mg g^{-1}) and flowering onset (Julian days)) with mean annual temperature (°C), vapour pressure deficit (kPa) and soil fertility (using centred predictor variables scaled to unit variance). Soil fertility increases from left to right along the x-axis.

2.3.3 Summary of results

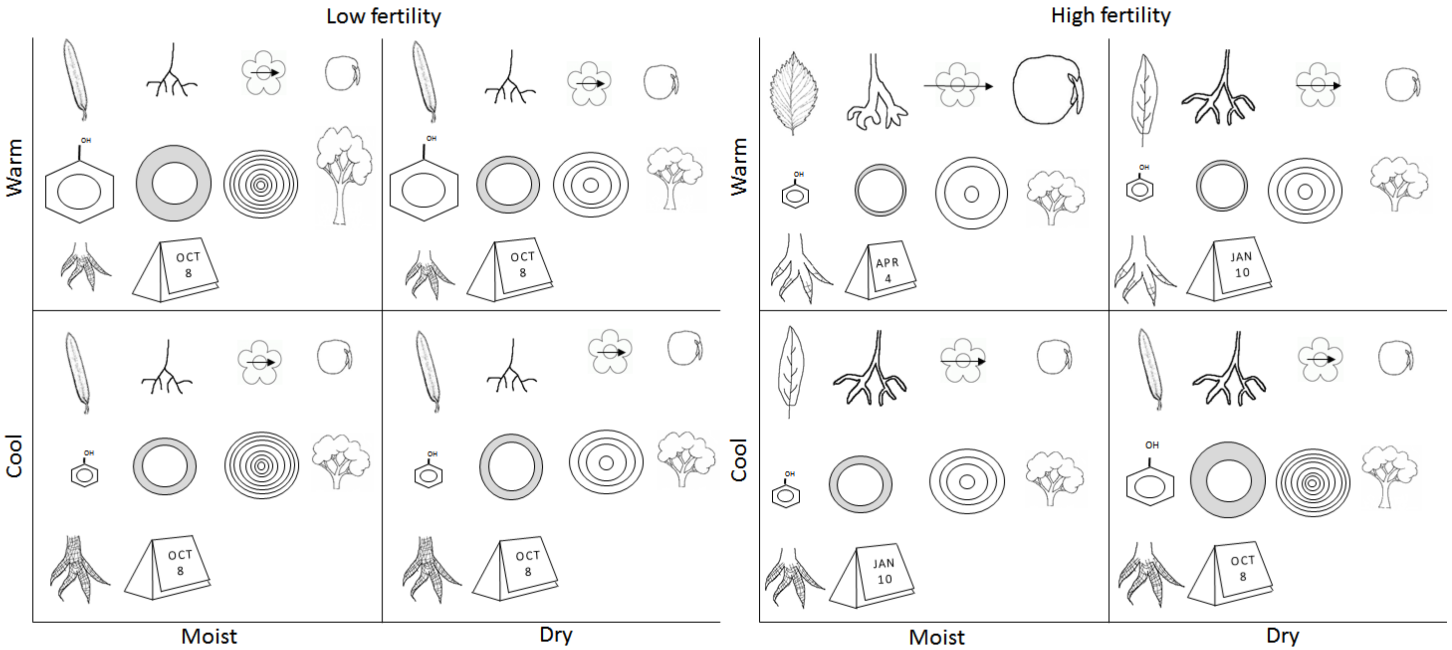
The variation in CWM traits across multiple plant organs is summarised in Figure 2.18. In environments with low fertility soil, across all climatic conditions, ‘slow’ leaf traits were dominant. In environments with high fertility soil, ‘slow’ leaf traits were favoured when conditions were cool and dry. However, in high fertility sites with higher temperature and moisture, leaf traits were ‘faster’.

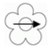
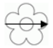
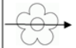
In sites with low fertility, across all climate conditions, low root diameter, short flowering duration and small seeds were favoured. In low fertility sites, leaf phenolic concentrations varied from low in cool conditions to high in warm conditions. In high fertility sites, leaf phenolic concentrations were moderate in cool and dry conditions, but low in all other climates. In sites with high fertility soil, root diameter was high in warm and moist sites, but moderate in all other conditions. In high fertility soils, flowering duration varied from long in warm and moist environments to short in cool and dry environments. In high fertility soils, seed mass was high in warm and moist conditions, but low in all other conditions.

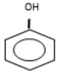
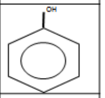
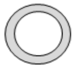
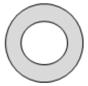
In sites with low fertility soil, across all climatic conditions, relative bark thickness and wood dry matter content were moderate to high. In high fertility sites, relative bark thickness and wood dry matter content varied from low in warm and moist conditions to high in cool and dry conditions.

In sites with low fertility, maximum height varied from tall in warm and moist conditions to short in cool and dry conditions. In sites with high fertility soil, maximum height was low across all climates, except cool and dry conditions where it was moderate.

In low fertility soils, root dry matter content varied from moderate in warm conditions to high in cool conditions. In high fertility soils, root dry matter content varied from low in warm conditions to moderate in cool conditions. In low fertility soils, flowering onset was early across all climatic conditions. Yet in high fertility soils, flowering onset varied from late in warm and moist conditions to early in cool and dry conditions.



Leaf economics traits	Slow		Moderate		Fast	
Root diameter	Low		Moderate		High	
Flowering duration	Short		Moderate		Long	

Seed mass	Low		High			
Leaf phenolics	Low		Moderate		High	
Relative bark thickness	Low		Moderate		High	

WDMC	Low		Moderate		High	
Maximum height	Short		Moderate		Tall	
RDMC	Low		Moderate		High	
Flowering onset	Early		Moderate		Late	

Figure 2.18: Summary of variation in CWM traits across soil fertility and climate gradients in New Zealand forests. Refer to symbol legend below plot.

2.4 Discussion

The results of this thesis indicated that (i) there were five dominant independent dimensions of variation among traits of New Zealand trees, and (ii) soil fertility was a more important predictor of CWM traits than climate variables, however, significant interaction effects between soil fertility and climate variables overrode the importance of the individual main effects.

Soil fertility has not been included in previous quantitative studies of community assembly in New Zealand forests at a national scale. Despite early recognition that forest community composition in New Zealand is affected by both climate and soil fertility (Wardle 1991), national-scale quantitative studies have focused predominantly on the climatic drivers of community distributions. Only in a few cases have such community ecology studies included soil variables such as soil water deficit, soil parent material, soil texture and rooting depth (Leathwick 1995; Leathwick *et al.* 1996; Leathwick & Whitehead 2001). Recent studies across terrestrial ecosystems worldwide have also found soil fertility to be a more important driver of trait-environment relationships than climate (Ordonez, *et al.* 2009; Maire, *et al.* 2015). The results from this thesis support the idea that soil fertility has a greater role in community assembly than previously acknowledged.

This thesis found significant effects of the interaction effects between soil fertility and climatic variables, on CWM traits in forest communities in New Zealand. Hence, the adaptive value of traits in particular climatic conditions depends upon the fertility of the soil. The importance of interaction effects between soil fertility and climate has not previously been assessed in plant communities, despite suggestions that there may be joint effects between these variables on traits (Dwyer, *et al.* 2015; Maire, *et al.* 2015).

The five intrinsic dimensions of trait variation recognised in this study represent variation across all plant organs. This aligns with previous recommendations that in order to ensure that functional variation between species is portrayed accurately it is important to consider four to eight trait dimensions, and traits from many plant organs (Laughlin 2014a). Identification of the intrinsic dimensionality of the dataset was valuable because it reduced the complexity of the interpretation. This was possible because the correlated traits within each dimension varied in similar patterns along the environmental gradients. The relationships between each of the thirteen traits within the five trait dimensions, and climate and soil fertility in New Zealand forests will be discussed in turn.

Principal component one: leaf economics traits

In environments with high fertility soils, CWM leaf economics traits varied from ‘slow’ leaves (with low SLA, low LNC and LPC, and high LDMC) in cool and dry environments to ‘fast’ leaves (with high SLA, high LNC, high LPC and low LDMC) in warm and moist environments, as previously described on a global scale (Wright, *et al.* 2005a). However, in environments with low fertility soils across all climatic conditions, ‘slow’ leaf economic traits (with low SLA, LNC, low LPC and high LDMC) tended to be favoured. This is an example of the importance of including interaction effects between climate and soil fertility. This thesis research supports the idea that variation in the adaptive values of CWM leaf economics traits across environmental gradients is more accurately portrayed when soil fertility is accounted for simultaneously with climate (Reich 2014).

Species that survive successfully in resource-limited sites tend to have ‘slow’ leaves. These traits enable the species to survive via a conservative strategy of utilising nutrient resources that are in low abundance (Grubb 1998; Richardson, *et al.* 2004). Traits of ‘slow’ leaves are advantageous in nutrient-poor environments because the leaves are more resistant to physical damage, and have lower nutrient foraging costs than ‘fast’ leaves (Wright, *et al.* 2004). ‘Slow’ leaves have low photosynthetic rates compared to ‘fast’ leaves, however ‘slow’ leaves have long leaf lifespans which mean that the high energetic and carbon investment in producing leaf tissue with greater structural integrity is offset by the benefits of continued photosynthesis over long leaf lifespans (Reich 2014). Proficient resorption of nutrients before leaf fall also reduces the construction costs of ‘slow’ leaves (Richardson, *et al.* 2008). Over-investing in ‘fast’ leaves when nutrients are scarce is not a viable strategy (Reich 2014). ‘Slow’ leaves are favoured in low fertility sites with a range of climates because any improvement in climate favourability is unable to offset the detrimental effects of resource limitation to leaf production (Richardson, *et al.* 2008).

In high fertility soils, where the stress of attaining sufficient nutrients is relaxed, climate is the sole driver of variation in CWM leaf economics traits. In sites with high fertility soil and cool, dry conditions, 'slow' leaf traits were favoured because they enhance survival when moisture and temperature are so low that investing in 'fast' leaf traits would be uneconomical. In these conditions, considerable savings are made by having long-lived leaves which are capable of photosynthesis despite harsh conditions, and have lower respiratory carbon and water loss than 'fast' leaves (Cunningham, *et al.* 1999; Farquhar, *et al.* 2002; Godoy, *et al.* 2011; Sanchez-Gomez, *et al.* 2013).

Only in sites with high fertility, warm and moist conditions were 'fast' leaves an economical and adaptive strategy. In these conditions, 'fast' leaves were advantageous because the potential for rapid photosynthesis was not limited by any factors (Grime 1977; Grime 1979). The productive strategy in which, high quantities of resources and water are used to rapidly acquire carbon, is successful in these productive conditions (Wright, *et al.* 2004). 'Fast' leaves have short leaf lifespans and high nutrient concentrations compared to slow leaves, but the rate of return on investment in 'fast' leaves is high enough in fertile, warm, and moist conditions to offset the costs (Reich 2014).

Principal component two: root diameter, flowering duration, seed mass and leaf phenolic concentration

In low fertility soils, across all climatic conditions, thin CWM root diameter was favoured. However, in high fertility soils, root diameter varied from moderate in cool and dry environments to thick in warm and moist environments. Thin roots are favoured in sites with low soil fertility because they enable a greater spread of roots within the soil to search for nutrients than would be possible with the same allocation of resources to thick roots (Hill, *et al.* 2006; Holdaway, *et al.* 2011). Thin roots also have lower requirements of external nutrients for maximum growth which is favourable under low nutrient availability (Hill, *et al.* 2006). In high fertility soils, thick, long-lived roots are selected for in warm and moist environments, where there are no restrictions on the potential for root growth (Powell 1974). In these conditions thick roots offer the best long-term opportunity for obtaining resources (McCormack, *et al.* 2012) by increasing the surface area for resource uptake and symbiotic interactions with mycorrhizae to occur (Newsham, *et al.* 1995; Wang & Qiu 2006). In high fertility, cool and dry environments, species with moderate root diameters are favoured. This is because thinner roots have lower risks of drought- or freezing- induced xylem cavitation, and lower costs of water uptake from soils, than thicker roots (Fitter 1987; Leuschner, *et al.* 2004; Alameda & Villar 2012; Olmo, *et al.* 2014). Thinner roots have lower metabolic costs which is also favoured for conservation of resources in cool conditions (Eissenstat 1992). The importance of including interaction effects is exemplified in this trait because root diameter varied with climate in high fertility soils, but not in low fertility soils.

In low fertility soils, across all climates, short flowering duration was favoured. However, in high fertility soils, flowering duration varied from short in cool and dry environments to long in warm and moist environments. In environments with low soil fertility, nutrient stress limits the availability of resources for allocation to reproduction. Hence a shorter flowering duration and strategy of using all available flowering resources at once is selected for. This allows plants to invest heavily in a short period of flowering in anticipation that successful pollination will occur during this time (Wolkovich & Ettinger 2014). If this period is synchronised with optimal conditions then chances of pollination are high, but if it is not then pollination success may be low (Aronson, *et al.* 1992). In environments with high soil fertility, and cool and dry conditions, short flowering durations are favoured. This is because water-stress tends to limit the duration of plant lifecycles and therefore also limit the duration of flowering (Aronson, *et al.* 1992). In environments with high fertility soils and warm, moist conditions, longer flowering duration is favoured. This trend follows previously recorded patterns of increasing flowering duration with increasing temperature (Bock, *et al.* 2014). In these conditions there are no limitations to how much the plants can afford to invest in flowering over an extended period of time. Hence long flowering duration has adaptive value because it may increase the chance of successful pollination by having flowers available over a longer period (Wolkovich & Cleland 2014).

Low seed mass was favoured in sites with low soil fertility across all climates. In high fertility soil, low seed mass was also favoured in all climates, except in warm and moist conditions where high seed mass was favoured. This trend of seed mass with environmental conditions supports the findings at a regional scale in Northland, New Zealand (Jager, *et al.* 2015). Larger seeds may be favoured in high fertility sites with warm and moist conditions because competition for light is highest in these conditions and therefore the greater ability of large seeds than small seeds, to tolerate shade may favoured (Coomes, *et al.* 2009). Large seeds provide support for slow-growing plants which have a greater tolerance of low light, and greater survival through early establishment, than plants with small seeds (Reich, *et al.* 1998; Moles, *et al.* 2007). The correlation of large seed mass with high temperatures in fertile sites may be driven by the increasing metabolic costs for respiration with in higher temperatures, as shown in Australia (Lord, *et al.* 1997; Murray, *et al.* 2004). The correlation of large seeds with moist, high fertility sites adds support to the argument that large seed mass is not associated with increased seedling establishment during drought (Wright & Westoby 1999; Leishman, *et al.* 2000).

In New Zealand forests, the production of a large number of small seeds in most environments appears to outweigh the benefits of producing a few large seeds (Aarssen & Jordan 2001; Henery & Westoby 2001). Only in environments with high soil fertility, warm and moist conditions, does the production of a small number of large seeds outweigh the benefits of producing many small seeds. It may take 8 weeks to 4 years for the higher survival of large seeds to counterbalance their higher costs of production compared to smaller seeds (Moles, *et al.* 2007). Hence, although large seeds provide an advantage in early life stages, small-seeded species may have survival advantages which accrue during other stages in the life-cycle (Moles, *et al.* 2007). In most combinations of soil fertility and climate in New Zealand, small seeds were favoured because the benefits of producing large seeds did not exceed the costs of producing them.

When soil fertility was high, low leaf phenolic concentration was favoured across all climates except cool and dry conditions. However, in low fertility soils, leaf phenolic concentration varied from low in cool environments to high in warm environments. Low leaf phenolic concentrations are advantageous in fertile sites with warm climates, as well as cool and moist climates, because the conditions are suitable for fast growth. There are no resource limitations, so producing leaves with low phenolic concentrations is an energetically and resource ‘cheap’ scheme that supports high productivity (Wright, *et al.* 2010). Moderate leaf phenolic concentrations in sites with high fertility soils, and cool and dry conditions may increase leaf defence against physical disturbances (Moles, *et al.* 2011b). The occurrence of higher leaf phenolic concentrations in low fertility, warm environments suggests that more conservative traits are favoured in these conditions. High phenolic concentration reduces rates of decomposition and N mineralisation and thereby regulates nutrient cycling (Kraus, *et al.* 2003). In nutrient limited sites, higher phenolic concentration is also advantageous because it enables leaves to have greater resistance to physical and biotic damage in such environments, where the cost of replacing damaged tissue is far greater than in more fertile sites (Moles, *et al.* 2011b).

The role of phenolics in defending leaves against herbivores is also worth considering, in light of these results. In low fertility sites, the increase of leaf phenolic concentration with increasing temperature suggests there may be an increasing importance of herbivore defence due to from an increased abundance of herbivores in warm climates (Schemske, *et al.* 2009). Some studies suggest that plants deploy a range of uncoordinated combinations of defence (Koricheva *et al.* 2004; Moles, *et al.* 2013). However, in the current results, the trend from high phenolic concentrations in sites with low fertility soil, warm conditions to low concentrations in high fertility sites, support studies that suggest that chemical defence tends to be more common in lower fertility sites while physical defences, such as spines, are more common in higher fertility soils (Owen-Smith & Cooper 1987). Physical defences such as spines, divarication and fibrous leaves of high tensile strength do seem to occur mainly in sites with higher fertility soils in New Zealand (Atkinson & Greenwood 1989). The demand for features which decrease palatability to herbivores may seem out of place in a country that lacks native browsing mammals, however, the occurrence of such defences may suggest coevolution of these traits with the herbivorous moa (Atkinson & Greenwood 1989) or phytophagous insects (Greenwood & Atkinson 1977). The role of moa is favoured because the evolution of visual mimicry (eg. *Alseuosmia pusilla* mimicing *Pseudowintera colorata*) would not be an effective defence against insects which select their food plants based on chemical cues (Barlow & Wiens 1977). Another option is that variation in traits implicated in defence may be largely explained by phylogeny, as was discovered in the alpine shrubs of New Zealand (Tanentzap, *et al.* 2011). For example, New Zealand conifers have high concentrations of phytoecdysteroids that would induce avoidance by invertebrates (Singh *et al.* 1978).

Further study is needed to confirm the role of defence chemicals such as phenolics in New Zealand trees.

Principal component three: relative bark thickness and wood dry matter content

Moderate to high relative bark thickness and wood dry matter content were favoured in sites with low fertility soil, across all climatic conditions. However, in high fertility soil, relative bark thickness and wood dry matter content varied from low in warm and moist climates to high in cool and dry climates. Moderately thick bark is advantageous in environments with low fertility because it has lower construction costs than thick bark (Lawes 2013), but still provides some benefits of defence against physical disturbances that may damage sensitive bark tissues (Herms & Mattson 1992; Niklas 1999; Paine 2010). Jager, *et al.* (2015) found that bark thickness of some New Zealand trees declined with increasing soil fertility. This thesis research shows that this pattern is more complicated when climatic conditions are accounted for simultaneously with soil fertility. Thin bark in fertile, warm conditions is likely to be selected for because it has lower construction and maintenance costs (Lawes 2013). Despite the lack of frequent fires in the evolutionary history of New Zealand trees (Lawes, *et al.* 2014; Perry *et al.* 2014), thick bark has evolved in some trees which tend to be selected for in sites with high soil fertility and cool, dry conditions. Thick bark in these conditions may provide defence against other forms of disturbance, such as abrasion (Jager, *et al.* 2015). As a result of the interaction effects, the expected trend of increasing bark thickness with increasing temperature (Vines 1968; Laughlin, *et al.* 2011; Lawes 2013; Rosell 2014) is followed in sites with low, but not high fertility soil in New Zealand forests.

Wood dry matter content was correlated with relative bark thickness and therefore showed the similar relationships with environmental gradients. In sites with low fertility, high or moderate wood dry matter content had a selective advantage because it infers greater resistance to disturbances (Putz, *et al.* 1983; Lawton 1984; Rowe & Speck 2005; Curran 2008), and freezing- or drought-induced cavitation (Sperry & Sullivan 1992; Sperry, *et al.* 1994; Swenson & Enquist 2007; Poorter, *et al.* 2010). Jager, *et al.* (2015) showed that wood dry matter content decreased with increasing soil fertility in trees in Northland, New Zealand. This trend is only apparent in moist environmental conditions at the national scale. This is another example of the importance of interaction effects between climate and soil fertility. In sites with high soil fertility and warm, moist conditions, low wood dry matter content is favourable because it has lower construction costs, and can supply nutrients and water efficiently to a larger total leaf area than high wood dry matter content (ter Steege 2001; Chave, *et al.* 2009). The favouring of high wood dry matter content in high fertility sites with cool and dry conditions is a novel result attained from assessing the effects of soil fertility and climate simultaneously. In these conditions, high wood dry matter content has the selective advantage of increasing resistance against drought-induced hydraulic cavitation (Hacke & Sperry 2001; Secchi & Zwieniecki 2011). The greater construction costs and slower growth rates associated with high wood dry matter content are offset by the increased safety inferred in these environments. The trend of increasing wood dry matter content with increasing temperature observed in other countries (Wiemann 2002; Chave 2006; Laughlin, *et al.* 2011) was not observed in this study. Instead, after soil fertility, moisture availability had a stronger influence than temperature on the adaptive values of wood dry matter content in community assembly of New Zealand forests.

Principal component four: maximum plant height

When soil fertility was high, moderate maximum height was favoured in cool and dry conditions while short height was favoured in other climates. However, in low fertility soils, maximum height varied from short in cool and dry environments to tall in warm and moist environments. This observed trend of maximum height contrasts the generally expected trend. Plant height is usually greatest in fertile, warm and moist sites where limitations to growth are minimal, and decreases with decreasing fertility (King 1990; Richardson, *et al.* 2004; Peltzer, *et al.* 2010). However, in this study, plant height was generally lower in high fertility sites than in low fertility sites. This follows the findings of Jager, *et al.* (2015). The negative relationship of plant height with soil fertility may result from differences in community dynamics. High fertility sites are favoured by species with a wide range of growth rates, making competition for light stronger than in low fertility sites (Coomes, *et al.* 2009). This enables a greater range of shade-tolerant niches and therefore a greater range of maximum heights to be possible in high fertility soils (Coomes, *et al.* 2009). Gap-disturbances also occur frequently in high fertility sites making it favourable for species to allocate more resources to fast establishment and growth strategies rather than to attaining tall height (Ogden *et al.* 1991). In contrast, in sites with low fertility, less frequent, but larger-scale disturbances, such as landslides, are common and slow-growing species that are able to tolerate such disturbances are favoured (Wells *et al.* 2001). The shortest maximum heights on low fertility sites occur where temperature and moisture availability are low. The risks of freezing- and drought-induced xylem cavitation are highest in these conditions so shorter trees are likely to be favoured for their greater resistance to hydraulic cavitation (Ryan & Yoder 1997; Koch, *et al.* 2004). In warm and moist sites with low fertility, the risks of drought and frost are reduced and therefore taller maximum height to enable greater competition for light is the adaptive trait value.

Principal component five: root dry matter content and flowering onset

In low fertility soils, the adaptive value of root dry matter content varied from moderate in warm climates to high in cool climates. However, in high fertility soils, root dry matter content tended to be scaled down and varied from low in warm climates to moderate in cool climates. These trends of root dry matter content closely follow those described by the ‘fast-slow’ plant economics spectrum (Reich 2014). In sites with high fertility soil, particularly in warm climates, low root dry matter content, reflecting the ‘fast’ strategy, is favoured. These environmental conditions are favourable for growth, so species can economically produce low density tissues that have low construction costs and a rapid return on investment over the short root lifespan (Freschet, *et al.* 2013a). In contrast, higher root dry matter content is favoured in high fertility sites, particularly in low temperatures. These harsh conditions make attaining sufficient nutrients challenging so a ‘slower’ growth strategy is favoured. A high amount of energy and resources are required to produce tissue in these conditions so thick, dense tissue is produced that is longer-lasting and more resistant to threats such as frost (Reich 2014). The high investment in roots with high root dry matter content is offset by the long-lifespan and the less frequent need for repair or replacement of such roots, compared to roots with lower dry matter content. The down-scaling of the adaptive values of root dry matter content from low to high fertility reflects the increasing demand for conservative traits in low fertility soils. This trend would not have been recognised if the effects of soil fertility and climate on CWM traits were not assessed simultaneously.

In low fertility soils, across all climates, early flowering onset was favoured. Early flowering in sites with low fertility soil, may have adaptive value in ensuring that reproduction can occur before competition for pollinators with other species becomes intense (Wolkovich & Cleland 2014; Wolkovich & Ettinger 2014). This may be particularly important in New Zealand where a large percentage of flowers are inconspicuous, pale coloured, small-sized, and characteristic of generalised pollinator relationships (Webb & Kelly 1993). The paucity of specialised pollinators relative to other countries suggests the need for differentiation in reproductive methods by other means (Lloyd 1985; Craig *et al.* 2000). In low fertility sites, early flowering may provide a means of differentiating flowering from other species, while ensuring a good chance for reproduction before competition with other species increases.

In high fertility soils, flowering onset varied from early in cool and dry conditions to late in warm and moist conditions. Early flowering onset in cool and dry conditions may be a response to drought stress (Aronson, *et al.* 1992). Conversely, late flowering onset in warm and moist conditions may be a response to the presence of favourable conditions (Aronson, *et al.* 1992). This trend with temperature is opposite to that found in previous studies (Sparks, *et al.* 2000; Menzel, *et al.* 2006; Cook, *et al.* 2012; Bock, *et al.* 2014). Later flowering onset in sites with high soil fertility and warm, moist conditions may have adaptive value if vernalisation is an important process controlling flowering in New Zealand trees. In sites with warm and moist climates, later winter temperatures may cause the vernalisation trigger of flowering to occur at a later Julian date. It is not yet known how many trees require vernalisation in New Zealand.

2.4.1 Summary of relationships between CWM traits and environmental factors

Interaction effects between climate and soil fertility were important drivers of the trends in the adaptive values of most of the CWM traits studied. Therefore, although New Zealand forests may follow previously observed trends in CWM traits with variation in either climate or soil fertility, when these factors vary simultaneously the relationships between CWM traits and the environment may be significantly different. For example, relative bark thickness was shown to decrease with increasing soil fertility at a regional scale in New Zealand (Jager, *et al.* 2015). In this nationwide study, bark thickness did decrease with increasing soil fertility, but only in warm climates. Likewise, in sites with high fertility soil, leaf economics traits varied from 'fast' in warm, moist conditions to 'slow' in cool, dry conditions as expected (Wright, *et al.* 2005a), but in sites with low fertility soil, the selective advantage for conservative growth was so high that 'slow' leaf traits were favoured regardless of climatic variation. Soil fertility, moisture and temperature have important influences on tree survival independently. However when variations in these factors occur simultaneously, the adaptive values of multiple CWM traits may differ from those when only one factor varies.

Some of the unexpected relationships between CWM traits and environmental factors in New Zealand forests that were identified in this research may be explained by physiological drivers that are yet to be fully understood. For example, variation in bark thickness does not relate to defence from fire (Lawes, *et al.* 2014) but may provide resistance against other disturbances. The observed trends in leaf phenolic concentrations may relate to the leaf economic spectrum, because 'fast' leaves in high fertility soils do not have as great a need for protective chemicals as do 'slow' leaves in resource-limited soils. However, the role of herbivores in driving this trend is yet to be assessed quantitatively. The unexpected trend of flowering onset with temperature, in sites with high soil fertility may be explained further by studies of vernalisation in New Zealand trees. The recognition of the importance of interaction effects between climate and soil fertility from this thesis research provides the basis of a deeper understanding of how environmental factors determine the adaptive values of multiple functional traits across varying habitats.

2.4.2 Comparisons to previous studies

This thesis research builds on previous forest ecology research in New Zealand. Leathwick (1995) developed models of the optimal environmental conditions for native New Zealand trees in relation to mean annual temperature, moisture and solar radiation. The findings of Leathwick (1995) were summarised in a three way triangle. In this broad-leaved trees occupied environments that are most favourable for plant growth with moist, mild, fertile and high light conditions. Beech trees occupied the sites which are reasonably stable but less favourable for plant growth.

Sites where disturbance or harsh conditions made broad-leaved species uncompetitive, were occupied by the opportunistic conifers (Bond 1989; Leathwick 1995). Comparison of these plant-environment associations to the results of this thesis illustrates the advantages of using a functional trait-based approach to understanding community assembly.

Community-weighted mean functional trait-environment relationships from this thesis can be overlaid onto the plant-environment triangle proposed by Leathwick (1995). In the top of the triangle where soil is fertile and climate is warm and moist, results from my thesis propose that species are expected to have productive leaf traits, thick roots, long flowering duration, short maximum height, low leaf phenolic content, low RDMC, late flower onset, large seeds, thin bark, and low WDMC. These are all traits of fast species with high growth rates and low investment in defence strategies (Reich 2014). These traits seem to fit well with Leathwick (1995)'s idea of broadleaved species occurring in the top of this triangle. In the left corner of the triangle where soil fertility is somewhat limited, climate is cool and dry and small scale/low intensity disturbance occurs, results from my thesis propose that species have less productive leaves, thinner roots, shorter flowering duration, higher maximum height, moderate leaf phenolic content, higher RDMC, earlier flowering onset, smaller seeds, thicker bark, and higher WDMC. Such traits typical of stressful environments reflect the importance of conservative traits in such harsh conditions and fit well with Leathwick (1995)'s suggestion of beech species occurring in this corner. In the right corner of the triangle where soil fertility is low, climate is variable and large scale/high intensity disturbance occurs, results from my thesis propose that species are expected to have 'slow' leaf traits, thin roots, short flowering duration, variable maximum height, high leaf phenolic content, high LDMC, moderate flowering onset, small seeds, thick bark, and high WDMC. These traits reflect the highly stressful environment in which angiosperm competition is reduced at the advantage of the slow-growing and stress-tolerant conifers (Leathwick 1995; Reich 2014). The trait-based perspective of this thesis follows the species-based results of Leathwick (1995). However, the trait-based method provides an unprecedented understanding of the physiological reasons why distinct communities occur in different environments. This mechanistic approach also provides a greater potential for developing accurate predictive models and is more generalizable across other parts of the world (Lavorel & Garnier 2002; Suding 2011; Laughlin 2014b).

Based on observations of New Zealand tree species, Wardle (1991) proposed a summary figure to illustrate the occurrence of species in relation to temperature, moisture and soil fertility. It would be possible to use the regression models from this thesis to clarify if the positions of species in environmental space proposed by Wardle (1991) are supported by mechanistic trait-based ecology. A challenge in doing so is quantifying the qualitative soil fertility gradient used by Wardle (1991) so that it aligns with that used in this research.

This is the first time that interaction effects between climate and soil fertility have been found to have a strong influence on multiple CWM traits. Previously most studies have focused on one of these factors at a time (eg. Frenette-Dussault *et al.*, 2013). This approach is unreasonably hopeful because climate and soil fertility have been recognised to be simultaneous drivers of plant distributions for many years (Schimper 1903; Prentice, *et al.* 1992). Maire, *et al.* (2015) first suggested the importance of interaction effects in driving community assembly, by showing that the joint effects of soil pH, soil P and moisture availability explain variation in CWM leaf traits better than any independent variable. Ordonez, *et al.* (2009) demonstrated the effect of interactions between soil C:N and mean annual precipitation on the adaptive values of SLA at a community-level globally. Dwyer, *et al.* (2015) followed this by demonstrating that interactions between soil P and moisture availability drive selection of CWM SLA, height, and seed mass. Yet, until now it has not been known whether these interaction effects influence the adaptive values of a large number and variety of CWM traits. In this thesis, the interaction effects of soil fertility × MAT, and soil fertility × VPD, overrode the importance of the individual environmental factors in driving variation in the adaptive values of CWM traits in New Zealand forests. This recognition of the importance of these interaction effects in driving community-level trait variation is an important contribution to the understanding of community assembly processes and these interaction effects will be crucial to include in future trait-based models.

3 Chapter Three: Synthesis

3.1 Conclusions

Trait-based ecology provides a mechanistic approach to understanding environmental filtering and community assembly. Previous research has shown that the adaptive values of traits vary along environmental gradients depending on their relative advantages in different environmental conditions. However, the potentially critical role of interaction effects between climate and soil fertility in driving variation in CWM traits was yet to be assessed, and nationwide trait-based studies had not been conducted in New Zealand forests. In this thesis, my overall aim was to determine the adaptive value of multiple functional traits across broad climate and soil fertility gradients in New Zealand forests.

This thesis identified there five intrinsic dimensions that explain trait variation in New Zealand tree species. Five dimensions is within the expected number of dimensions needed to ensure that functional differences between species are accurately detected (Laughlin 2014a). In addition, these five dimensions represent all major plant organs, as recommended when attempting to assess variation in traits across environmental gradients (Laughlin 2014a). The identification of these intrinsic dimensions provided a logical order in which to explain the relationships between CWM traits and environmental gradients.

This research contributes to the overall body of knowledge concerning variation in plant functional traits across environmental gradients and highlights how the adaptive values of multiple CWM traits vary across broad climate and soil fertility gradients in New Zealand forests. In environments with high fertility soil, the adaptive values of leaf economics traits varied with climate as expected (Wright, *et al.* 2005a), from 'fast' in warm and moist climates to 'slow in cool and dry climates. However, in environments with low fertility soil, 'slow' leaf traits were favoured regardless of climatic conditions. Thin root diameter, short flowering duration and small seeds were also favoured in environments with low fertility soil, across all climates. However, in environments with high fertility soils, the adaptive values of root diameter, flowering duration and seed mass varied from high in warm and moist conditions, to moderate or low in all other climates. In low fertility sites, leaf phenolic concentration varied from high in warm conditions to low in cool conditions, but in high fertility sites, leaf phenolic concentration was moderate in cool and dry conditions and low in all other climates. In low fertility soils, relative bark thickness and wood dry matter content were moderate in dry conditions and high in moist conditions. Yet, in high fertility soils, these two traits varied from low in warm and moist climates to high in cool and dry climates. In low fertility sites, the adaptive value of maximum plant height varied from tall in warm and moist conditions to short in cool and dry conditions. In contrast, in high fertility sites, the adaptive value of maximum height was moderate in cool and dry conditions but low in all other climates. In low fertility soils, root dry matter content varied from moderate in warm climates to high in cool climates, but in high fertility soils, this trait varied from low in warm climates to moderate in cool climates. The adaptive value of flowering onset was early in low fertility sites across all climates but in high fertility sites flowering onset varied from early in cool and dry conditions to late in warm and moist conditions. The significant role of the interaction effects is evidenced by the differing adaptive values of CWM traits with climatic factors depending on soil fertility.

This study highlights for the first time, the importance of including the interaction effects between climate and soil fertility when investigating community assembly in plant environments. The main effect of soil fertility was a stronger predictor of CWM traits in native New Zealand forests than were climate variables. However, the interaction effects between soil fertility and climate were significant predictors of most CWM traits in New Zealand forests. Therefore, climate and soil interact in a way that influences the adaptive values of CWM traits independently from the influence of each factor and the inclusion of interaction effects is highly important for understanding how community-level traits are sorted along environmental gradients. For example, the adaptive value of leaf economics traits depends not only on climate but also on soil fertility. The environment of plants is a multi-dimensional space. This environmental complexity needs to be accurately represented when trying to understand environmental filtering, or else incorrect and confounded conclusions will be made.

3.2 Limitations

Shortfalls in biodiversity knowledge may have affected the results (Brito 2010; Feeley 2015). Maximum plant height and flowering data were extracted from regional floras for this research. The reliability of these traits would likely be improved by further field measurements. It would also be of incredible value to conduct a similar study to this thesis research, on other plant forms, such as shrubs, ferns and epiphytes. This would enable inclusion of these species in models of species distributions and interactions to aid restoration planning and models of carbon storage.

This study of trait-based community assembly focused on the environmental filters because they are dominant and easier to study at this broad scale than biotic factors (Laliberté *et al.* 2014). However, it will be important for future studies to incorporate an understanding of biotic factors, such as the influences of competition between (Huston 1979; Feeley 2015) and within species (Jung *et al.* 2010; Laughlin, *et al.* 2012; Kraft *et al.* 2015). Although a species may have traits that are environmentally suited to a site, it may be excluded by factors such as plant-soil interactions that are difficult to detect when observing environmental factors only (Van der Putten *et al.* 2010). Likewise, a species with traits that are not environmentally suited to a site may actually be able to inhabit it because of biotic factors such as intraspecific competition (Laughlin, *et al.* 2012). Incorporation of biotic factors into trait-based studies alongside environmental factors will be vital for improving our understanding of community assembly.

Biotic processes, such as competition for limiting resources, tend to limit the functional similarity of co-occurring species (Macarthur & Levins 1967). This results in the divergence of trait values within communities (Mayfield & Levine 2010) and can lead to intraspecific trait variation. The relative importance of environmental filtering versus trait divergence may vary across sites (Laughlin, *et al.* 2012). This thesis research included a large number of tree species and sampling sites. However, intraspecific variation in traits was not included. The inclusion of intraspecific variation into trait-based ecology may be important for improving the understanding of community assembly (Violle *et al.* 2012).

3.3 Applications and recommendations for future work

The greater importance of soil fertility than climate in determining CWM traits in New Zealand trees is supported by global studies (Maire, *et al.* 2015). However, the influence of soil fertility on CWM plant traits is poorly quantified in comparison to that of climate both in New Zealand and worldwide (Maire, *et al.* 2015). This thesis supports the idea that soil fertility should be included into future studies of community assembly and species distributions.

This thesis provides the first evidence that climate and soil fertility interact in a way that influences the adaptive values of traits independently from the influence of each predictor variable independently. Due to the global recognition of the shared importance of these factors in driving species distributions (Prentice, *et al.* 1992), it is expected that this is a globally occurring interaction of extreme importance to community assembly. Despite this, it would be beneficial to test for the influence of the interaction effects of soil fertility and climate in different biomes worldwide, in order to confirm the generality of their importance.

The occurrence of interaction effects between soil fertility and climate driving community-level selection of traits is relevant to future studies of community assembly, species distributions and conservation studies. In future studies of community assembly it will also be important to include an interaction effect between climate and soil fertility. Failing to include this may lead to confounded or misleading results.

It would be interesting to use the relationships between adaptive trait values of communities and environmental gradients recognised in this thesis to predict community assembly and consequently the expected relative abundance of native tree species across sites in New Zealand. This could be achieved using the community-weighted mean trait data collected in this study (Shipley, *et al.* 2011) or more completely by incorporating intraspecific trait variation (Laughlin, *et al.* 2012). Doing so would provide answers to questions, such as how gaps in the distributions of beech trees relate to climate and soil gradients (Veblen & Stewart 1982; Wardle & Lee 1990). Predictive models such as these may also enable more rigorous comparisons to previous studies of species distributions in relation to climate such as that by Leathwick (1995). It is expected that the inclusion of soil fertility and the interaction effects of soil fertility and climate will result in at least slightly different predictions of relationships between plant communities and environmental gradients than those made by Leathwick (1995). This is likely to lead to altered predictions of potential forest patterns prior to human arrival (Leathwick 2001), altered predictions of changes in species distributions with changes in climate and land-use (Whitehead *et al.* 1992; Leathwick*, et al.* 1996; Thuiller *et al.* 2008; Ahteensuu & Lehvavirta 2014) and potentially altered conservation priorities (Elith & Leathwick 2009). For instance, when soil fertility is included into predictions of changes in community distribution patterns with climate change, communities with large thin leaves on average will be favoured in warm and moist climates, but only when soil fertility is high. Without including soil fertility, it would be have been predicted that such communities would be favoured in all warm and moist climates, as per Wright*, et al.* (2005a). Therefore the implications of climate change for vegetation depend on soil fertility as well. Such models could also provide a mechanistic way of predicting species for restoration projects that are functionally suitable and will lead to desired ecosystem functions (Laughlin 2014b). Other possible applications include predicting where productivity may change (Craine *et al.* 2002; Coomes *et al.* 2014), or combining with other datasets, to forecast where invasive species may to increase in dominance (Moles, *et al.* 2008). Nevertheless, more testing of the relationships between CWM traits and environmental and biotic factors is needed before we are able to test the more applied questions. In the short term, it is feasible and recommended to test a trait-based model to predict community and species distributions in New Zealand forests.

It may also be valuable to consider how variation in traits of the species in this study change with ontogeny. Resource allocation patterns may differ among ontogenetic stages (Day & Greenwood 2011), and soil and climate may influence seedlings and saplings differently to adult plants (Spasojevic *et al.* 2014). There are currently studies that have found significant correlations between the traits of seedling and adult plants (Cornelissen*, et al.* 2003b; Freschet *et al.* 2010; Martin *et al.* 2013), as well as those that have demonstrated decoupling of trait variation between juvenile and adult stages (Baraloto*, et al.* 2010; Houter & Pons 2012; Spasojevic*, et al.* 2014). Therefore it would be interesting to see where New Zealand trees occur among these varying results. Data from this study could be combined with traits from greenhouse-grown seedlings in order to test the effects of ontogeny on multiple traits. Differences in trait variation between different ontogenetic stages may be important for understanding the process of community assembly across environmental gradients and when using trait-based ecology to aid forestry (Boege & Marquis 2005) and restoration planning (Suding 2011).

It would also be interesting to delve further into the drivers of variation in leaf phenolic concentrations in New Zealand trees. For instance, determining if variation in climate and soil fertility, or defence from herbivory are more significant drivers of variation in leaf phenolic concentrations would be valuable. The role of herbivory could be explored using methods similar to those of Tanentzap, *et al.* (2011). Thereby, the relative occurrence of chemical and physical defences against herbivory in New Zealand trees and whether phytophagous insects or large birds (such as moa) are the primary drivers of the evolution of these defences could be assessed. To provide the foundations for such research, the data collected during this thesis on leaf concentrations of cellulose, fibre, tannin, lignin and total phenolics could be combined with data on leaf structural defences, such as those recorded by Bond *et al.* (2004).

References

Aarssen, L. W. & Jordan, C. Y. (2001) Between-species patterns of covariation in plant size, seed size and fecundity in monocarpic herbs. *Ecoscience*. **8**, 471-477.

Adams, J. M., Rehill, B., Zhang, Y. & Gower, J. (2009) A test of the latitudinal defense hypothesis: Herbivory, tannins and total phenolics in four North American tree species. *Ecological Research*. **24**, 697-704.

Aerts, R. (1999) Interspecific competition in natural plant communities: Mechanisms, trade-offs and plant-soil feedbacks. *Journal of Experimental Botany*. **50**, 29-37.

Aerts, R. & Chapin, F. S. I. (2000) The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Advances in Ecological Research*. **30**, 1-37.

Agrawal, A. A. F., M. (2006) Plant defense syndromes. *Ecology*. **87**, S132-S149.

Ahteensuu, M. & Lehvavirta, S. (2014) Assisted migration, risks and scientific uncertainty, and ethics: A comment on Albrecht et al.'s review paper. *Journal of Agricultural & Environmental Ethics*. **27**, 471-477.

Alameda, D. & Villar, R. (2012) Linking root traits to plant physiology and growth in *Fraxinus angustifolia* Vahl. seedlings under soil compaction conditions. *Environmental and Experimental Botany*. **79**, 49-57.

Albrecht, G. A., Brooke, C., Bennett, D. H. & Garnett, S. T. (2013) The ethics of assisted colonization in the age of anthropogenic climate change. *Journal of Agricultural & Environmental Ethics*. **26**, 827-845.

Allan, H. H. (1961) *Flora of New Zealand. Vol. I. Indigenous Tracheophyta: Psilopsida, Lycopsida, Filicopsida, Gymnospermae, Dicotyledones*. Government Printer, Wellington, New Zealand.

Allen, R. B., Reif, A. & Hall, G. M. J. (1991) Elevational distribution of conifer-broadleaved hardwood forests on South Island, New Zealand. *Journal of Vegetation Science*. **2**, 323-330.

Allen, R. B., Bellingham, P. J., Holdaway, R. J. & Wiser, S. K. (2013) New Zealand’s indigenous forests and shrublands. *Ecosystem services in New Zealand: Conditions and trends* (ed. J. R. Dymond), pp. 34-48. Manaaki Whenua Press, Lincoln, New Zealand.

Alvarez-Uria, P. & Koerner, C. (2011) Fine root traits in adult trees of evergreen and deciduous taxa from low and high elevation in the Alps. *Alpine Botany*. **121**, 107-112.

Amasino, R. M. (1996) Control of flowering time in plants. *Current Opinion in Genetics & Development*. **6**, 480-487.

Anacker, B., Rajakaruna, N., Ackerly, D., Harrison, S., Keeley, J. & Vasey, M. (2011) Ecological strategies in California chaparral: Interacting effects of soils, climate, and fire on specific leaf area. *Plant Ecology & Diversity*. **4**, 179-188.

Aronson, J., Kigel, J., Shmida, A. & Klein, J. (1992) Adaptive phenology of desert and Mediterranean populations of annual plants grown with and without water stress. *Oecologia*. **89**, 17-26.

Atkinson, I. A. E. & Greenwood, R. M. (1989) Relationships between moa and plants. *New Zealand Journal of Ecology*. **12**, 67-96.

Ausín, I., Alonso-Blanco, C. & Martínez-Zapater, J. (2005) Environmental regulation of flowering. *International Journal of Developmental Biology*. **49**, 689-705.

Austin, M. P. & Smith, T. M. (1989) A new model for the continuum concept. *Vegetatio*. **83**, 35-47.

Baas, P., Ewers, F. W., Davis, S. D. & Wheeler, E. A. (2004) Evolution of xylem physiology. *The evolution of plant physiology* (eds. A. R. Hemsley & I. Poole), pp. 273–295. Elsevier Academic Press, London, UK.

Barajas-Morales, J. (1987) Wood specific gravity in species from two tropical forests in Mexico. *Iawa Bulletin*. **8**, 143-148.

Baraloto, C., Timothy Paine, C., Poorter, L., Beauchene, J., Bonal, D., Domenach, A. M., Hérault, B., Patino, S., Roggy, J. C. & Chave, J. (2010) Decoupled leaf and stem economics in rain forest trees. *Ecology Letters*. **13**, 1338-1347.

Barlow, B. A. & Wiens, D. (1977) Host-parasite resemblance in Australian mistletoes: The case for cryptic mimicry. *Evolution*. **31**, 69-84.

Bazzaz, F. A. & Pickett, S. T. A. (1980) Physiological ecology of tropical succession: A comparative review. *Annual Review of Ecology and Systematics*. **11**, 287-310.

Bellingham, P. J., Tanner, E. V. J. & Healey, J. R. (1995) Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology*. **76**, 2562-2580.

Bennett, R. N. & Wallsgrove, R. M. (1994) Tansley Review No. 72. Secondary metabolites in plant defence mechanisms. *New Phytologist*. **127**, 617-633.

Bernier, G. & Perilleux, C. (2005) A physiological overview of the genetics of flowering time control. *Plant Biotechnology Journal*. **3**, 3-16.

Best, H. A. & Bellingham, P. (1991) *A detailed habitat study of North Island kokako in Puketi Forest, Northland* Science and Research Internal Report No.103. Department of Conservation, Wellington, New Zealand.

Bier, H. (1999) *Strength properties of small clear specimens of New Zealand-grown timbers*. New Zealand Forest Research Institute, Rotorua, New Zealand.

Binkley, D. & Fisher, R. F. (2013) *Ecology and management of forest soils* (4th ed.). Wiley-Blackwell, Hoboken, NJ.

Binkley, D., Driscoll, C. T., Allen, H. L., Schoeneberger, P. & McAvoy, D. (2011) *Acidic deposition and forest soils: Context and case studies of the southeastern United States*. Springer-Verlag, New York, NY.

Birouste, M., Zamora-Ledezma, E., Bossard, C., Pérez-Ramos, I. M. & Roumet, C. (2014) Measurement of fine root tissue density: A comparison of three methods reveals the potential of root dry matter content. *Plant and Soil*. **374**, 299-313.

Blakemore, L. C., Searle, P. L. & Daly, B. K. (1987) *Methods for chemical analysis of soils.* NZ Soils Bureau Report No. 80. Lower Hutt, New Zealand, DSIR Land Resources. 103p.

Bloom, A. J., Chapin, F. S. & Mooney, H. A. (1985) Resource limitation in plants: An economic analogy. *Annual Review of Ecology and Systematics*. **16**, 363-392.

Bock, A., Sparks, T. H., Estrella, N., Jee, N., Casebow, A., Schunk, C., Leuchner, M. & Menzel, A. (2014) Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey. *Global Change Biology*. **20**, 3508-3519.

Boege, K. & Marquis, R. J. (2005) Facing herbivory as you grow up: The ontogeny of resistance in plants. *Trends in Ecology & Evolution*. **20**, 441-448.

Bond, W. J. (1989) The tortoise and the hare: Ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society*. **36**, 227-249.

Bond, W. J., Lee, W. G. & Craine, J. M. (2004) Plant structural defences against browsing birds: A legacy of New Zealand's extinct moas. *Oikos*. **104**, 500-508.

Borch, K., Bouma, T. J., Lynch, J. P. & Brown, K. M. (1999) Ethylene: A regulator of root architectural responses to soil phosphorus availability. *Plant Cell and Environment*. **22**, 425-431.

Brando, P. M., Nepstad, D. C., Balch, J. K., Bolker, B., Christman, M. C., Coe, M. & Putz, F. E. (2012) Fire-induced tree mortality in a neotropical forest: The roles of bark traits, tree size, wood density and fire behavior. *Global Change Biology*. **18**, 630-641.

Brito, D. (2010) Overcoming the Linnean shortfall: Data deficiency and biological survey priorities. *Basic and Applied Ecology*. **11**, 709-713.

Burns, B. R. & Leathwick, J. R. (1996) Vegetation-environment relationships at Waipoua Forest, Northland, New Zealand. *New Zealand Journal of Botany*. **34**, 79-92.

Campbell, B. D. & Grime, J. P. (1992) An experimental test of plant strategy theory. *Ecology*. **73**, 15-29.

Cavender-Bares, J., Kozak, K. H., Fine, P. V. & Kembel, S. W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*. **12**, 693-715.

Chao, K. J., Phillips, O. L., Gloor, E., Monteagudo, A., Torres-Lezama, A. & Martinez, R. V. (2008) Growth and wood density predict tree mortality in Amazon forests. *Journal of Ecology*. **96**, 281-292.

Chapin, F. S. (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*. **11**, 233-260.

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G. & Zanne, A. E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*. **12**, 351-366.

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., ter Steege, H. & Webb, C. O. (2006) Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological Applications*. **16**, 2356-2367.

Chudnoff, M. (1976) Density of tropical timbers as influenced by climatic life zones. *Commonwealth Forestry Review*. **55**, 203-217.

Clarkson, B. D. (1985a) The vegetation of the Kaitake Range Egmont National Park, New Zealand. *New Zealand Journal of Botany*. **23**, 15-31.

Clarkson, D. T. (1985b) Factors affecting mineral nutrient acquisition by plants. *Annual Review of Plant Physiology*. **36**, 77-115.

Close, D. C. & McArthur, C. (2002) Rethinking the role of many plant phenolics–protection from photodamage not herbivores? *Oikos*. **99**, 166-172.

Cockayne, L. (1928) *The vegetation of New Zealand*. Cambridge University Press, New York, NY.

Coley, P. D. & Aide, T. M. (1991) Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. *Plant-animal interactions: Evolutionary ecology in tropical and temperate regions* (eds. P. W. Price, T. M. Lewinsohn, G. W. Fernandes & W. W. Benson), pp. 25-49. Wiley, New York, NY.

Comas, L. & Eissenstat, D. (2009) Patterns in root trait variation among 25 co‐existing North American forest species. *New Phytologist*. **182**, 919-928.

Comas, L. H. & Eissenstat, D. M. (2004) Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Functional Ecology*. **18**, 388-397.

Cook, B. I., Wolkovich, E. M. & Parmesan, C. (2012) Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences of the United States of America*. **109**, 9000-9005.

Coomes, D. A., Kunstler, G., Canham, C. D. & Wright, E. (2009) A greater range of shade-tolerance niches in nutrient-rich forests: An explanation for positive richness-productivity relationships? *Journal of Ecology*. **97**, 705-717.

Coomes, D. A., Flores, O., Holdaway, R., Jucker, T., Lines, E. R. & Vanderwel, M. C. (2014) Wood production response to climate change will depend critically on forest composition and structure. *Global Change Biology*. **20**, 3632-3645.

Cornelissen, J., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D., Reich, P., Ter Steege, H., Morgan, H. & Van Der Heijden, M. (2003a) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*. **51**, 335-380.

Cornelissen, J. H. C., Cerabolini, B., Castro-Diez, P., Villar-Salvador, P., Montserrat-Marti, G., Puyravaud, J. P., Maestro, M., Werger, M. J. A. & Aerts, R. (2003b) Functional traits of woody plants: Correspondence of species rankings between field adults and laboratory-grown seedlings? *Journal of Vegetation Science*. **14**, 311-322.

Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Perez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T. V., Diaz, S., Garnier, E., Gurvich, D. E., Kazakou, E., Klein, J. A., Read, J., Reich, P. B., Soudzilovskaia, N. A., Vaieretti, M. V. & Westoby, M. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*. **11**, 1065-1071.

Cortina, J., Green, J. J., Baddeley, J. A. & Watson, C. A. (2008) Root morphology and water transport of *Pistacia lentiscus* seedlings under contrasting water supply: A test of the pipe stem theory. *Environmental and Experimental Botany*. **62**, 343-350.

Craig, J., Anderson, S., Clout, M., Creese, B., Mitchell, N., Ogden, J., Roberts, M. & Ussher, G. (2000) Conservation issues in New Zealand. *Annual Review of Ecology and Systematics*. **31**, 61-78.

Craine, J. M. (2009) *Resource strategies of wild plants*. Princeton University Press, Princeton, NJ.

Craine, J. M. & Lee, W. G. (2003) Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. *Oecologia*. **134**, 471-478.

Craine, J. M., Lee, W. G., Bond, W. J., Williams, R. J. & Johnson, L. C. (2005) Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology*. **86**, 12-19.

Craine, J. M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M. & Knops, J. (2002) Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology*. **16**, 563-574.

Craufurd, P. Q., Wheeler, T. R., Ellis, R. H., Summerfield, R. J. & Williams, J. H. (1999) Effect of temperature and water deficit on water-use efficiency, carbon isotope discrimination, and specific leaf area in peanut. *Crop Science*. **39**, 136-142.

Cunningham, S. A., Summerhayes, B. & Westoby, M. (1999) Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecological Monographs*. **69**, 569-588.

Curran, T. J., Gersbach, L. N., Edwards, W. & Krockenberger, A. K. (2008) Wood density predicts plant damage and vegetative recovery rates caused by cyclone disturbance in tropical rainforest tree species of north Queensland, Australia. *Austral Ecology*. **33**, 442-450.

Darwin, C. (1859) *The origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. John Murray, London, UK.

Davies, W. C. (1961) *New Zealand native plant studies*. Reed, Wellington, New Zealand.

Day, M. E. & Greenwood, M. S. (2011) Regulation of ontogeny in temperate conifers. *Tree Physiology*. **4**, 91-119.

De Frenne, P., Graae, B. J., Rodriguez-Sanchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., Gruwez, R., Hermy, M., Lenoir, J., Plue, J., Coomes, D. A. & Verheyen, K. (2013) Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology*. **101**, 784-795.

de Lange, P. J., Norton, D. A., Courtney, S. P., Heenan, P. B., Barkla, J. W., Cameron, E. K., Hitchmough, R. & Townsend, A. J. (2009) Threatened and uncommon plants of New Zealand (2008 revision). *New Zealand Journal of Botany*. **47**, 61-96.

Díaz, S., Cabido, M., Zak, M., Martínez Carretero, E. & Araníbar, J. (1999) Plant functional traits, ecosystem structure and land‐use history along a climatic gradient in central‐western Argentina. *Journal of Vegetation Science*. **10**, 651-660.

Dijkgraaf, A. C. (2002) Phenology and frugivory of large-fruited species in northern New Zealand and the impacts of introduced mammals. Unpublished PhD thesis, University of Auckland, Auckland, New Zealand.

Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*. **38**, 209-221.

Druitt, D. G., Enright, N. J. & Ogden, J. (1990) Altitudinal zonation in the mountain forests of Mt Hauhungatahi, North Island, New Zealand. *Journal of Biogeography*. **17**, 205-220.

Dwyer, J. M., Hobbs, R. J., Wainwright, C. E. & Mayfield, M. M. (2015) Climate moderates release from nutrient limitation in natural annual plant communities. *Global Ecology and Biogeography*. **24**, 549-561.

Ehrlich, P. R. & Raven, P. H. (1964) Butterflies and plants: A study in coevolution. *Evolution*. **18**, 586-608.

Eissenstat, D. M. (1992) Costs and benefits of constructing roots of small diameter. *Journal of Plant Nutrition*. **15**, 763-782.

Elith, J. & Leathwick, J. (2009) Conservation prioritisation using species distribution modelling. *Spatial conservation prioritization: Quantitative methods and computational tools*, pp. 70-93. Oxford University Press, Oxford, UK.

Enquist, B. J., West, G. B., Charnov, E. L. & Brown, J. H. (1999) Allometric scaling of production and life-history variation in vascular plants. *Nature*. **401**, 907-911.

Environmental Systems Research Institute (2011) *ArcGIS Desktop: Release 10*. Retrieved 1 August 2014 from http://www.esri.com/software/arcgis/arcgis-for-desktop.

Esler, A. E. (1969) Leaf fall and flowering of nikau. *Bulletin of the Wellington Botanical Society*. **36**, 18-23.

Falster, D. S. & Westoby, M. (2003) Plant height and evolutionary games. *Trends in Ecology & Evolution*. **18**, 337-343.

Farjon, A. (2005) *A monograph of Cupressaceae and Sciadopitys*. Kew Publishing, Kew, UK.

Farquhar, G. D., Buckley, T. N. & Miller, J. M. (2002) Optimal stomatal control in relation to leaf area and nitrogen content. *Silva Fennica*. **36**, 625-637.

Farrell, B. D., Dussourd, D. E. & Mitter, C. (1991) Escalation of plant defense: Do latex and resin canals spur plant diversification? *American Naturalist*. **138**, 881-900.

Feeley, K. J. (2015) Moving forward with species distributions. *American Journal of Botany*. **102**, 173-175.

Fernandez-Going, B. M., Harrison, S. P., Anacker, B. L. & Safford, H. D. (2013) Climate interacts with soil to produce beta diversity in Californian plant communities. *Ecology*. **94**, 2007-2018.

Ferry, B., Morneau, F., Bontemps, J. D., Blanc, L. & Freycon, V. (2010) Higher treefall rates on slopes and waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *Journal of Ecology*. **98**, 106-116.

Fitter, A. H. (1987) An architectural approach to the comparative ecology of plant root systems. *New Phytologist*. **106**, 61-77.

Fitter, A. H. & Fitter, R. S. R. (2002) Rapid changes in flowering time in British plants. *Science*. **296**, 1689-1691.

Fitter, A. H., Atkinson, D., Read, D. J. & Usher, M. B. (1985) Functional significance of root morphology and root architecture. *Ecological interactions in soil: Plants, microbes and animals* (Vol. 4) (ed. A. H. Fitter), pp. 87-106. Blackwell Scientific, Oxford, UK.

Fonseca, C. R., Overton, J.M., Collins, B., Westoby, M. (2000) Shifts in trait combinations along rainfall and phosphorus gradients. *Journal of Ecology*. **88**, 964-977.

Fox, J. (2003) Effect displays for generalized linear models. *Journal of Statistical Software*. **8**, 1-27.

Frenette-Dussault, C., Shipley, B., Meziane, D. & Hingrat, Y. (2013) Trait-based climate change predictions of plant community structure in arid steppes. *Journal of Ecology*. **101**, 484-492.

Freschet, G. T., Cornelissen, J. H., Van Logtestijn, R. S. & Aerts, R. (2010) Evidence of the ‘plant economics spectrum’in a subarctic flora. *Journal of Ecology*. **98**, 362-373.

Freschet, G. T., Bellingham, P. J., Lyver, P. O. B., Bonner, K. I. & Wardle, D. A. (2013a) Plasticity in above- and belowground resource acquisition traits in response to single and multiple environmental factors in three tree species. *Ecology and Evolution*. **3**, 1065-1078.

Freschet, G. T., Cornwell, W. K., Wardle, D. A., Elumeeva, T. G., Liu, W. D., Jackson, B. G., Onipchenko, V. G., Soudzilovskaia, N. A., Tao, J. P. & Cornelissen, J. H. C. (2013b) Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. *Journal of Ecology*. **101**, 943-952.

Funk, J. L. & Cornwell, W. K. (2013) Leaf traits within communities: Context may affect the mapping of traits to function. *Ecology*. **94**, 1893-1897.

Fürst, G. & Ghisletta, P. (2009) Statistical interaction between two continuous (latent) variables. *11th Congress of the Swiss Psychological Society, August 19th-20th, Neuchâtel, Switzerland*, pp. 19-20.

Gaston, K. J., Genney, D. R., Thurlow, M. & Hartley, S. E. (2004) The geographical range structure of the holly leaf ‐ miner. IV. Effects of variation in host ‐ plant quality. *Journal of Animal Ecology*. **73**, 911-924.

Geng, Y., Wang, L., Jin, D. M., Liu, H. Y. & He, J. S. (2014) Alpine climate alters the relationships between leaf and root morphological traits but not chemical traits. *Oecologia*. **175**, 445-455.

Ghosh, D. (2006) Bark is the hallmark. *Resonance*. **11**, 41-50.

Godoy, O., de Lemos, J. P. & Valladares, F. (2011) Invasive species can handle higher leaf temperature under water stress than Mediterranean natives. *Environmental and Experimental Botany*. **71**, 207-214.

Gourlet-Fleury, S., Rossi, V., Rejou-Mechain, M., Freycon, V., Fayolle, A., Saint-André, L., Cornu, G., Gérard, J., Sarrailh, J.-M., Flores, O., Baya, F., Billand, A., Fauvet, N., Gally, M., Henry, M., Hubert, D., Pasquier, A. & Picard, N. (2011) Environmental filtering of dense-wooded species controls above-ground biomass stored in African moist forests. *Journal of Ecology*. **99**, 981-990.

Graça, M. A. & Cressa, C. (2010) Leaf quality of some tropical and temperate tree species as food resource for stream shredders. *International Review of Hydrobiology*. **95**, 27-41.

Grace, J. (1987) Climatic tolerance and the distribution of plants. *New Phytologist*. **106**, 113-130.

Greene, D. & Johnson, E. (1994) Estimating the mean annual seed production of trees. *Ecology*. **75**, 642-647.

Greenwood, R. & Atkinson, I. (1977) Evolution of divaricating plants in New Zealand in relation to moa browsing. *Proceedings of the New Zealand Ecological Society*. **24**, 21-33.

Grime, J. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American naturalist*. **111**, 1169-1194.

Grime, J., Thompson, K., Hunt, R., Hodgson, J., Cornelissen, J., Rorison, I., Hendry, G., Ashenden, T., Askew, A. & Band, S. (1997) Integrated screening validates primary axes of specialisation in plants. *Oikos*. **79**, 259-281.

Grime, J. P. (1979) *Plant strategies and vegetation processes*. John Wiley and sons, New York, NY.

Grime, J. P. (1993) Ecology sans frontieres. *Oikos*. **68**, 385-392.

Grubb, P. J. (1998) A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology, Evolution and Systematics*. **1**, 3-31.

Hacke, U. G. & Sperry, J. S. (2001) Functional and ecological xylem anatomy. *Perspectives in Plant Ecology, Evolution and Systematics*. **4**, 97-115.

Hallam, A. & Read, J. (2006) Do tropical species invest more in anti-herbivore defence than temperate species? A test in *Eucryphia* (Cunoniaceae) in eastern Australia. *Journal of Tropical Ecology*. **22**, 41-51.

Harrington, L., Rosier, S., Dean, S. M., Stuart, S. & Scahill, A. (2014) The role of anthropogenic climate change in the 2013 drought over North Island, New Zealand. *Bulletin of the American Meteorological Society*. **95**, S45-S48.

Harris, J. A., Hobbs, R. J., Higgs, E. & Aronson, J. (2006) Ecological restoration and global climate change. *Restoration Ecology*. **14**, 170-176.

Hättenschwiler, S. & Vitousek, P. M. (2000) The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends in Ecology & Evolution*. **15**, 238-243.

Heal, O., Anderson, J. & Swift, M. (1997) Plant litter quality and decomposition: An historical overview. *Driven by nature: Plant litter quality and decomposition* (eds. G. Cadisch & K. E. Giller), pp. 3-30. CAB International, Wallingford, UK.

Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A.-L. & Totland, Ø. (2009) How does climate warming affect plant-pollinator interactions? *Ecology Letters*. **12**, 184-195.

Henery, M. L. & Westoby, M. (2001) Seed mass and seed nutrient content as predictors of seed output variation between species. *Oikos*. **92**, 479-490.

Herms, D. A. & Mattson, W. J. (1992) The dilemma of plants: To grow or defend. *Quarterly Review of Biology*. **67**, 283-335.

Hill, J. O., Simpson, R. J., Moore, A. D. & Chapman, D. F. (2006) Morphology and response of roots of pasture species to phosphorus and nitrogen nutrition. *Plant and Soil*. **286**, 7-19.

HilleRisLambers, J., Adler, P., Harpole, W., Levine, J. & Mayfield, M. (2012) Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*. **43**, 227.

Hobbie, S. E., Nadelhoffer, K. J. & Högberg, P. (2002) A synthesis: The role of nutrients as constraints on carbon balances in boreal and arctic regions. *Plant and Soil*. **242**, 163-170.

Hobbs, R. J., Higgs, E. & Harris, J. A. (2009) Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology & Evolution*. **24**, 599-605.

Holdaway, R. J., Richardson, S. J., Dickie, I. A., Peltzer, D. A. & Coomes, D. A. (2011) Species- and community-level patterns in fine root traits along a 120 000-year soil chronosequence in temperate rain forest. *Journal of Ecology*. **99**, 954-963.

Holdridge, L. R. (1947) Determination of world formations from simple climatic data. *Science*. **105**, 367-368.

Houter, N. C. & Pons, T. L. (2012) Ontogenetic changes in leaf traits of tropical rainforest trees differing in juvenile light requirement. *Oecologia*. **169**, 33-45.

Howell, T. A. & Dusek, D. A. (1995) Comparison of vapor-pressure-deficit calculation methods: Southern High Plains. *Journal of Irrigation & Drainage Engineering*. **121**, 191.

Hura, T., Hura, K., Dziurka, K., Ostrowska, A., Baczek-Kwinta, R. & Grzesiak, M. (2012) An increase in the content of cell wall-bound phenolics correlates with the productivity of triticale under soil drought. *Journal of Plant Physiology*. **169**, 1728.

Huston, M. (1979) A general hypothesis of species diversity. *American Naturalist*. **113**, 81-101.

Huston, M. A. (2012) Precipitation, soils, NPP, and biodiversity: Resurrection of Albrecht's curve. *Ecological Monographs*. **82**, 277-296.

IPCC (2007) *Climate Change 2007: Synthesis Report.* Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland, IPCC. 104p.

Jackson, S. T. & Hobbs, R. J. (2009) Ecological restoration in the light of ecological history. *Science*. **325**, 567.

Jager, M. M. (2014) Plant traits and their role in determining forest community structure along a soil fertility gradient. Unpublished MSc thesis, University of Waikato, Hamilton, New Zealand.

Jager, M. M., Richardson, S. J., Bellingham, P. J., Clearwater, M. J. & Laughlin, D. C. (2015) Soil fertility induces coordinated responses of multiple independent functional traits. *Journal of Ecology*. **103**, 374-385.

Janz, N. (2011) Ehrlich and Raven revisited: Mechanisms underlying codiversification of plants and enemies. *Annual Review of Ecology, Evolution, and Systematics*. **42**, 71-89.

Jenny, H. (1941) *Factors of soil formation: A system of quantitative pedology*. McGraw-Hill, New York, NY.

Jones, H. G. (1992) *Plants and microclimate: A quantitative approach to environmental plant physiology* (2nd ed.). Cambridge University Press, Cambridge, UK.

Jump, A. S., Matyas, C. & Penuelas, J. (2009) The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology & Evolution*. **24**, 694-701.

Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. (2010) Intraspecific variability and trait-based community assembly. *Journal of Ecology*. **98**, 1134-1140.

Karl, T. R. & Trenberth, K. E. (2003) Modern global climate change. *Science*. **302**, 1719-1723.

Kaspar, T. C. & Bland, W. L. (1992) Soil temperature and root growth. *Soil Science*. **154**, 290-299.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., Van Bodegom, P. M., Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin, O., Bahn, M., Baker, T. R., Baldocchi, D., Bekker, R., Blanco, C. C., Blonder, B., Bond, W. J., Bradstock, R., Bunker, D. E., Casanoves, F., Cavender-Bares, J., Chambers, J. Q., Chapin Iii, F. S., Chave, J., Coomes, D., Cornwell, W. K., Craine, J. M., Dobrin, B. H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W. F., Fang, J., FernÁNdez-MÉNdez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G. T., Fyllas, N. M., Gallagher, R. V., Green, W. A., Gutierrez, A. G., Hickler, T., Higgins, S. I., Hodgson, J. G., Jalili, A., Jansen, S., Joly, C. A., Kerkhoff, A. J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J. M. H., Kramer, K., KÜHn, I., Kurokawa, H., Laughlin, D., Lee, T. D., Leishman, M., Lens, F., Lenz, T., Lewis, S. L., Lloyd, J., LlusiÀ, J., Louault, F., Ma, S., Mahecha, M. D., Manning, P., Massad, T., Medlyn, B. E., Messier, J., Moles, A. T., MÜLler, S. C., Nadrowski, K., Naeem, S., Niinemets, Ü., NÖLlert, S., NÜSke, A., Ogaya, R., Oleksyn, J., Onipchenko, V. G., Onoda, Y., OrdoÑEz, J., Overbeck, G., Ozinga, W. A., PatiÑO, S., Paula, S., Pausas, J. G., PeÑUelas, J., Phillips, O. L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J. F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S. J., Yguel, B., Zaehle, S., Zanne, A. E. & Wirth, C. (2011) TRY: A global database of plant traits. *Global Change Biology*. **17**, 2905-2935.

Kauppi, P. & Posch, M. (1985) Sensitivity of boreal forests to possible climatic warming. *Climatic Change*. **7**, 45-54.

Keddy, P. A. (1992) Assembly and response rules: Two goals for predictive community ecology. *Journal of Vegetation Science*. **3**, 157-164.

Kembel, S. W., De Kroon, H., Cahill, J. F., Jr. & Mommer, L. (2008) Improving the scale and precision of hypotheses to explain root foraging ability. *Annals of Botany*. **101**, 1295-1301.

King, D. A. (1990) The adaptive significance of tree height. *American Naturalist*. **135**, 809-828.

Kirschbaum, M. U. F., Watt, M. S., Tait, A. & Ausseil, A. G. E. (2012) Future wood productivity of *Pinus radiata* in New Zealand under expected climatic changes. *Global Change Biology*. **18**, 1342-1356.

Kleiman, D. & Aarssen, L. W. (2007) The leaf size/number trade-off in trees. *Journal of Ecology*. **95**, 376–382.

Koch, G. W., Sillett, S. C., Jennings, G. M. & Davis, S. D. (2004) The limits to tree height. *Nature*. **428**, 851-854.

Koricheva, J., Nykanen, H. & Gianoli, E. (2004) Meta-analysis of trade-offs among plant antiherbivore defenses: Are plants jacks-of-all-trades, masters of all? *American Naturalist*. **163**, E64-E75.

Körner, C. (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia*. **115**, 445-459.

Kozlowski, T. T. (1992) Carbohydrate sources and sinks in woody plants. *Botanical Review*. **58**, 107-222.

Kraft, N. J., Adler, P. B., Godoy, O., James, E. C., Fuller, S. & Levine, J. M. (2015) Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*. **29**, 592-599.

Kraft, N. J. B., Valencia, R. & Ackerly, D. D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*. **322**, 580-582.

Kramer-Walter, K. R. (2015) Root traits of New Zealand trees: Community-level responses to a soil fertility gradient, and plastic responses to nutrient availability. Unpublished MSc thesis, University of Waikato, Hamilton, New Zealand.

Kraus, T. E., Dahlgren, R. A. & Zasoski, R. J. (2003) Tannins in nutrient dynamics of forest ecosystems: A review. *Plant and Soil*. **256**, 41-66.

Laine, K. M. & Henttonen, H. (1987) Phenolics/nitrogen ratios in the blueberry *Vaccinium myrtillus* in relation to temperature and microtine density in Finnish Lapland. *Oikos*. **50**, 389-395.

Laliberté, E., Zemunik, G. & Turner, B. L. (2014) Environmental filtering explains variation in plant diversity along resource gradients. *Science*. **345**, 1602-1605.

Lambers, H., Raven, J. A., Shaver, G. R. & Smith, S. E. (2008) Plant nutrient acquisition strategies change with soil age. *Trends in Ecology & Evolution*. **23**, 95-103.

Lambers, H., Brundrett, M. C., Raven, J. A. & Hopper, S. D. (2010) Plant mineral nutrition in ancient landscapes: High plant species diversity on infertile soils is linked to functional diversity for nutritional strategies. *Plant and Soil*. **334**, 11-31.

Lambers, H., Shane, M. W., Cramer, M. D., Pearse, S. J. & Veneklaas, E. J. (2006) Root structure and functioning for efficient acquisition of phosphorus: Matching morphological and physiological traits. *Annals of Botany*. **98**, 693–713.

Laughlin, D. C. (2011) Nitrification is linked to dominant leaf traits rather than functional diversity. *Journal of Ecology*. **99**, 1091-1099.

Laughlin, D. C. (2014a) The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*. **102**, 186-193.

Laughlin, D. C. (2014b) Applying trait-based models to achieve functional targets for theory-driven ecological restoration. *Ecology Letters*. **17**, 771-784.

Laughlin, D. C., Richardson, S. J., Wright, E. & Bellingham, P. J. (2015) Environmental filtering and positive plant litter feedback simultaneously explain correlations between leaf traits and soil fertility. *Ecosystems*. **In press**.

Laughlin, D. C., Fule, P. Z., Huffman, D. W., Crouse, J. & Laliberte, E. (2011) Climatic constraints on trait-based forest assembly. *Journal of Ecology*. **99**, 1489-1499.

Laughlin, D. C., Joshi, C., van Bodegom, P. M., Bastow, Z. A. & Fulé, P. Z. (2012) A predictive model of community assembly that incorporates intraspecific trait variation. *Ecology Letters*. **15**, 1291-1299.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*. **16**, 545-556.

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Pellet, G. & Douzet, R. (2011) Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *Journal of Ecology*. **99**, 135-147.

Lawes, M. J., Richardson, S. J., Clarke, P. J., Midgley, J. J., McGlone, M. S. & Bellingham, P. J. (2014) Bark thickness does not explain the different susceptibility of Australian and New Zealand temperate rain forests to anthropogenic fire. *Journal of Biogeography*. **41**, 1467-1477.

Lawes, M. J., Midgley, J. J. & Clarke, P. J. (2013) Costs and benefits of relative bark thickness in relation to fire damage: A savanna/forest contrast. *Journal of Ecology*. **101**, 517-524.

Lawes, M. J., Richards, A., Dathe, J. & Midgley, J. J. (2011) Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology*. **212**, 2057-2069.

Lawton, J. H. (1999) Are there general laws in ecology? *Oikos*. **84**, 177-192.

Lawton, R. O. (1984) Ecological constraints on wood density in a tropical montane rain forest. *American Journal of Botany*. **71**, 261-267.

Leathwick, J., Morgan, F., Wilson, G., Rutledge, D., McLeod, M. & Johnston, K. (2002) *Land Environments of New Zealand: A Technical Guide.* Wellington, New Zealand, Ministry for the Environment.

Leathwick, J. R. (1984) *Phenology of some common trees, shrubs, and lianes in four central North Island forests.* FRI Bulletin No. 72. Rotorua, New Zealand, Forest Research Institute. 46p.

Leathwick, J. R. (1995) Climatic relationships of some New Zealand forest tree species. *Journal of Vegetation Science*. **6**, 237-248.

Leathwick, J. R. (1998) Are New Zealand's *Nothofagus* species in equilibrium with their environment? *Journal of Vegetation Science*. **9**, 719-732.

Leathwick, J. R. (2001) New Zealand's potential forest pattern as predicted from current species ‑ environment relationships. *New Zealand Journal of Botany*. **39**, 447-464.

Leathwick, J. R. (2003) *Land environments of New Zealand, Ngā taiao o Aotearoa*. David Bateman, Auckland, New Zealand.

Leathwick, J. R. & Whitehead, D. (2001) Soil and atmospheric water deficits and the distribution of New Zealand's indigenous tree species. *Functional Ecology*. **15**, 233-242.

Leathwick, J. R., Whitehead, D. & McLeod, M. (1996) Predicting changes in the composition of New Zealand's indigenous forests in response to global warming: A modelling approach. *Environmental Software*. **11**, 81-90.

Lee, J. A. & Verleyson, M. (2007) *Nonlinear Dimensionality Reduction*. Springer, New York, NY.

Lee, K. E. (1959) *The earthworm fauna of New Zealand*. New Zealand DSIR Bulletin No. 130. Wellington, New Zealand, New Zealand Department of Scientific and Industrial Research. 486p.

Leishman, M. R., Wright, I. J., Moles, A. T. & Westoby, M. (2000) The evolutionary ecology of seed size. *Seeds: The ecology of regeneration in plant communities* (ed. M. Fenner), pp. 31–57. CAB International, Wallingford, UK.

Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P. & Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*. **320**, 1768-1771.

Leuschner, C., Hertel, D., Schmid, I., Koch, O., Muhs, A. & Hölscher, D. (2004) Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. *Plant and Soil*. **258**, 43-56.

Littell, J. S., Peterson, D. L. & Tjoelker, M. (2008) Douglas-fir growth in mountain ecosystems: Water limits tree growth from stand to region. *Ecological Monographs*. **78**, 349-368.

Liu, X. J., Swenson, N. G., Wright, S. J., Zhang, L. W., Song, K., Du, Y. J., Zhang, J. L., Mi, X. C., Ren, H. B. & Ma, K. P. (2012) Covariation in plant functional traits and soil fertility within two species-rich forests. *PloS One*. **7**, e34767.

Lloyd, D. G. (1985) Progress in understanding the natural history of New Zealand plants. *New Zealand Journal of Botany*. **23**, 707-722.

Lohbeck, M., Poorter, L., Lebrija-Trejos, E., Martínez-Ramos, M., Meave, J. A., Paz, H., Pérez-García, E. A., Romero-Pérez, I. E., Tauro, A. & Bongers, F. (2013) Successional changes in functional composition contrast for dry and wet tropical forest. *Ecology*. **94**, 1211-1216.

Long, S. P. & Ort, D. R. (2010) More than taking the heat: Crops and global change. *Current Opinion in Plant Biology*. **13**, 241-248.

Lord, J., Egan, J., Clifford, T., Jurado, E., Leishman, M., Williams, D. & Westoby, M. (1997) Larger seeds in tropical floras: Consistent patterns independent of growth form and dispersal mode. *Journal of Biogeography*. **24**, 205-211.

Lusk, C. H., Jorgensen, M. A. & Bellingham, P. J. (2015) A conifer-angiosperm divergence in the growth vs. shade tolerance trade-off underlies the dynamics of a New Zealand warm-temperate rain forest. *Journal of Ecology*. **103**, 479-488.

Lynch, J. P. & St.Clair, S. B. (2004) Mineral stress: The missing link in understanding how global climate change will affect plants in real world soils. *Field Crops Research*. **90**, 101-115.

Macarthur, R. & Levins, R. (1967) Limiting similarity, convergence and divergence of coexisting species. *American Naturalist*. **101**, 377-385.

Mackintosh, L. (2001) *Overview of New Zealand climate*. Teaching resources. Retrieved 9 May, 2015, from https://www.niwa.co.nz/education-and-training/schools/resources/climate/overview.

Maire, V., Wright, I. J., Prentice, I. C., Batjes, N. H., Bhaskar, R., Bodegom, P. M., Cornwell, W. K., Ellsworth, D., Niinemets, Ü. & Ordonez, A. (2015) Global effects of soil and climate on leaf photosynthetic traits and rates. *Global Ecology and Biogeography*. **24**, 706-717.

Martin, A. R., Thomas, S. C. & Zhao, Y. (2013) Size-dependent changes in wood chemical traits: A comparison of neotropical saplings and large trees. *AoB PLANTS*. **5**, plt039.

Martz, F., Peltola, R., Fontanay, S., Duval, R. E., Julkunen-Tiitto, R. & Stark, S. (2009) Effect of latitude and altitude on the terpenoid and soluble phenolic composition of juniper (*Juniperus communis*) needles and evaluation of their antibacterial activity in the boreal zone. *Journal of Agricultural and Food Chemistry*. **57**, 9575-9584.

Mason, N. W. H., de Bello, F., Dolezal, J. & Leps, J. (2011) Niche overlap reveals the effects of competition, disturbance and contrasting assembly processes in experimental grassland communities. *Journal of Ecology*. **99**, 788-796.

Mason, N. W. H., Richardson, S. J., Peltzer, D. A., de Bello, F., Wardle, D. A. & Allen, R. B. (2012) Changes in coexistence mechanisms along a long-term soil chronosequence revealed by functional trait diversity. *Journal of Ecology*. **100**, 678-689.

Mayfield, M. M. & Levine, J. M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology letters*. **13**, 1085-1093.

McCormack, M. L., Adams, T. S., Smithwick, E. A. H. & Eissenstat, D. M. (2012) Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist*. **195**, 823-831.

McCully, M. E. (1999) Roots in soil: Unearthing the complexities of roots and their rhizospheres. *Annual Review of Plant Physiology and Plant Molecular Biology*. **50**, 695-718.

McCune, B. & Grace, J. B. (2002) *Analysis of ecological communities*. MjM Software Design, Oregon, USA.

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G. & Yepez, E. A. (2008) Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*. **178**, 719-739.

McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*. **21**, 178-185.

McGlone, M., Walker, S., Hay, R. & Christie, J. (2010a) Climate change, natural systems and their conservation in New Zealand. *Climate change adaptation in New Zealand: Future scenarios and some sectoral perspectives* (eds. R. A. C. Nottage, D. S. Wratt, J. F. Bornman & K. Jones), pp. 82-99. New Zealand Climate Change Centre, Wellington, New Zealand.

McGlone, M. S., Richardson, S. J. & Jordan, G. J. (2010b) Comparative biogeography of New Zealand trees: Species richness, height, leaf traits and range sizes. *New Zealand Journal of Ecology*. **34**, 137-151.

McGlone, M. S., Dungan, R. J., Hall, G. M. & Allen, R. B. (2004) Winter leaf loss in the New Zealand woody flora. *New Zealand Journal of Botany*. **42**, 1-19.

McLaren, R. G. & Cameron, K. C. (1996) *Soil science: Sustainable production and environmental protection* (2nd. ed.). Oxford University Press, Auckland, New Zealand.

McNab, W. H. (1993) A topographic index to quantify the effect of mesoscale landform on site productivity. *Canadian Journal of Forest Research*. **23**, 1100-1107.

McNabb, R. F. R. (1958) The mycorrhizas of some New Zealand plants. Unpublished MSc thesis, University of Otago, Dunedin, New Zealand.

Meinzer, F. C., Clearwater, M. J. & Goldstein, G. (2001) Water transport in trees: Current perspectives, new insights and some controversies. *Environmental and Experimental Botany*. **45**, 239-262.

Meisner, A., Hol, W. H. G., de Boer, W., Krumins, J. A., Wardle, D. A. & van der Putten, W. H. (2014) Plant-soil feedbacks of exotic plant species across life forms: A meta-analysis. *Biological Invasions*. **16**, 2551-2561.

Memmott, J., Craze, P. G., Waser, N. M. & Price, M. V. (2007) Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*. **10**, 710-717.

Menzel, A., Sparks, T. H., Estrella, N. & Roy, D. B. (2006) Altered geographic and temporal variability in phenology in response to climate change. *Global Ecology and Biogeography*. **15**, 498-504.

Messier, J., McGill, B. J. & Lechowicz, M. J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*. **13**, 838-848.

Metson, A. J., Blakemore, L. C. & Rhoades, D. A. (1979) Methods for the determination of soil organic carbon: A review, and application to New Zealand soils. *New Zealand Journal of Science*. **22**, 205-228.

Meurk, C. D. (1984) Bioclimatic zones of the Antipodes: And beyond? *New Zealand Journal of Ecology*. **7**, 175-182.

Middleton, E. M. & Teramura, A. H. (1993) The role of flavonol glycosides and carotenoids in protecting soybean from ultraviolet-B damage. *Plant Physiology*. **103**, 741-752.

Ministry for the Environment (2001) *Climate change impacts on New Zealand.* Publication ME 396. Wellington, New Zealand, New Zealand Government. 39p.

Mokany, K. & Ash, J. (2008) Are traits measured on pot grown plants representative of those in natural communities? *Journal of Vegetation Science*. **19**, 119-126.

Moles, A. T. & Westoby, M. (2003) Latitude, seed predation and seed mass. *Journal of Biogeography*. **30**, 105-128.

Moles, A. T. & Westoby, M. (2004) Seedling survival and seed size: A synthesis of the literature. *Journal of Ecology*. **92**, 372-383.

Moles, A. T., Gruber, M. A. M. & Bonser, S. P. (2008) A new framework for predicting invasive plant species. *Journal of Ecology*. **96**, 13-17.

Moles, A. T., Bonser, S. P., Poore, A. G., Wallis, I. R. & Foley, W. J. (2011a) Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology*. **25**, 380-388.

Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., Pitman, A., Hemmings, F. A. & Leishman, M. R. (2009) Global patterns in plant height. *Journal of Ecology*. **97**, 923-932.

Moles, A. T., Ackerly, D. D., Tweddle, J. C., Dickie, J. B., Smith, R., Leishman, M. R., Mayfield, M. M., Pitman, A., Wood, J. T. & Westoby, M. (2007) Global patterns in seed size. *Global Ecology and Biogeography*. **16**, 109-116.

Moles, A. T., Wallis, I. R., Foley, W. J., Warton, D. I., Stegen, J. C., Bisigato, A. J., Cella-Pizarro, L., Clark, C. J., Cohen, P. S. & Cornwell, W. K. (2011b) Putting plant resistance traits on the map: A test of the idea that plants are better defended at lower latitudes. *New Phytologist*. **191**, 777-788.

Moles, A. T., Peco, B., Wallis, I. R., Foley, W. J., Poore, A. G. B., Seabloom, E. W., Vesk, P. A., Bisigato, A. J., Cella-Pizarro, L., Clark, C. J., Cohen, P. S., Cornwell, W. K., Edwards, W., Ejrnæs, R., Gonzales-Ojeda, T., Graae, B. J., Hay, G., Lumbwe, F. C., Magaña-Rodríguez, B., Moore, B. D., Peri, P. L., Poulsen, J. R., Stegen, J. C., Veldtman, R., von Zeipel, H., Andrew, N. R., Boulter, S. L., Borer, E. T., Cornelissen, J. H. C., Farji-Brener, A. G., DeGabriel, J. L., Jurado, E., Kyhn, L. A., Low, B., Mulder, C. P. H., Reardon-Smith, K., Rodríguez-Velázquez, J., De Fortier, A., Zheng, Z., Blendinger, P. G., Enquist, B. J., Facelli, J. M., Knight, T., Majer, J. D., Martínez-Ramos, M., McQuillan, P. & Hui, F. K. C. (2013) Correlations between physical and chemical defences in plants: Tradeoffs, syndromes, or just many different ways to skin a herbivorous cat? *New Phytologist*. **198**, 252-263.

Moles, A. T., Perkins, S. E., Laffan, S. W., Flores-Moreno, H., Awasthy, M., Tindall, M. L., Sack, L., Pitman, A., Kattge, J., Aarssen, L. W., Anand, M., Bahn, M., Blonder, B., Cavender-Bares, J., Cornelissen, J. H. C., Cornwell, W. K., Diaz, S., Dickie, J. B., Freschet, G. T., Griffiths, J. G., Gutierrez, A. G., Hemmings, F. A., Hickler, T., Hitchcock, T. D., Keighery, M., Kleyer, M., Kurokawa, H., Leishman, M. R., Liu, K. W., Niinemets, U., Onipchenko, V., Onoda, Y., Penuelas, J., Pillar, V. D., Reich, P. B., Shiodera, S., Siefert, A., Sosinski, E. E., Soudzilovskaia, N. A., Swaine, E. K., Swenson, N. G., van Bodegom, P. M., Warman, L., Weiher, E., Wright, I. J., Zhang, H. X., Zobel, M. & Bonser, S. P. (2014) Which is a better predictor of plant traits: Temperature or precipitation? *Journal of Vegetation Science*. **25**, 1167-1180.

Molloy, L. (1998) *Soils in the New Zealand landscape: The living mantle* (2nd ed.). New Zealand Society of Soil Science, Lincoln, New Zealand.

Mouradov, A., Cremer, F. & Coupland, G. (2002) Control of flowering time: Interacting pathways as a basis for diversity. *Plant Cell*. **14**, S111-S130.

Muller-Landau, H. C. (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*. **36**, 20-32.

Murray, B. R. & Gill, A. M. (2001) A comparative study of interspecific variation in fruit size among Australian eucalypts. *Ecography*. **24**, 651-658.

Murray, B. R., Brown, A. H. D. & Grace, J. P. (2003) Geographical gradients in seed size among and within perennial Australian *Glycine* species. *Australian Journal of Botany*. **51**, 47-57.

Murray, B. R., Brown, A., Dickman, C. & Crowther, M. (2004) Geographical gradients in seed mass in relation to climate. *Journal of Biogeography*. **31**, 379-388.

Murray, M., Cannell, M. & Smith, R. (1989) Date of budburst of fifteen tree species in Britain following climatic warming. *Journal of Applied Ecology*. **26**, 693-700.

Newsham, K., Fitter, A. & Watkinson, A. (1995) Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends in Ecology & Evolution*. **10**, 407-411.

Niinemets, Ü. (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*. **82**, 453-469.

Niklas, K. J. (1999) The mechanical role of bark. *American Journal of Botany*. **86**, 465-469.

Niklas, K. J. (2007) Maximum plant height and the biophysical factors that limit it. *Tree Physiology*. **27**, 433-440.

Norton, D. A. (1998) *Impacts of tree coring on indigenous trees.* Conservation Advisory Science Notes No. 186. Wellington, New Zealand, Department of Conservation. 6p.

Novotny, V., Drozd, P., Miller, S. E., Kulfan, M., Janda, M., Basset, Y. & Weiblen, G. D. (2006) Why are there so many species of herbivorous insects in tropical rainforests? *Science*. **313**, 1115-1118.

Nychka, D., Reinhard, F. & Stephan, S. (2015) *Fields: Tools for Spatial Data*. R package version 8.2-1. Retrieved 25 March 2015 from http://cran.r-project.org/web/packages/fields/index.html.

Ogden, J., Fordham, R., Pilkington, S. & Serra, R. (1991) Forest gap formation and closure along an altitudinal gradient in Tongariro National Park, New Zealand. *Journal of Vegetation Science*. **2**, 165-172.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. & Wagner, H. (2011) *Vegan: Community Ecology Package*. R package version 2.0-2. Retrieved 25 March 2015 from http:/CRAN.R-project.org/package=vegan.

Olmo, M., Lopez-Iglesias, B. & Villar, R. (2014) Drought changes the structure and elemental composition of very fine roots in seedlings of ten woody tree species. Implications for a drier climate. *Plant and Soil*. **384**, 113-129.

Ordonez, A. & Olff, H. (2013) Do alien plant species profit more from high resource supply than natives? A trait-based analysis. *Global Ecology and Biogeography*. **22**, 648-658.

Ordonez, J. C., van Bodegom, P. M., Witte, J. P. M., Wright, I. J., Reich, P. B. & Aerts, R. (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*. **18**, 137-149.

Osunkoya, O. O., Sheng, T. K., Mahmud, N. A. & Damit, N. (2007) Variation in wood density, wood water content, stem growth and mortality among twenty-seven tree species in a tropical rainforest on Borneo Island. *Austral Ecology*. **32**, 191-201.

Owen-Smith, N. & Cooper, S. M. (1987) Palatability of woody plants to browsing ruminants in a South African savanna. *Ecology*. **68**, 319-331.

Paine, C. E. T., Stahl, C., Courtois, E. A., Patiño, S., Sarmiento, C. & Baraloto, C. (2010) Functional explanations for variation in bark thickness in tropical rain forest trees. *Functional Ecology*. **24**, 1202-1210.

Palmer, M. A., Ambrose, R. F. & Poff, N. L. (1997) Ecological theory and community restoration ecology. *Restoration Ecology*. **5**, 291-300.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*. **421**, 37-42.

Payton, I. J., Newell, C. L. & Beets, P. N. (2004) *New Zealand Carbon Monitoring System: Indigenous forest and shrubland data collection manual.* Report prepared for New Zealand Climate Change Office. Christchurch, New Zealand, Ministry for the Environment. 68p.

Peco, B., Carmona, C. P., de Pablos, I. & Azcárate, F. M. (2012) Effects of grazing abandonment on functional and taxonomic diversity of Mediterranean grasslands. *Agriculture, Ecosystems & Environment*. **152**, 27-32.

Peltzer, D. A., Wardle, D. A., Allison, V. J., Baisden, W. T., Bardgett, R. D., Chadwick, O. A., Condron, L. M., Parfitt, R. L., Porder, S., Richardson, S. J., Turner, B. L., Vitousek, P. M., Walker, J. & Walker, L. R. (2010) Understanding ecosystem retrogression. *Ecological Monographs*. **80**, 509-529.

Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N., Funes, G., Quetier, F., Hodgson, J. G., Thompson, K., Morgan, H. D., ter Steege, H., van der Heijden, M. G. A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A. C., Aquino, S. & Cornelissen, J. H. C. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*. **61**, 167-234.

Perry, G. L. W., Wilmshurst, J. M. & McGlone, M. S. (2014) Ecology and long-term history of fire in New Zealand. *New Zealand Journal of Ecology*. **38**, 157-176.

Petanidou, T., Kallimanis, A. S., Sgardelis, S. P., Mazaris, A. D., Pantis, J. D. & Waser, N. M. (2014) Variable flowering phenology and pollinator use in a community suggest future phenological mismatch. *Acta Oecologica*. **59**, 104-111.

Pfanz, H., Aschan, G., Langenfeld-Heyser, R., Wittmann, C. & Loose, M. (2002) Ecology and ecophysiology of tree stems: Corticular and wood photosynthesis. *Naturwissenschaften*. **89**, 147-162.

Poorter, L. (2008) The relationships of wood-, gas-and water fractions of tree stems to performance and life history variation in tropical trees. *Annals of Botany*. **102**, 367-375.

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J. C., Peña‐Claros, M., Sterck, F., Villegas, Z. & Sass‐Klaassen, U. (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist*. **185**, 481-492.

Poorter, L., McNeil, A., Hurtado, V.-H., Prins, H. H. T. & Putz, F. E. (2014) Bark traits and life-history strategies of tropical dry- and moist forest trees. *Functional Ecology*. **28**, 232-242.

Powell, C. L. (1974) Effect of P fertilizer on root morphology and P uptake of *Carex coriacea*. *Plant and Soil*. **41**, 661-667.

Pratt, R. B., Jacobsen, A. L., Ewers, F. W. & Davis, S. D. (2007) Relationships among xylem transport, biomechanics and storage in stems and roots of nine Rhamnaceae species of the California chaparral. *New Phytologist*. **174**, 787-789.

Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A. & Solomon, A. M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*. **19**, 117-134.

Primack, D., Imbres, C., Primack, R. B., Miller-Rushing, A. J. & Del Tredici, P. (2004) Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany*. **91**, 1260-1264.

Putz, F. E., Coley, P. D., Lu, K., Montalvo, A. & Aiello, A. (1983) Uprooting and snapping of trees: Structural determinants and ecological consequences. *Canadian Journal of Forest Research*. **13**, 1011-1020.

R Development Core Team (2014) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing Vienna, Austria. Retrieved 20 August 2014 from http://www.R-project.org/.

Rathcke, B. & Lacey, E. P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*. **16**, 179-214.

Reich, P. B. (2014) The world‐wide ‘fast‐slow’ plant economics spectrum: A traits manifesto. *Journal of Ecology*. **102**, 275-301.

Reich, P. B. & Oleksyn, J. (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America*. **101**, 11001-11006.

Reich, P. B., Tjoelker, M. G., Walters, M. B., Vanderklein, D. W. & Bushena, C. (1998) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology*. **12**, 327-338.

Reich, P. B., Wright, I.J., Cavender-Bares, J., Craine, M., Oleksyn, J., Westoby, M., Walters, M.B. (2003) The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences*. **164**, S143–S164.

Richardson, S., Peltzer, D., Allen, R., McGlone, M. & Parfitt, R. (2004) Rapid development of phosphorus limitation in temperate rainforest along the Franz Josef soil chronosequence. *Oecologia*. **139**, 267-276.

Richardson, S. J., Allen, R. B. & Doherty, J. E. (2008) Shifts in leaf N : P ratio during resorption reflect soil P in temperate rainforest. *Functional Ecology*. **22**, 738-745.

Richardson, S. J., Allen, R. B., Buxton, R. P., Easdale, T. A., Hurst, J. M., Morse, C. W., Smissen, R. D. & Peltzer, D. A. (2013) Intraspecific relationships among wood density, leaf structural traits and environment in four co-occurring species of *Nothofagus* in New Zealand. *PloS One*. **8**, e58878.

Roberts, M. R. & Paul, N. D. (2006) Seduced by the dark side: Integrating molecular and ecological perspectives on the influence of light on plant defence against pests and pathogens. *New Phytologist*. **170**, 677-699.

Romero, C. & Bolker, B. M. (2008) Effects of stem anatomical and structural traits on responses to stem damage: An experimental study in the Bolivian Amazon. *Canadian Journal of Forest Research*. **38**, 611-618.

Rosell, J. A., Gleason, S., Méndez ‐ Alonzo, R., Chang, Y. & Westoby, M. (2014) Bark functional ecology: Evidence for tradeoffs, functional coordination, and environment producing bark diversity. *New Phytologist*. **201**, 486-497.

Rosenzweig, C. & Parry, M. L. (1994) Potential impact of climate change on world food supply. *Nature*. **367**, 133-138.

Rowe, N. & Speck, T. (2005) Plant growth forms: An ecological and evolutionary perspective. *New Phytologist*. **166**, 61-72.

Rustad, L. E., Campbell, J. L., Marion, G., Norby, R., Mitchell, M., Hartley, A., Cornelissen, J. & Gurevitch, J. (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*. **126**, 543-562.

Ryan, M. G. & Yoder, B. J. (1997) Hydraulic limits to tree height and tree growth. *Bioscience*. **47**, 235-242.

Ryan, M. G., Phillips, N. & Bond, B. J. (2006) The hydraulic limitation hypothesis revisited. *Plant, Cell & Environment*. **29**, 367-381.

Saito, T. & Terashima, I. (2004) Reversible decreases in the bulk elastic modulus of mature leaves of deciduous *Quercus* species subjected to two drought treatments. *Plant, Cell & Environment*. **27**, 863-875.

Sakai, A. (1979) Freezing avoidance mechanism of primordial shoots of conifer buds. *Plant and Cell Physiology*. **20**, 1381-1390.

Salisbury, E. (1949) Leaf form and function. *Nature*. **163**, 515-518.

Salmon, J. T. (1985) *Collins guide to the alpine plants of New Zealand* (Revised ed.). Collins, Auckland, New Zealand.

Sanchez-Gomez, D., Robson, T. M., Gasco, A., Gil-Pelegrin, E. & Aranda, I. (2013) Differences in the leaf functional traits of six beech (*Fagus sylvatica* L.) populations are reflected in their response to water limitation. *Environmental and Experimental Botany*. **87**, 110-119.

Sandel, B., Corbin, J. D. & Krupa, M. (2011) Using plant functional traits to guide restoration: A case study in California coastal grassland. *Ecosphere*. **2**, UNSP 23.

Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M. & Roy, K. (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology, Evolution, and Systematics*. **40**, 245-269.

Schimper, A. F. W. (1903) *Plant-geography upon a physiological basis*. Clarendon Press, Oxford, UK.

Scholz, F. G., Bucci, S. J., Goldstein, G., Meinzer, F. C., Franco, A. C. & Miralles-Wilhelm, F. (2007) Biophysical properties and functional significance of stem water storage tissues in Neotropical savanna trees. *Plant Cell and Environment*. **30**, 236-248.

Schulze, E. D., Turner, N. C., Nicolle, D. & Schumacher, J. (2006) Leaf and wood carbon isotope ratios, specific leaf areas and wood growth of *Eucalyptus* species across a rainfall gradient in Australia. *Tree Physiology*. **26**, 479-492.

Seastedt, T. R., Hobbs, R. J. & Suding, K. N. (2008) Management of novel ecosystems: Are novel approaches required? *Frontiers in Ecology and the Environment*. **6**, 547-553.

Secchi, F. & Zwieniecki, M. A. (2011) Sensing embolism in xylem vessels: The role of sucrose as a trigger for refilling. *Plant Cell and Environment*. **34**, 514-524.

Shigo, A. L. (1984) Compartmentalization: A conceptual framework for understanding how trees grow and defend themselves. *Annual Review of Phytopathology*. **22**, 189-214.

Shipley, B., Vile, D. & Garnier, E. (2006) From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science*. **314**, 812-814.

Shipley, B., Laughlin, D. C., Sonnier, G. & Otfinowski, R. (2011) A strong test of a maximum entropy model of trait-based community assembly. *Ecology*. **92**, 507-517.

Sinclair, M. R., Wratt, D. S., Henderson, R. D. & Gray, W. R. (1997) Factors affecting the distribution and spillover of precipitation in the Southern Alps of New Zealand: A case study. *Journal of Applied Meteorology*. **36**, 428-442.

Singh, P., Fenemore, P. G., Dugdale, J. S. & Russell, G. B. (1978) The insecticidal activity of foliage from New Zealand conifers. *Biochemical Systematics and Ecology*. **6**, 103-106.

Siska, E. L., Pennings, S. C., Buck, T. L. & Hanisak, M. D. (2002) Latitudinal variation in palatability of salt-marsh plants: Which traits are responsible? *Ecology*. **83**, 3369-3381.

Smith, T. & Huston, M. (1989) A theory of the spatial and temporal dynamics of plant communities. *Vegetatio*. **83**, 49-69.

Society for Ecological Restoration International Science & Policy Working Group (2004) *The SER International Primer on Ecological Restoration*. www.ser.org & Tucson, Society for Ecological Restoration International. 13p.

Sparks, T. H., Jeffree, E. P. & Jeffree, C. E. (2000) An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *International Journal of Biometeorology*. **44**, 82-87.

Sparks, T. H., Mizera, T., Wójtowicz, W. & Tryjanowski, P. (2012) Synchrony in the phenology of a culturally iconic spring flower. *International Journal of Biometeorology*. **56**, 407-409.

Spasojevic, M. J., Yablon, E. A., Oberle, B. & Myers, J. A. (2014) Ontogenetic trait variation influences tree community assembly across environmental gradients. *Ecosphere*. **5**, Article no. 129.

Sperry, J. S. & Sullivan, J. E. M. (1992) Xylem embolism in response to freeze-thaw cycles and water-stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiology*. **100**, 605-613.

Sperry, J. S., Nichols, K. L., Sullivan, J. E. M. & Eastlack, S. E. (1994) Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology*. **75**, 1736-1752.

Stark, S., Julkunen-Tiitto, R., Holappa, E., Mikkola, K. & Nikula, A. (2008) Concentrations of foliar quercetin in natural populations of white birch (*Betula pubescens*) increase with latitude. *Journal of Chemical Ecology*. **34**, 1382-1391.

Steinbauer, M. J. (2010) Latitudinal trends in foliar oils of eucalypts: Environmental correlates and diversity of chrysomelid leaf ‐ beetles. *Austral Ecology*. **35**, 204-213.

Stephens, P., Smith, B. & Lincoln, R. (2007) New Zealand: Forest carbon reporting and the role of forests in climate change policy. *Forests, Carbon and Climate Change Local and International Perspectives COFORD Conference* (eds. E. Hendrick & K. G. Black), pp. 9-13. COFORD, National Council for Forest Research and Development, Dublin, Ireland.

Suding, K. N. (2011) Toward an era of restoration in ecology: Successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics*. **42**, 465-487.

Suding, K. N. & Goldstein, L. J. (2008) Testing the Holy Grail framework: Using functional traits to predict ecosystem change. *New Phytologist*. **180**, 559-562.

Sumbele, S., Fotelli, M. N., Nikolopoulos, D., Tooulakou, G., Liakoura, V., Liakopoulos, G., Bresta, P., Dotsika, E., Adams, M. A. & Karabourniotis, G. (2012) Photosynthetic capacity is negatively correlated with the concentration of leaf phenolic compounds across a range of different species. *AoB PLANTS*. **2012**, pls025.

Swenson, N. G. & Enquist, B. J. (2007) Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*. **94**, 451-459.

Taiz, L. & Zeiger, E. (2002) *Plant physiology* (5th ed.). Sinauer Associates, Sunderland, MA.

Tanentzap, A. J., Lee, W. G., Dugdale, J. S., Patrick, B. P., Fenner, M., Walker, S. & Coomes, D. A. (2011) Differential responses of vertebrate and invertebrate herbivores to traits of New Zealand subalpine shrubs. *Ecology*. **92**, 994-999.

ter Steege, H., Pitman, N. C. A., Phillips, O. L., Chave, J., Sabatier, D., Duque, A., Molino, J.-F., Prevost, M.-F., Spichiger, R., Castellanos, H., von Hildebrand, P. & Vasquez, R. (2006) Continental-scale patterns of canopy tree composition and function across Amazonia. *Nature*. **443**, 444-447.

ter Steege, H. H., D. S. (2001) Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology*. **82**, 3197-3212.

Thompson, L. G., Mosley-Thompson, E., Davis, M. E. & Brecher, H. H. (2011) Tropical glaciers, recorders and indicators of climate change, are disappearing globally. *Annals of Glaciology*. **52**, 23-34.

Thorpe, A. S. & Stanley, A. G. (2011) Determining appropriate goals for restoration of imperilled communities and species. *Journal of Applied Ecology*. **48**, 275-279.

Thuiller, W., Albert, C., Araujo, M. B., Berry, P. M., Cabeza, M., Guisan, A., Hickler, T., Midgely, G. F., Paterson, J., Schurr, F. M., Sykes, M. T. & Zimmermann, N. E. (2008) Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology Evolution and Systematics*. **9**, 137-152.

Trockenbrodt, M. (1990) Survey and discussion of the terminology used in bark anatomy. *IAWA Bulletin*. **11**, 141-166.

Tyree, M. T. & Zimmermann, M. H. (2002) *Xylem structure and the ascent of sap* (2nd ed.). Springer-Verlag, Berlin, Germany.

Urban, M. C. (2015) Accelerating extinction risk from climate change. *Science*. **348**, 571-573.

Valverde-Barrantes, O. J., Smemo, K. A. & Blackwood, C. B. (2014) Fine root morphology is phylogenetically structured, but nitrogen is related to the plant economics spectrum in temperate trees. *Functional Ecology*. **29**, 796-807.

Van Buuren, S. & Groothuis-Oudshoorn, K. (2011) mice: Multivariate Imputation by Chained Equations in R. *Journal of Statistical Software*. **45**, 1-67.

Van der Putten, W. H., Macel, M. & Visser, M. E. (2010) Predicting species distribution and abundance responses to climate change: Why it is essential to include biotic interactions across trophic levels. *Philosophical Transactions of the Royal Society: Biological Sciences*. **365**, 2025-2034.

Van der Putten, W. H., Bardgett, R. D., Bever, J. D., Bezemer, T. M., Casper, B. B., Fukami, T., Kardol, P., Klironomos, J. N., Kulmatiski, A., Schweitzer, J. A., Suding, K. N., Van de Voorde, T. F. J. & Wardle, D. A. (2013) Plant-soil feedbacks: The past, the present and future challenges. *Journal of Ecology*. **101**, 265-276.

Van Noordwijk, M., Martikainen, P., Bottner, P., Cuevas, E., Rouland, C. & Dhillion, S. S. (1998) Global change and root function. *Global Change Biology*. **4**, 759-772.

Van Rees, K. (2006) Forest ecosystems: Soils associated with major. *Encyclopedia of Soil Science* (Vol. 1) (ed. R. Lal), pp. 722 - 724. Taylor & Francis, New York, NY.

Vance, C. P. (2001) Symbiotic nitrogen fixation and phosphorus acquisition: Plant nutrition in a world of declining renewable resources. *Plant Physiology*. **127**, 390-397.

Veblen, T. T. & Stewart, G. H. (1982) On the conifer regeneration gap in New Zealand: The dynamics of *Libocedrus bidwillii* stands on South Island. *Journal of Ecology*. **70**, 413-436.

Vellend, M. (2010) Conceptual synthesis in community ecology. *The Quarterly Review of Biology*. **85**, 183-206.

Verkaik, E. & Braakhekke, W. G. (2007) Kauri trees (*Agathis australis*) affect nutrient, water and light availability for their seedlings. *New Zealand Journal of Ecology*. **31**, 39-46.

Verkaik, E., Berendse, F. & Gardner, R. O. (2007) Low soil water and nutrient availability below New Zealand kauri (*Agathis australis* (D. Don) Lindl.) trees increase the relative fitness of kauri seedlings. *Plant Ecology*. **191**, 163-170.

Veteli, T. O., Kuokkanen, K., Julkunen ‐ Tiitto, R., Roininen, H. & Tahvanainen, J. (2002) Effects of elevated CO_2 and temperature on plant growth and herbivore defensive chemistry. *Global Change Biology*. **8**, 1240-1252.

Vines, R. (1968) Heat transfer through bark, and the resistance of trees to fire. *Australian Journal of Botany*. **16**, 499-514.

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*. **116**, 882-892.

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V. & Messier, J. (2012) The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology & Evolution*. **27**, 244-252.

Vitousek, P. M., Turner, D. R. & Kitayama, K. (1995) Foliar nutrients during long-term soil development in Hawaiian montane rain forest. *Ecology*. **76**, 712-720.

Vitousek, P. M., Aplet, G., Turner, D. & Lockwood, J. J. (1992) The Mauna Loa environmental matrix: Foliar and soil nutrients. *Oecologia*. **89**, 372-382.

Vitt, P., Havens, K. & Hoegh-Guldberg, O. (2009) Assisted migration: Part of an integrated conservation strategy. *Trends in Ecology & Evolution*. **24**, 473-474.

Vitt, P., Havens, K., Kramer, A. T., Sollenberger, D. & Yates, E. (2010) Assisted migration of plants: Changes in latitudes, changes in attitudes. *Biological Conservation*. **143**, 18-27.

Wainhouse, D., Ashburner, R., Ward, E. & Rose, J. (1998) The effect of variation in light and nitrogen on growth and defence in young Sitka Spruce. *Functional Ecology*. **12**, 561-572.

Wang, B. & Qiu, Y.-L. (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza*. **16**, 299-363.

Wardle, D. A., Jonsson, M., Bansal, S., Bardgett, R. D., Gundale, M. J. & Metcalfe, D. B. (2012) Linking vegetation change, carbon sequestration and biodiversity: Insights from island ecosystems in a long-term natural experiment. *Journal of Ecology*. **100**, 16-30.

Wardle, J. (1984) *The New Zealand Beeches*. New Zealand Forest Service, Wellington, New Zealand.

Wardle, P. (1964) Facets of the distribution of forest vegetation in New Zealand. *New Zealand Journal of Botany*. **2**, 352-366.

Wardle, P. (1991) *Vegetation of New Zealand*. Cambridge University Press, Cambridge, UK.

Wardle, P. & Lee, W. G. (1990) Environmental and floristic gradients in Westland, New Zealand and the discontinuous distribution of *Nothofagus*: Comment. *New Zealand Journal of Botany*. **28**, 479-481.

Webb, C. & Kelly, D. (1993) The reproductive biology of the New Zealand flora. *Trends in Ecology & Evolution*. **8**, 442-447.

Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I. & Poff, N. L. (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters*. **13**, 267-283.

Webb, E. L., van de Bult, M., Fa'aumu, S., Webb, R. C., Tualaulelei, A. & Carrasco, L. R. (2014) Factors affecting tropical tree damage and survival after catastrophic wind disturbance. *Biotropica*. **46**, 32-41.

Webb, L. J. (1959) A physiognomic classification of Australian rain forests. *Journal of Ecology*. **47**, 551-570.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999) Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science*. **10**, 609-620.

Weiher, E. K., P. A. (1995) Assembly rules, null models, and trait dispersion: New questions from old patterns. *Oikos*. **74**, 159-164.

Wells, A., Duncan, R. P. & Stewart, G. H. (2001) Forest dynamics in Westland, New Zealand: The importance of large, infrequent earthquake-induced disturbance. *Journal of Ecology*. **89**, 1006-1018.

Westerling, A. L., Hidalgo, H. G., Cayan, D. R. & Swetnam, T. W. (2006) Warming and earlier spring increase western US forest wildfire activity. *Science*. **313**, 940-943.

Westoby, M. & Wright, I. J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology & Evolution*. **21**, 261-268.

Westoby, M., Jurado, E. & Leishman, M. (1992) Comparative evolutionary ecology of seed size. *Trends in Ecology & Evolution*. **7**, 368-372.

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. & Wright, I. J. (2002) Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*. **33**, 125.

White, P. S. & Walker, J. L. (1997) Approximating nature’s variation: Selecting and using reference information in restoration ecology. *Restoration Ecology*. **5**, 338-349.

Whitehead, D., Leathwick, J. & Hobbs, J. (1992) How will New Zealand’s forests respond to climate change? Potential changes in response to increasing temperature. *New Zealand Journal of Forestry Science*. **22**, 39-53.

Wiemann, M. C. W., G. B. (2002) Geographic variation in wood specific gravity: Effects of latitude, temperature, and precipitation. *Wood and Fiber Science*. **34**, 96-107.

Williams, J. & Eamus, D. (1997) Plant ecophysiology: Linking pattern and process. A review. *Australian Journal of Botany*. **45**, 351-357.

Williamson, G. B. & Wiemann, M. C. (2010) Measuring wood specific gravity...Correctly. *American Journal of Botany*. **97**, 519-524.

Wilson, H. D. (1994) *Field guide: Stewart Island plants*. Manuka Press, Christchurch, New Zealand.

Wiser, S. K., Hurst, J. M., Wright, E. F. & Allen, R. B. (2011) New Zealand's forest and shrubland communities: A quantitative classification based on a nationally representative plot network. *Applied Vegetation Science*. **14**, 506-523.

Wolkovich, E. M. & Ettinger, A. K. (2014) Back to the future for plant phenology research. *New Phytologist*. **203**, 1021-1024.

Wolkovich, E. M. & Cleland, E. E. (2014) Phenological niches and the future of invaded ecosystems with climate change. *AoB PLANTS*. **6**, plu013.

Woodward, F. I. & McKee, I. F. (1991) Vegetation and climate. *Environment International*. **17**, 535-546.

Wright, D. M., Jordan, G. J., Lee, W. G., Duncan, R. P., Forsyth, D. M. & Coomes, D. A. (2010) Do leaves of plants on phosphorus ‐ impoverished soils contain high concentrations of phenolic defence compounds? *Functional Ecology*. **24**, 52-61.

Wright, I. J. & Westoby, M. (1999) Differences in seedling growth behaviour among species: Trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *Journal of Ecology*. **87**, 85-97.

Wright, I. J., Ackerly, D. D., Bongers, F., Harms, K. E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Paz, H. & Pitman, N. C. (2007) Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals of Botany*. **99**, 1003-1015.

Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Groom, P. K., Hikosaka, K., Lee, W., Lusk, C. H., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Warton, D. I. & Westoby, M. (2005a) Modulation of leaf economic traits and trait relationships by climate. *Global Ecology & Biogeography*. **14**, 411-421.

Wright, I. J., Reich, P. B., Cornelissen, J. H. C., Falster, D. S., Garnier, E., Hikosaka, K., Byron, B. L., Lee, W., Oleksyn, J., Osada, N., Poorter, H., Villar, R., Warton, D. I. & Westoby, M. (2005b) Assessing the generality of global leaf trait relationships. *New Phytologist*. **166**, 485-496.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M. L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas, S. C., Tjoelker, M. G., Veneklaas, E. J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature*. **428**, 821-827.

Wyse, S. V., Burns, B. R. & Wright, S. D. (2014) Distinctive vegetation communities are associated with the long ‐ lived conifer *Agathis australis* (New Zealand kauri, Araucariaceae) in New Zealand rainforests. *Austral Ecology*. **39**, 388-400.

Yang, Z., Sinclair, T. R., Zhu, M., Messina, C. D., Cooper, M. & Hammer, G. L. (2012) Temperature effect on transpiration response of maize plants to vapour pressure deficit. *Environmental and Experimental Botany*. **78**, 157-162.

Zimmerman, J. K., Everham, E. M., Waide, R. B., Lodge, D. J., Taylor, C. M. & Brokaw, N. V. L. (1994) Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: Implications for tropical tree life histories. *Journal of Ecology*. **82**, 911-922.

Zotov, V. D. (1938) Some correlations between vegetation and climate in New Zealand. *New Zealand Journal of Science and Technology*. **19**, 474-487.