FACTORS INFLUENCING FUTURE CANOPY COMPOSITION AT TIROMOANA BUSH, NORTH CANTERBURY, NEW ZEALAND

A THESIS

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by

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Abstract

The purpose of this study was to investigate seedling recruitment beneath kanuka forest at Tiromoana Bush, North Canterbury. The regeneration of broadleaved tree species is evident throughout Tiromoana Bush. This research aimed to quantify the biotic and abiotic factors influencing the distribution of small and large seedlings of canopy tree species, their relative growth rates, their survival, abundance and composition throughout the forest understorey of Tiromoana Bush. Tiromoana Bush is a forest restoration area of 410 hectares adjacent to the Kate Valley landfill.

To determine the future tree species composition at Tiromoana Bush, seedling recruitment, growth and survival was quantified through remeasuring tagged seedlings in 26 permanent vegetation monitoring plots located in the major forest patches at Tiromoana Bush. In addition, seedling data from 78 temporary vegetation survey plots established in three major forest patches were used to assess the influence of different factors on seedling abundance.

At Tiromoana Bush, the most common canopy tree species as seedlings in the permanent vegetation monitoring plots was mahoe followed by fivefinger. Mahoe seedling density was significantly affected by canopy openness, distance to seed sources, light index, shrub cover and slope, but not by aspect, basal area and time. For fivefinger, seedlings increased in abundance with time, but the difference was not statistically significant. The relative growth rate of mahoe in the 20-49cm height class (in which most seedlings occurred) was significantly affected by shrub cover, light index and canopy openness. Mahoe seedling recruits were significantly affected by light index and canopy openness. Survivability of mahoe was affected by aspect. For fivefinger, individual relative growth rates were significantly affected by canopy openness and light index.

Similar results were found for tree species seedlings present in the temporary survey plots provided with mahoe and fivefinger again the most common species, followed by kohuhu. Light index significantly affected golden akeake small seedlings as well as canopy openness. Light index significantly affected ngaio large seedling distribution. Aspect was the only significant factor for kohuhu large seedling distribution. Distance from seed sources significantly affected fivefinger small seedling distribution as seedlings are dependent upon dispersal away from the parent trees. Slope significantly affected the distribution of red matipou small seedlings.

The most important environmental attribute influencing seedling abundance is light. This is evident in both the permanent seedling monitoring plots and the temporary vegetation survey plots. Based on data from the temporary vegetation survey plots, mahoe, fivefinger and kohuhu are most abundant suggesting that these three canopy tree species will dominate the forest canopy at Tiromoana Bush once the kanuka starts to senesce.

Keywords: Seedling Recruitment; Seedling Abundance; Light; Small Seedlings; Large Seedlings; Tiromoana Bush

Thesis Layout

Chapter One:	Provides an overview of forest dynamics, and its role in forest development and succession. Impacts of land clearing in the lowlands for agricultural development are discussed, along with remediation of forest in these lands. The thesis goals and objectives conclude this chapter.
Chapter Two:	Describes Tiromoana Bush and the Tiromoana Bush Restoration Project Management Plan, outlining the major goals and objectives for achieving successful restoration of indigenous vegetation at Tiromoana Bush.
Chapter Three:	An outline of the methods used in this thesis determining the future forest canopy composition at Tiromoana Bush, and the factors contributing or limiting the future canopy composition at Tiromoana Bush.
Chapter Four:	Describes the results found at Tiromoana Bush. Relative growth rates, number of recruits, survival, tree species abundance and species composition are discussed.
Chapter Five:	Provides an overall evaluation on the findings of the results: restoration implications; study limitations and areas for further research.
Chapter Six:	Summarises the major findings of this study and provides an outline of the future strategies for restoration based on the Tiromoana Bush Project Management Plan.

Chapter One: Introduction

1.1. Overview

The main thrust of this research is to gain an understanding of the dynamics of a regenerating forest. Future forest canopies are influenced by both biotic and abiotic factors that influence species enabling to establish beneath the existing forest canopy, whether this be an old-growth canopy or a young regenerating (seral) canopy. Seedling establishment, growth and survival are the key stages influencing future canopy composition and are influenced by a host of abiotic and biotic factors including light (Raich and Gong, 1990; Nicotra *et al*. 1999), soil moisture and nutrients (Itoh, 1995; Brearley *et al*. 2003), litter fall and cover (Aide, 1987; Molofsky and Augspurger, 1992; Hammond, 1995), seed dispersal (Howe and Schupp, 1985; Webb and Peart, 2001), seed and seedling predation, herbivory and pathogen attack (Molofsky and Fisher, 1993; Hulme, 1996; Notman and Gorchov, 2001) and competition from established vegetation (Denslow *et al*. 1991; Wang and Augspurger, 2004).

Development of ecologically sound strategies for conservation management of forests requires a good knowledge of forest dynamics, succession and regeneration (Dupuy and Chazdon, 2008). This is particularly important when considering the future development of a regenerating forest that has established as part of a restoration project. Environmental factors that differentially affect the recruitment and mortality of seedlings of forest tree species contribute to the diversity of regeneration niches thus ultimately affecting community composition and hence plant diversity in the future forest (Grubb, 1977; Harper, 1977). The number of seedlings that are present in the forest understorey and their growth and survival rates determine the number of saplings that will potentially be available to replace trees lost through natural mortality (James, 1998) and through disturbance events, such as landslides or wind-throw. The large spatial and temporal scales at which these replacement processes function requires long-term studies at the landscape scale (Dupuy and Chazdon, 2008).

The great losses of indigenous forest cover as a result of expanding agricultural lands leads to significant reductions and possibly extinctions of native plants and animals. In many temperate areas worldwide, natural lowland forests have been fragmented during extensive agricultural development (Burns *et al*. 2011). An example of this is happening here in New Zealand. In New Zealand, agriculture has been one of the greatest causes of land use change and habitat destruction (Morad and Jay, 2000). Before European settlement in New Zealand, areas associated with the highest biodiversity were the coastal lowlands (Morad and Jay, 2000) where agriculture is now most intense. Recognition of land-use history, particularly the type of agriculture used, is important regarding land-use changes. This phenomenon is likely to affect future forest composition, in particular in areas when agriculture later ceases (Foster *et al*. 2003). At stand to landscape scales, differences in land-use history influence modern vegetation patterns (Zimmerman *et al*. 1995; Motzkin *et al*. 1999a, 1999b). Currently, most of the land below 300 m is privately owned, and contains only fragments of the original vegetation (Morad and Jay, 2000; Burns *et al*. 2011).

Loss of natural forest in New Zealand has been greatest on the lowlands. In these areas, almost all of the forest that remains is on private land in small fragments or remnants. The loss of natural forest in New Zealand occurred during both Polynesian and European settlement, as a result of fire and forest harvesting or felling. Recent evidence suggests that the pre-human vegetation in lowland environments included podocarp forests and other woody species (Clark *et al*. 1996). With the current conflicting issues around agriculture and sustaining native biodiversity, the need for environmental planners to encourage landowners and farmers to retain all areas of native vegetation, or in part, is crucial to allow for survival of some of the native flora present in the lowlands (Morad and Jay, 2000). In New Zealand, management actions such as fencing and control of invasive pests and weeds are likely to reduce threats to indigenous biodiversity through preventing grazing and trampling damage by livestock (Burns *et al.* 2000; Smale *et al*. 2005). Studies encompassing the exclusion of livestock form fragments in New Zealand reported that change in understorey composition is evident, there is a decreased number of adventive species and there are increases in richness of indigenous species and in tree seedling and sapling numbers (Timmins, 2002; Smale *et al*. 2005; Dodd and Power, 2007).

1.2. Review of Forest Dynamics in Relation to Forest Canopy Development

Understanding how forest species are able to colonise disturbed areas, either naturally or via human intervention, is important for restoration ecology. The review below addresses the components of natural forest regeneration and how limitations of these components may arrest future canopy development. In particular, the review provides insight to forest regeneration in areas initially used for farming practices but are now regenerating back into native forest. In New Zealand, agriculture over the past 1150 years has been prominent on the lowlands, resulting in large losses of indigenous flora and fauna (McGlone, 1989; Wilmshurst *et al*. 2004). Ex-pasture sites, known as old-field sites, are known to provide habitat for regenerating native species otherwise restricted to small remnants in fragmented agricultural landscapes (Standish *et al*. 2009). Since European settlement, abandonment of farmland occurred during times of depression and abolition of subsidies during the late 1980s (Standish *et al*. 2009). The removal of agricultural subsidies in the late 1980s meant that substantial areas of farmland had become less attractive for farming and some areas since have been allowed to revert back into native woody vegetation allowing a succession of native forest to start developing.

1.2.1. Seed Dispersal

The life history of seed plants is comprised of two ecologically distinct phases. These are known as sessile and dispersal phases (Eriksson and Ehrlen, 1992). The term dispersal is characterised by the movement of individuals away from their parents (Nathan *et al*. 2003) to sites where seeds can germinate and survive to produce the next generation (Chanthorn and Brockelman, 2008). Dispersal has been noted as a key factor affecting species distributions (Primack and Miao, 1992) and dispersal limitation can impede seedling recruitment of plant species. A wide array of seed and dispersal features exists among plants (Eriksson and Ehrlen, 1992) and it is inevitable that considerable between-species variation in patterns of recruitment occurs. Seed dispersal is a topic of much interest to ecologists, however until the last few decades the ecology of dispersal has not received rigorous attention scientifically (Willson and Traveset, 2000).

Dispersed offspring survive and reproduce more readily than those that are not dispersed away from the parent; this is due mainly to detrimental conditions they may encounter close to parents. When dispersed farther away, however seedlings encounter similar conditions, but from a different perspective (Willson and Traveset, 2000), for example herbivory and microsite availability. Darwin (1859) pointed out that adaptations of seed dispersal and means of long-distance transportation are particularly important to plants. Long-distance dispersal is favoured in order for offspring to colonise unvegetated habitat and limits competition with extant vegetation (Koch *et al*. 2010). Dispersal over modest distances ensures seeds are distributed within proximity to the source that supported the parent(s) (Koch *et al*. 2010).

The dispersal potential of different dispersal modes varies immensely (Willson and Traveset, 2000). Seeds can be dispersed via wind or water (abiotic), or through vertebrate movement (biotic) means (e.g. birds), while for some species dispersal simply occurs via gravity: the seed has no special dispersal mechanism. Dispersal by wind or animals enable seeds to travel greater distances away from the parent tree.

Dispersal of offspring away from the natal site is one way that genes move through a population or into new populations (Willson and Traveset, 2000). This prevents in-breeding among individuals of the same species. Seed dispersal has major influences on plant fitness and whether seedlings subsequently live or die (Wenny, 2001). In theory, plants may increase their fitness level if higher numbers of seeds are dispersed to areas where offspring gain a higher potential of survival relative to other sites; this is termed directed dispersal (Wenny, 2001).

The lack of information regarding long-distance seed dispersal (Nathan *et al*. 2003) is unfortunate since long-distance dispersal events influence many key aspects of plant biology, including population dynamics, the evolutionary ecology of plant populations, biological invasions and the overall health (diversity) of ecological communities (Harper, 1977; Sauer, 1988; Hengeveld, 1989; Hanski and Gilpin, 1997; Hovestadt *et al*. 1999). Concerning recruitment dynamics, two models describe the effect of proximity of seedlings to parent trees and distance away from parents, how these situations affect seedling recruitment. The Janzen-Connell model (Figure 1a) developed by Janzen (1970), and Connell (1971), hypothesises that seedling mortality is virtually 100% close to parent trees, thus recruitment is limited conversely, most seedlings appear at some distance away from the parent (*sensu* escape hypothesis; Howe and Smallwood, 1982; Bustamante and Simonetti, 2000), but because the number of seeds present declines with increasing distance, actual seedling numbers peak and then drop off again. In the Hubbell model (Figure 1b; Hubbell, 1980), seedling mortality, although high, is less than 100% near the parent, because seed density is highest nearer the parent, suggesting that recruitment will also be higher there (Houle, 1995).

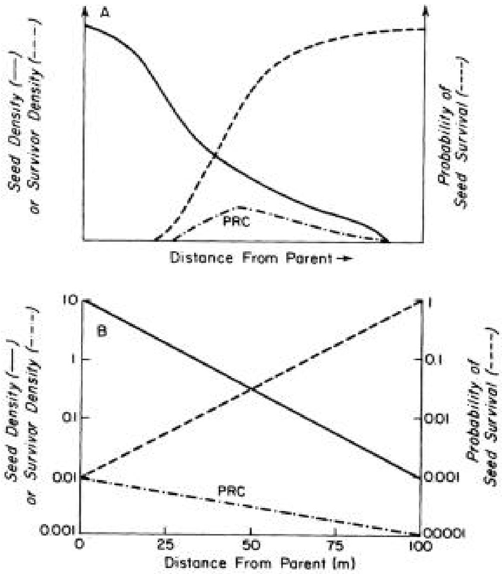

Figure 1. a) Janzen's graphical model of the effects of seed predation on tree spacing. The population recruitment curve (PRC) is expected to rise above zero only beyond some minimal distance from a parent tree, and is maximal where the product of seed density and probability of survival to maturity is highest. b) Hubbell's revised model depicts that seed density values span a greater range than the probability of the survival curve. This revised model assumes a non-zero percentage of seeds escapes predators near the parent tree. The two curves results in the PRC reaching its maximum near the parent. Reproduced from Augspurger, 1983

1.2.2. Seedling Recruitment: What does seedling recruitment in forests encompass?

The term recruitment is defined in several ways. With respect to this study, seedling recruitment refers to the entry of new individuals into a population (Ribbens *et al*. 1996). Seedling recruitment represents an interface between the sessile and dispersal phases discussed above (Eriksson and Ehrlen, 1992). In many populations, seedling recruitment represents a demographic bottleneck, particularly for species without the ability to grow clonally (Gurevitch *et al*. 2002; McEuen and Curran, 2006). Ribbens *et al*. (1996) define a seedling recruit as a propagule that has germinated and is later able to survive without maternal resources. Successful regeneration and species migration by plants generally depend on seeds or other propagules being dispersed to sites where they can germinate, become seedlings and then survive to form part of the existing vegetation (Dungan *et al*. 2001). Seedling recruitment is a critical stage in the plant life cycle, because most seeds fail to reach sites where establishment can occur and even for those seeds that do reach suitable sites, most fail to establish as seedlings (Clark *et al*. 1998; Clark *et al*. 1999).

Predictions of where new seedling recruits will occur poses challenges (Sagnard *et al*. 2007), especially with regard to seed dispersal, and ecological tradeoffs, for example the seed size/number ratio (Leishman, 2001). The abundance of and spatial pattern of seedling recruitment are influenced by seed distributions established during the time of seed dispersal (Augspurger, 1983, 1984). Newly recruited seedlings ultimately form the next forest cohort; such recruits form the basis of forest turnover over time, and hence forest composition. Growth and survival of established seedlings in a heterogeneous forest understorey are important components that determine subsequent canopy replacement (Grubb, 1977; Clark *et al*. 1999; Nakashizuka, 2001).

Recruitment is therefore important as it drives the overall long-term health of the forest.

Indigenous woody plant recruitment may be constrained at different life stages (Wang *et al*. 2010), where ecologists have long recognised that tree seedling recruitment is limited by both the supply of seeds and the availability of sites suitable for seedling establishment (Caspersen and Saprunoff, 2005). Clark *et al*. (1999) pose two views concerning the role of recruitment in forest dynamics. Firstly, trees that provide low or uncertain levels of seed supply negatively affect plant populations which inevitably results in limited recruitment and establishment of seedlings (Clark *et al*. 1999). This is among the causes leading to species rarity or absence. Second, recruitment ascribes a more limited role to seed supply and thus the establishment of seedlings (Clark *et al*. 1999). Limited recruitment can exert striking effects on the composition of plant communities (Leak and Graber, 1976), and recruitment limitations may operate through differing spatial and temporal scales (Ribbens *et al*. 1996). Recruitment limitation potentially involves numerous stages, where the relative importance is likely to differ over space and time, climatic fluctuations and appearances of canopy gaps, nurse logs and litter (Clark *et al*. 1999).

In many forested regions, understorey vegetation, namely herbaceous and shrub plants often form thick patches that ultimately shift patterns and rates of tree species recruitment during critical juvenile stages (Mallik, 2003; Royo and Carson, 2006) as they can outcompete the establishing seedlings (e.g. for light). Forests consistent of large, long-lived trees creating dense canopies influencing environmental conditions in the understorey (Boettcher and Kalisz, 1990), and later determine patterns of seedling regeneration (recruitment) beneath them (Forcier, 1975; Pacala *et al*. 1996).

Knowledge of species-specific requirements for seedling recruitment and interactions between environmental factors and different species within the same community type is poor and thus is an area where more research is needed (Silvertown and Tremlett, 1989; Edwards and Crawley, 1999). Integrated approaches combining information concerning seed dispersal are needed in order for better understanding of seedling recruitment processes (Schupp, 1995; LePage *et al*. 2000).

1.2.3. Biotic and abiotic factors controlling seedling recruitment in forests

Numerous abiotic and biotic factors are known to control seedling establishment. In forests, factors such as competition (neighbouring plants), desiccation, seed predation and herbivory (Fenner, 1985) all play roles in how seedlings are impacted once they have germinated. Below-ground (root) competition together with above-ground competition (space and light) both affect seedling survival (Brockie, 1992).

Natural disturbance regimes that create canopy openings (treefall gaps; Stewart *et al*. 1991) are important for forest dynamics, composition, structure and heterogeneity (Brokaw 1985a,b; Uhl *et al*. 1988; Runkel, 1982). The formation of small canopy openings by natural disturbances, for example windstorms, is typical of temperate forests including those of New Zealand (Wardle, 1984; Stewart 1986; Stewart and Rose, 1989, 1990). Gaps provide regeneration opportunities from seed in the seed bank, or established seedlings, or through invasion of new seedlings from outside the site (Pakeman and Small, 2005) as they increase light resources in the forest understorey.

In forest ecosystems, light is a major abiotic factor needed for the establishment of seedlings. Reduced light together with seed availability are two limitations for seedling establishment. Light availability is found to be an important determinant of seedling regeneration dynamics in temperate forests (Pacala *et al*. 1996; Finzi and Canham, 2000). Species show varying responses to light availability (particularly for seedling and sapling growth and survival; Brokaw, 1987; Van der Meer *et al*. 1998) where differences are likely to drive the spatial and temporal course of succession (Pacala *et al*. 1994; Kobe *et al*. 1995; Bazzaz, 1996). The degree of light penetration as well as root competition determines seedling abundance beneath the forest canopy (Gilman and Ogden, 2005); this also includes seedlings established underneath fern fronds. Greater light intensities in some forest communities could promote seedling survival through fungal pathogen suppression (Vaartaja, 1952; Augspurger, 1983).

Soil compaction influences seedling recruitment and plant development through increased soil strength, decreased oxygen availability and altered water storage and availability (Bassett *et al*. 2005). Compaction potential differs according to soil type, and plants are known to be affected differently (McQueen *et al*. 1994). Compacted soils reduce root growth hence plant anchorage is limited. This increases susceptibility to disturbance namely windthrow events (Kodrik and Kodrik, 2002). The reduction and size of soil macropores impedes root elongation (growth; Kozlowski *et al*. 1999) reducing root length hence limited soil exploitation (Materechera *et al*. 1991; Panayiotopoulos *et al*. 1994). Reduction of soil pores (and their volume) limits oxygen levels, potentially leading to toxic gas build up within the soil profile (Hillel, 1971). With respect to natural regeneration in New Zealand, effects of soil compaction on seedling establishment are important as many forest remnants have been grazed by domestic livestock (Bassett *et al*. 2005).

Physical damage by litterfall is another factor known to affect seedling recruitment (Gilman and Ogden, 2005; Alvarez – Clare and Kitajima, 2009). Litterfall is an important cause of seedling damage and mortality in many forest ecosystems (Gilman, and Ogden, 2005). For example, in a New Zealand temperate forest (Huapai) Gilman and Ogden (2005) found that litterfall contributed to 18% of seedling mortality. On the other hand, litter significantly decreases evaporative losses from the soil via temperature reduction that controls the transfer of water vapour (Williams *et al*. 1990; McAlpine, and Drake, 2002). Taxa likely to create elevated levels of litter accumulation include plants that shed large, heavy leaves and trees that drop limbs (Gilman and Ogden, 2005).

Seedlings are also at great risk of damage and death from herbivorous animals. Seedlings are tender and highly nutritious; herbivores tend to prey upon plants within reach more frequently and at the same time benefit their (herbivore) persistence. Reductions in woody seedling density have been noted in New Zealand forests post mammalian herbivore introductions in the 19th and 20th centuries (Husheer *et al*. 2006), whilst fencing to exclude domestic grazing animals results in significant increases in seedling densities.

Seedling establishment is affected both by seed dispersal and by environmental attributes of the site(s). In highly fragmented systems that have been heavily modified by past farming (agricultural) activities, the long-term development of future forest canopies could be compromised by a range of biotic and abiotic factors which will affect what tree species are able to regenerate hence grow beneath the initial “nurse” woody canopy.

1.3. Thesis Goals and Objectives

This study will add to our understanding of how regenerating forests in New Zealand function in particular the factors that might influence future canopy cover/composition. The main focus here is on the recruitment of seedlings of angiosperm tree species underneath a seral kanuka (*Kunzea ericoides*; Myrtaceae) forest. Kanuka trees are known to act as nurse species for seedlings, for example through providing shade and reduced exposure to weather phenomena, including desiccation (*sensu* Stevenson and Smale, 2005). Plant regeneration long-term beneath kanuka canopies has been noted and commented in the past (Cockayne 1919; Wilson, 1994; Reay and Norton, 1999a; Williams and Karl, 2002; Sullivan et al. 2007), suggesting that regeneration is made possible via the presence of these nurse plants.

Seedling recruitment (establishment, growth and survival) determines the next cohort of the forest. In order to gain a better understanding of this process, an understanding of ecological factors that determine seedling recruitment underneath existing seral kanuka canopies is required. More specifically, this research addresses the following questions:

1. What species are likely to dominate the future forest canopy at Tiromoana Bush?

2. What factors influence the abundance of potential canopy species in the understorey and, hence determine future canopy composition?

These questions will be addressed using the following approaches:

1. Data from existing permanent vegetation monitoring plots will be used to quantify recruitment, growth and mortality of seedlings under intact kanuka canopies as a basis for better understanding seedling dynamics.

2. Using stratified random plots, the influence of a range of biotic (dispersal distances, competition) and abiotic (light, slope, and aspect) factors on seedling abundance will be determined.

Chapter Two: Study Site

2.1. Study Site

This research took place at Tiromoana Bush in North Canterbury. Tiromoana Bush is a restoration project area covering 423 ha within the Motunau Ecological District (MED) (Lowry Ecological Region; North Canterbury); grid reference 43° 06’S, 172° 51’E (Figure 2).

Figure 2. Tiromoana Bush study location.

2.2. Geology of North Canterbury and Tiromoana Bush

All basement rocks beneath the Canterbury Region belong to the Torlesse Composite (Rakaia and Pahau) Terrane. The Pahau Terrane rocks, of late Jurassic to early Cretaceous age (160 million and 100 million years ago), occur to the north, and are probably derived from the Rakaia Terrane (Bradshaw, 1989). Most of North Canterbury comprises Late Cretaceous strata that rest with angular unconformity on the Torlesse Supergroup basement rocks (Nicol, 1993). These strata comprise the Broken River and Conway formations, which are thin (less than 200 m) and are locally completely absent (Nicol, 1993). The Kowai formation (formed during the Pliocene; 5.3 to 1.8 million years ago) comprises the stone types sandstone, siltstone, mudstone and carbonaceous layers, also occurs widely throughout North Canterbury (Forsyth *et al*. 2008).

The geology of the Tiromoana Bush area primarily comprises tertiary sedimentary rocks, as well as Quaternary outwash gravels, coastal gravels and sands (Norton, 2005). The coastal hills surrounding Tiromoana Bush are dominated by soft rocks and soils from the Tertiary and early Quaternary periods (that is, between 65 million and 1.8 million years ago), on former seabed strata on the coastal side of Mt Cass, and is consequently underlain by generally fine-grained compacted sedimentary deposits. Tiromoana Bush in geological terms is bounded in an area known as the Teviotdale syncline and the Kate anticline folds. The basement rock formation beneath Tiromoana Bush, known as the Kowai formation, formed during the Pliocene, between 5.3 and 1.8 million years ago, consists of brown, weathered greywacke-clast conglomerate with sandstone, siltstone and mudstone which are more common towards the base, where shellbeds and carbonaceous layers among this formation were scattered (Forsyth *et al*. 2008). The valley has moderately steep sides where surface erosion is evident.

The topography of Tiromoana Bush ranges from sea level to 346 m above sea level comprising hills and valleys, draining to the east by small rivers. Soils in the area are known as Stoneyhurst Hill soils where sandy loams predominate (Norton, 2005; Figure 3). The coastal environment consists of narrow sand and shingle beaches covered at high tide (Russell and Brown, 1990). The beaches are backed by coastal cliffs up to 60 m high. Slumping has occurred at the cliffs of the lower reaches of Kate Valley and nearby streams (Russell and Brown 1990; Norton, 2005).

2.3. Climate

The climate of North Canterbury is greatly dependent upon the lie of the Southern Alps to the west. Summer temperatures are generally warm, but during foehn northwesterly conditions (air blowing over the Alps and plains), temperatures can become hot. Mean annual rainfall is low and long, dry spells can occur, especially through summer. Typical summer daytime maximum air temperatures range from 18 °C to 26 °C[1], but may rise to more than 30 °C. Coastal North Canterbury experiences cool northeasterly breezes, cooling down temperatures in summer. Winters are cold, and frosts occur frequently. Typical winter daytime maximum air temperatures range from 7 °C to 14 °C. The North Canterbury coast for much of the year experiences northeasterly airflow, whilst southwesterlies become frequent during winter.

Tiromoana Bush experiences a temperate climate; a mild annual temperature of 10-12.5 °C, while the minimum temperature ranges from 0-3 °C (Leathwick, 2001),

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[1] Sourced from NIWA 2011

where in the summer of 2010, the average temperature was *circa*. 16 °C (max. 31 °C; min. 5 °C), and during winter, the average temperature is rather cold with an average of *circa*. 7 °C (max. 19 °C; min. 0.1 °C). The 2010 data collected at Kate Valley (near Tiromoana Bush) is for rainfall and temperature. The rainfall of 2010 at Kate Valley was 919 mm, where most rain was experienced in the winter months (*circa*. 380 mm) and least during the spring (*circa*. 160 mm). The humidity levels (relative humidity) at Tiromoana Bush are moderate where during 2010, the summer was 68% and in winter the humidity was higher at *circa*. 80%.

2.4. Vegetation History of North Canterbury

The commencement of the Holocene (about 10,000 years ago) was marked by rapid climatic ameliorations in which Late Glacial shrubland-grasslands of the South Island were replaced by tall forests (Worthy, 1990). By 9,500 BP, the eastern lowlands of the South Island had tall matai-totara-kahikatea forests (Worthy, 1990). The modern distribution of forest was largely reached by 2,500 BP, where fertile lowlands on the eastern South Island were in tall to low podocarp-broadleaved forest (Worthy, 1990; McWethy *et al*. 2010), and also *Nothofagus* spp. (beech) in wetter, and higher locations (McWethy *et al*. 2010).

Information gained form pollen analyses and from mapping of the potential vegetation cover of New Zealand suggests that the Motunau Ecological District would have been covered by an almost continuous cover of forest before human settlement (Norton, 2005). Information regarding pre-human vegetation specifically came from a pollen diagram (Figure 4) at Amberley (Moar, 1971), where this diagram showed the dominance of Podocarpaceae and *Nothofagus* pollen in the regional pollen rain and based on this, it was suggested that the pre-human vegetation was likely to have consisted of mainly totara (*Podocarpus totara*), matai (*Prymnopitys taxifolia*) and black beech (*N. solandri* var *solandri*) (Norton, 2005). Moar (1970) described the vegetation around the Pyramid Valley area, further inland, as covered by a mosaic of forest and shrubland. However, a more general construction of the potential vegetation cover shows that the Motunau Ecological District supported a mixture of lowland conifer forest and conifer/*N. solandri* forest (Leathwick *et al*. 2003).

It is likely the podocarp-broadleaved forests would have been the most widespread vegetation type. This forest would have comprised emergent podocarps (totara, matai and maybe kahikatea (*Dacrycarpus dacrydioides*)) above a mixed broadleaved angiosperm canopy including lemonwood (*Pittosporum eugenioides*), lowland ribbonwood (*Plagianthus regius*), kowhai (*Sophora microphylla*), narrow-leaved lacebark (*Hoheria angustifolia*) broadleaf (*Griselinia littoralis*), ngaio (*Myoporium laetum*), five-finger (*Pseudopanax arboreus*) and mahoe (*Melicytus ramiflorus*). Black beech would have been localised, confined to isolated “difficult” sites – sites where podocarp-broadleaved species were less competitive such as steep slopes and sites with soil moisture and nutrient limitations. Along the coastal fringe of the area, mixed broadleaved forest including ngaio and coastal akeake (*Dodonea viscosa*) would have been common (David Norton pers. comm. 2005).

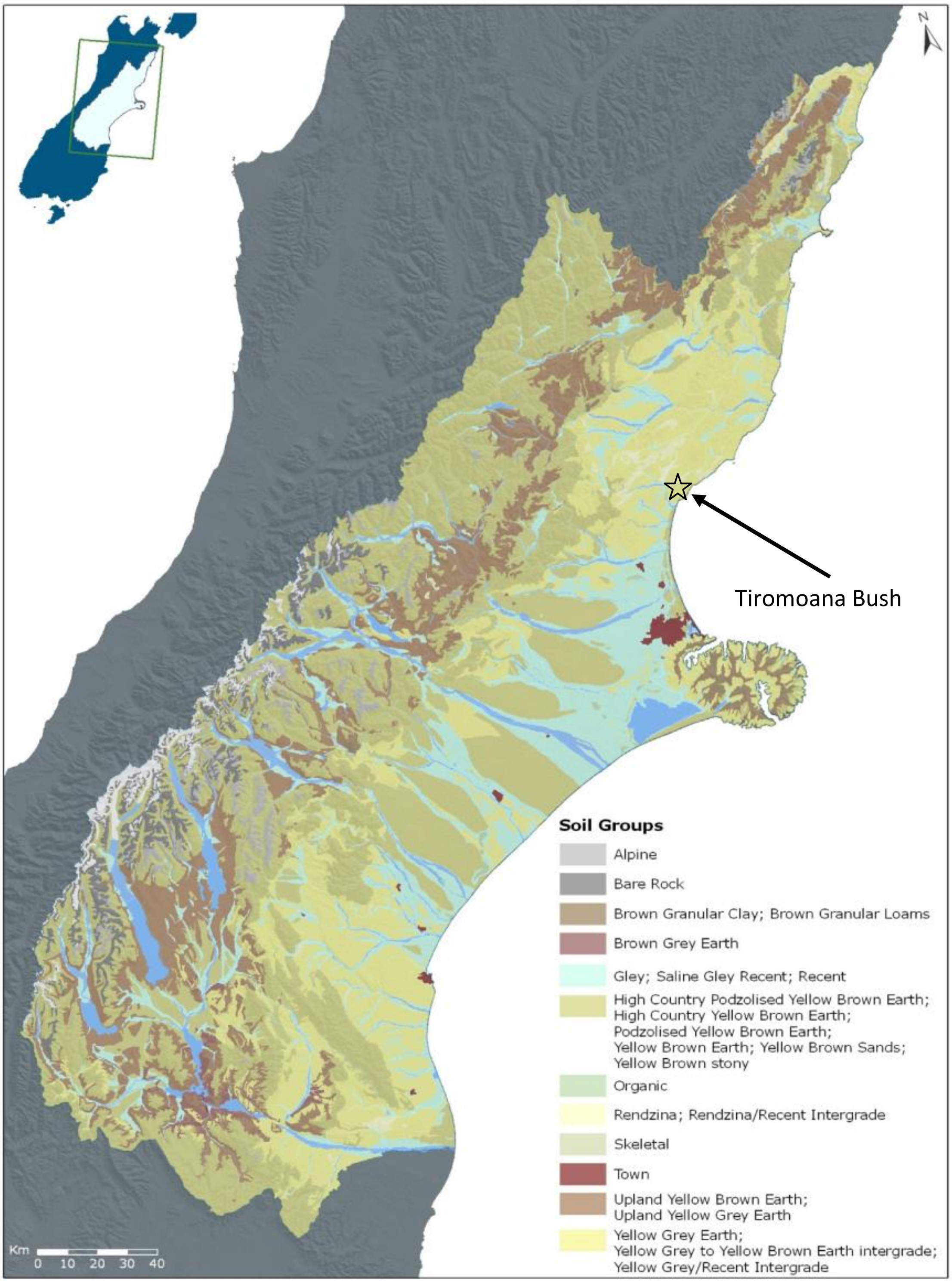

Figure 3. Soil groups of Canterbury. Tiromoana Bush (star) consists mainly of Yellow Grey Earth and Rendzina. Source: Environment Canterbury

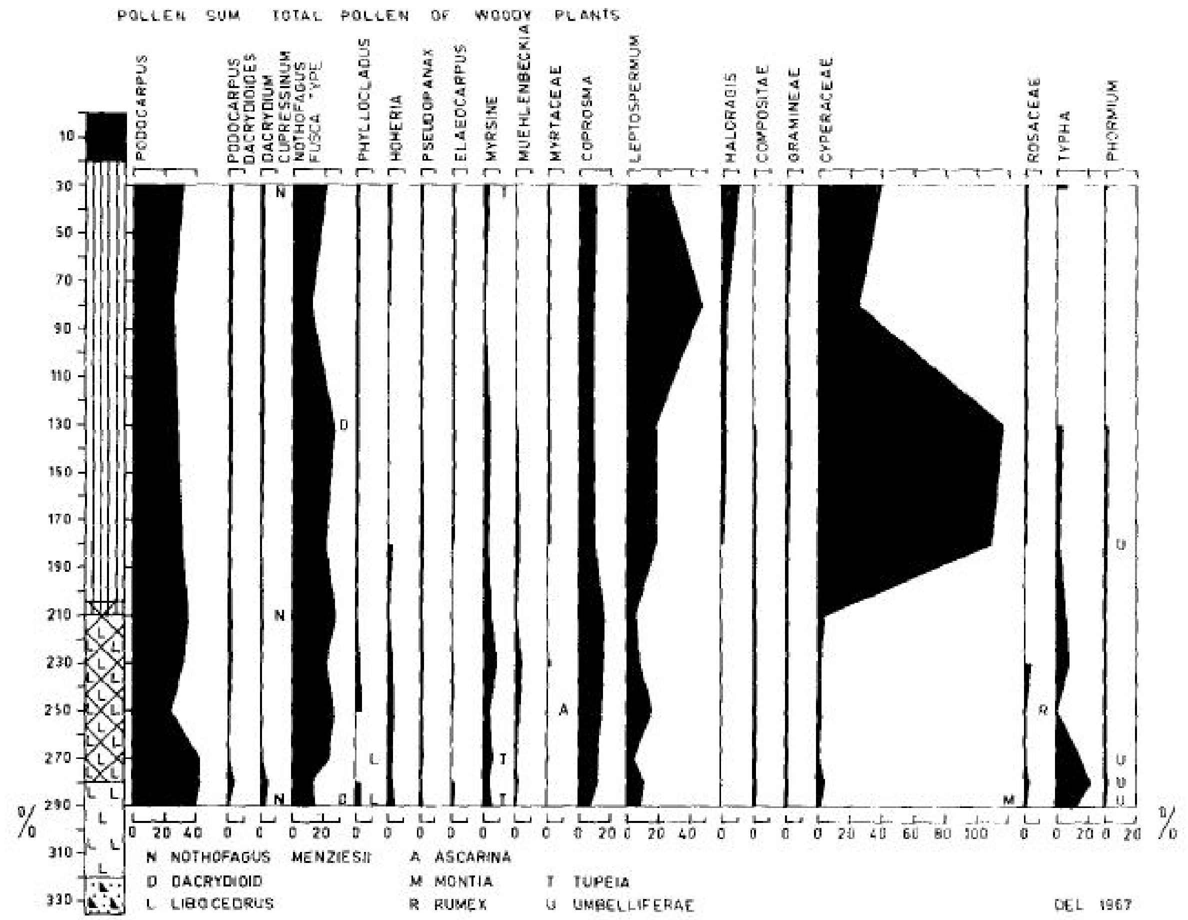

Figure 4. Pollen diagram, Swinton Park Farm, Amberley, North Canterbury. Reproduced from Moar, 1971

2.5. Vegetation loss in the Eastern South Island – Human Impacts

Similar to most land cover destruction in New Zealand, Tiromoana Bush suffered great losses of vegetation through burning, grazing and agricultural development. Fossil record evidence suggests that deforestation of the Motunau Ecological District was solely by fire (Norton, 2005), and that fires most likely occurred around 600-800 years ago. Other sites (other than Amberley) where pollen data was available (for example Travis Swamp in Christchurch) indicated that the severity of deforestation during the initial burning period (IBP; initial Maori arrival) occurred in moderate to low rainfall regions, where these large fire events caused shifts in vegetation types, such as beech and podocarps to bracken (*Pteridium esculentum*), grasses (*Poa* spp.), and small trees and shrubs (for example *Coprosma* spp., *Coriaria* spp. and kanuka (McWethy *et al*. 2010).

2.6. Current Vegetation Pattern of Tiromoana Bush

Present vegetation at Tiromoana Bush includes a range of exotic grasses, small to large areas of regenerating kanuka forest, shrublands, where these are dominated mainly of gorse, broom and *Coprosma propinqua*, mixed angiosperm forest (regenerating vegetation mainly mahoe, fivefinger, lancewood (*Pseudopanax crassifolius*), *Pittosporum* spp. and lesser species), wetland vegetation surrounding ponds and waterways, and a small remnant of black beech forest.

Pastures at Tiromoana Bush are dominated by a range of grasses, clover and herbaceous vegetation, and vary in composition with differing moisture levels and exposure.

The kanuka shrublands and forests range from kanuka monocultures, through to mixed stands with cabbage tree (*Cordyline australis*), small leaved *Coprosma* species, native broom (*Carmichaelia* spp.), and matagouri (*Discaria toumatou*), whilst the taller stands contain a mixture of five finger, mahoe, lancewood, and marbleleaf (*Carpodetus serratus*). Ngaio and golden akeake (*Olearia paniculata*) are more common nearer the coast. These shrublands and forests have recolonised sites where former forests had previously existed. The stands of lowland forest dominated by kanuka appear to post-date European settlement, and have most likely replaced grassland communities.

The shrublands are generally scattered through the valley, and are interspersed with areas of pasture. In these areas, silver tussock (*Poa cita*) is occasionally present. There are conifer plantations, to the northeast (radiata pine) and other hilly areas are planted with macrocarpa trees.

The black beech remnant is dominated by this species as well as other woody tree species, namely, kanuka, mahoe, lemonwood, lancewood and lesser species. Beneath the canopy is sparse, though there are small areas or thickets of mingimingi (*Coprosma propinqua*) and other species around. This remnant is located amongst stands of kanuka and broadleaved species.

2.7. Fauna of Tiromoana Bush

A range of animals inhabit Tiromoana Bush. A total of 20 indigenous and 15 introduced birds have been recorded at Tiromoana Bush during field surveys in October from 2005 to 2009 inclusive (Buckingham and Holster, 2010). These include bush and open pasture bird species, namely bellbird (*Anthornis melanura*), silvereye (*Zosterops lateralis*), grey warbler (*Gerygone igata*), fantail (*Rhipidura fuliginosa*), occasional sightings of tomtit (*Petroica macrocephala*) and brown creeper (*Mohoua novaeseelandiae*). Other birds that may visit Tiromoana Bush from time to time, or seasonally, possibly include New Zealand falcon (*Falco novaeseelandiae*), morepork (*Ninox novaeseelandiae*), long-tailed cuckoo (*Urodynamis taitensis*) and kakariki (*Cyanoramphus* spp.) (Buckingham and Holster, 2010). The only threatened species of birds recorded at Tiromoana Bush was black shag (*Phalocrocorax carbo novaehollandiae*) (At risk: Naturally Uncommon; Townsend *et al*. 2008). Kereru is no longer regarded as threatened (Buckingham and Holster, 2010).

Indigenous birds observed on the wetlands include paradise shelduck (*Tadorna variegata*), Australasian shoveler (*Anas rhynchotis*; first-time record), New Zealand scaup (*Aythya novaeseelandiae*), grey teal (*Anas gracilis*) and pied stilt (*Himantopus himantopus*). Welcome swallows (*Hirundo tahitica neoxena*) are common flying around the wetland areas and other parts of Tiromoana Bush (Buckingham and Holster, 2010).

Open pasture species include chaffinch (*Fringilla coelebs*), greenfinch (*Carduelis chloris*), redpoll (*Carduelis flammea*), yellowhammer (*Emberiza citronella*), magpie (*Gymnorhina tibicen*) and spur-winged plover (*Vanellus miles novaehollandiae*). Canada geese (*Branta canadensis*) were the most abundant and conspicuous introduced bird in wetlands.

Animal pests at Tiromoana Bush include the brushtail possum (*Trichosurus vulpecula*), mustelid species (stoats, ferrets and weasels; *Mustela* spp.), rodents (mice; Genus: *Apodemus* and rats; Genus: *Rattus*), and occasional deer (*Cervus* spp.). These animals pose threats to existing common and rare native plant and animal populations throughout Tiromoana Bush. Tiromoana Bush however is no longer grazed by domestic livestock.

2.8. Tiromoana Bush Restoration Project

2.8.1. General

Tiromoana Bush is now being managed as a restoration project based on a vision and series of management goals.

The restoration project at Tiromoana Bush was developed as a biodiversity offset, which the landfill company, Transwaste Canterbury Limited, proposed in 2002 (Norton, 2008) as part of their application for a resource consent under the Resource Management Act 1991 for establishing the landfill. Biodiversity offsets are a form of compensation for losses of biodiversity values elsewhere (Norton, 2008). Tiromoana Bush lies adjacent to the Canterbury Regional landfill of Kate Valley, where about 70% of waste is industrial.

The vision for this project sees, in 300 years time, Tiromoana Bush as a fully functional restored forest ecosystem where natural dynamic processes occur with minimal human intervention. The vision is broken down into short (5 year) and long term (35 years; 300 years) goals and outcomes which outline the approach to restoration and enable the assessment of restoration success (Norton, 2005).

2.8.2. Thirty-five year goals and outcomes

At the end of the 35-year resource consent period of the Kate Valley landfill, the leading outcomes will have been achieved within the Kate Valley Conservation Management Area as a direct result of the Tiromoana Bush restoration plan (Norton, 2005):

1. Vigorous regeneration will be occurring within the existing areas of shrubland and forest to ensure that natural successional processes are leading towards the development of mature lowland forest;
2. The existing bellbird population has expanded and kereru are now residing in the area and expanding the forest area sufficiently to improve forest connectivity;
3. The continued monitoring of biodiversity recovery; and
4. Promoting the public use of Tiromoana Bush (recreationally and scientifically).

2.8.3. Five year management goals

In order to meet the 35-year outcomes of the management plan for Tiromoana Bush, 8 outcomes for the first 5 years have been implemented. Five years as an appropriate time frame for these outcomes, as employed, is regarded as a short time frame to meet realistic, achievable goals (Norton, 2005), but long enough to see existent change(s) at Tiromoana Bush.

After the first 5-year term of the management plan, the outcomes need careful assessment. Concerning the development of subsequent 5-year term(s), reasoning for outcomes as to why they were not achieved need evaluation and thus measures need to be established to address the outcomes (Norton, 2005). Below, is a list of the outcomes that have been developed in the 5-year term(s), in order to meet the 35-year outcomes:

1. Appropriate restoration planning has been implemented. The size of the conservation area managed (*circa*. 410 ha), public interest of the area, and management actions ordering to meet the 35-year goals, requires management planning and annual reviews.
2. Ecological integrity for both existing remnants of native woody vegetation and restoration plantings has become protected. Presently, the area is heavily grazed by sheep and cattle, and this is placing adverse impacts upon the native vegetation and hence ecosystem condition. Removal of stock is thus a high management priority.
3. The Kate Valley Management Area is free of animal pests of high significance. The single threat from pest animals is their roles in the destruction of vegetation – natural and restored, as well as predacious animals impacting upon the fauna.
4. Plant pests are controlled to standards to limit threats to restoration (or other values). Plant pests, like animals, also threaten both natural regeneration and restoration plantings, especially through competition (light and nutrients), although this plan is realistic and recognises that not all exotic plants are

necessarily pests. Gorse, *Ulex europaeus*, for example is an exotic that can assist with regeneration (Wilson, 1994).

5. Restoration plantings covering an area of 5 ha minimum are growing vigorously and purposefully located plantings have been established as plants become available. The primary objective of restoring landscapes is to enhance connectivity between, in this case, existing native shrubland and forest remnants, and to enhance the black beech remnant also. Additionally, the establishment of enrichment plantings of key native species such as totara, matai, and kowhai to facilitate long-term succession and to provide food resources for native avifauna.
6. A biodiversity monitoring programme has been launched that enables the success of the restoration programme to be assessed in a quantitative manner. For restoration management, the monitoring process is an integral component as this allows success of the methods undertaken to be assessed. Nevertheless, monitoring needs careful intentions to ensure that it can supply information that updates management without negative cost to restoration.
7. Interests from communities, including the local community, together with the broader Canterbury community are informed about the restoration project. As an activity, restoration is deemed exciting, especially with the outcomes are almost always encouraging, and results can be observed in only a few years.
8. The Conservation Management Area of Kate Valley is used for recreation (walking) and opportunities exist for the public to view the coastline, on foot, together with appreciating the native forest ecosystems nearby. Additionally, the area offers extensive educational and research opportunities.

Chapter Three: Methods

3.1. Field Methods

3.1.1. Data Collection

For this study, data collected came from two sources: Permanent vegetation monitoring plots and temporary vegetation survey plots.

3.1.2. Permanent Vegetation Monitoring Plots

Monitoring of vegetation at Tiromoana Bush is based on a series of transects initially established in November 2005. The vegetation plots are located along 13 transects spread through the major areas of native woody vegetation within Tiromoana Bush (Figure 5). Each transect comprises three sample points, which were initially established as bird monitoring sites, but only two of these (which were randomly selected) are used for vegetation monitoring. The permanent vegetation monitoring sites comprise a 10 x 10 m plot (n = 26) with metal standards in each corner. A yellow cattle ear tag is nailed to a prominent tree to label each site.

Two 1.5 x 1.5 m seedling plots (n = 52) are located on a diagonal line across the plot (Figure 6). All four corners of the seedling plots are marked with a wooden stake. The first measurements undertaken for seedling height took place in 2007, where all seedlings of woody species greater than 20 cm in height were measured and individual plants were tagged using aluminium tags wired onto the stem.

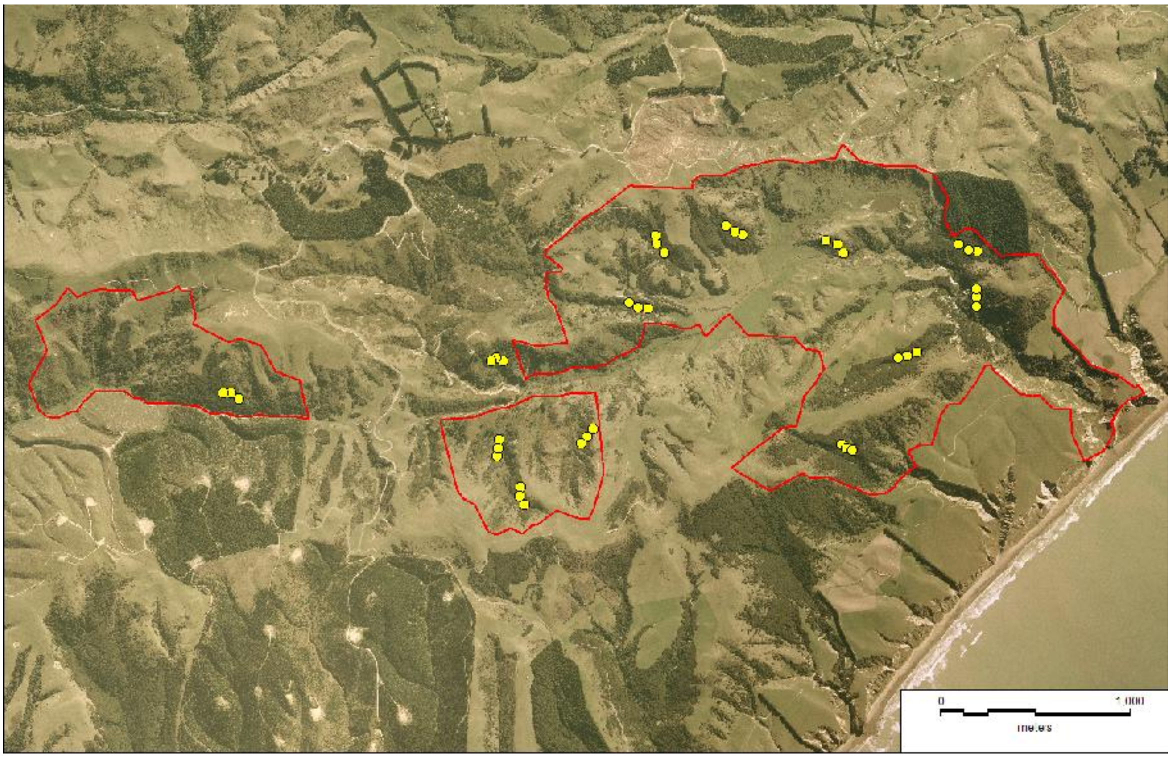

Figure 5. Thirteen transects in the major forest patches with associated permanent vegetation monitoring plots. The red outlines depict the conservation areas within Tiromoana Bush

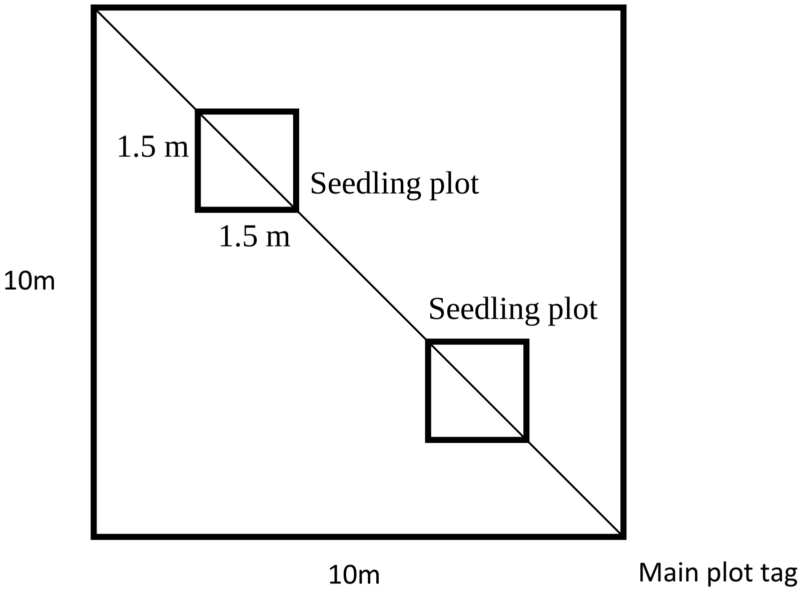

Figure 6. Permanent vegetation monitoring plot layout showing the location of the seedling plots

3.1.3. Permanent Vegetation Monitoring Plots – 2010 data collection

All plots were revisited in 2010/11 (summer and autumn), when all seedlings were remeasured. For each of the 52 seedling plots, all seedlings of woody species were measured (Figure 7). Newly recruited seedlings within these plots were also recorded and tagged, provided they were greater than 20 cm in height. Newly recruited seedlings less than 20 cm were counted by species, in order to determine species abundance, but were not tagged. Throughout this procedure in all plots, notes on mortality (death), and browsing were also made, especially when seedling tips were notably browsed, especially for mahoe.

A spherical densiometer (Jennings *et al*. 1999) was used to quantify canopy cover for each plot, and readings were taken from each corner of the plots, as suggested by Strickler, (1959). The spherical densiometer contained twenty-four 1 cm diameter squares (Figure 8a). To measure canopy cover, each 1 cm square was visually divided into 4 smaller squares (Figure 8b), and the presence or absence of canopy vegetation recorded. This gives a total of 96 squares. All densiometer readings were then averaged (all plot corner readings; Jennings 1999) to give overall canopy cover for each plot.

Figure 7. The author measuring a mahoe seedling

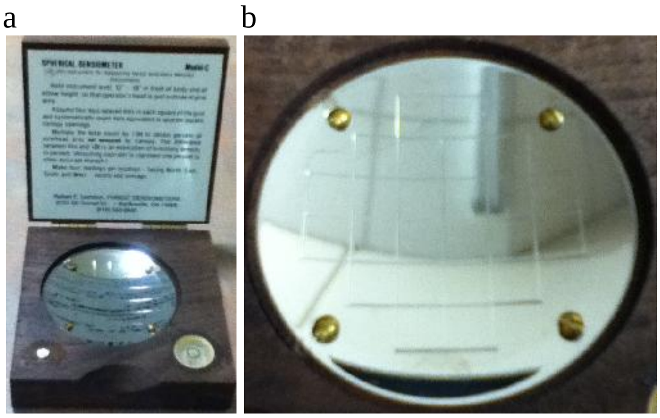

Figure 8. (a) Spherical densiometer instrument used to measure light interception in the kanuka understorey; (b) concave (model C) mirror with twenty-four 1 cm squares

3.1.4. Temporary Vegetation Survey Plots

In this second part of the study, a more wide-ranging survey of seedling abundance was undertaken across three substantial areas of kanuka forest (Figure 9) and involved recording seedlings of all woody plant species beneath the kanuka canopy in stratified random plots. The 4 x 4 m plots were located at 50 m distances along systematically placed transect lines crossing the three areas (Figure 10). The location of the first plot along each transect line was randomly determined. Transect lengths varied as the forest sites chosen had different areas of forest cover. Transects in all sites followed a compass bearing from the forest edge. Plots near forest edges were established provided that canopy cover was sufficient. Any unusual plot (site) characteristics such as soil erosion or other typographic means were noted.

In each of these plots, all woody seedlings were recorded. Seedlings below 5 cm in height were ignored as these were considered ephemeral. Small seedlings were defined as 5-30 cm in height and large seedlings were defined as > 30 cm in height and < 2 cm dbh. Non-shrub/tree species such as the vines *Muehlenbeckia* and *Parsonsia* were not recorded, although notes on their abundance were made.

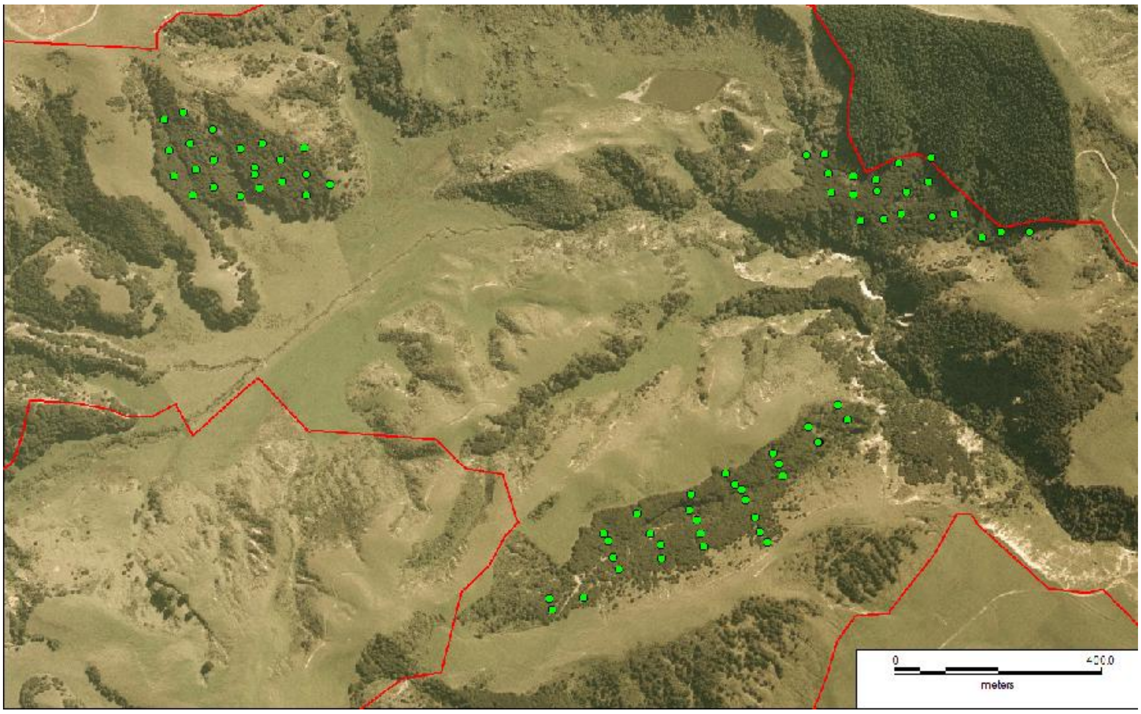

Figure 9. The three study sites at Tiromoana Bush with their associated vegetation survey plots. The red outlines are walking tracks and 4 x 4 tracks

Figure 10. The 4 x 4 m temporary vegetation survey plot layout (design)

For each plot, the following attributes were also recorded:

- GPS co-ordinates;
- Aspect;
- Slope;
- Physiography (terrace, ridge, gully and face);
- Surface cover (% coverage of litter, rock, bare ground, vascular and non-vascular vegetation);
- Height of canopy trees; and
- Canopy cover

Slope and aspect were measured using a Sunto clinometer and compass. Plots with more than one physiographic type had their slopes averaged: For example, plots with gully and terrace formations as part of their land form. The slopes were measured for both these forms and then were averaged to give the overall slope of the plot. GPS co-ordinates were taken at the centre point of each transect.

Canopy cover was estimated as a percentage, and the dominant species present noted (usually kanuka). Height of the canopy for all plots was also estimated. As for the permanent vegetation monitoring plots a spherical densiometer was used to quantify canopy cover and hence light entering through the canopy to the ground. Overall, a total of 78 plots were measured, across 20 transects from 3 forest patches.

3.1.5. Seed Source Mapping and Data Collection

For each of the forest patches where the temporary vegetation survey plots were established, the location of potential seed sources for seedlings was recorded. As the majority of the canopy was kanuka, a survey using binoculars and ground truthing was undertaken which enabled the location of the main areas of seed sources for the species recorded as seedlings to be mapped onto high resolution aerial photos of the site. Most seed source trees were located in or near gully areas.

Then from the aerial photo mapping, distances were determined from each survey plot to the nearest potential seed source for each species recorded in the plot. The average of these measurements was then used as an index of distance to seed sources. In addition, each plot was subjectively assigned to three approximate dispersal distance zones to reflect their overall location from seed sources:

- zone 1 (seed sources within 100 m of the plot);
- zone 2 (seed sources 100-500 m from plot); and
- zone 3 (seed sources >500 m from plot)

This same approach was also undertaken for the permanent vegetation monitoring plots, to understand new seedling recruits entering these plots and this relationship between distances to seed source trees.

3.2. Analytical Methods

3.2.1. Permanent Vegetation Monitoring Plots

Linear regression analyses were undertaken to determine the effect of environmental attributes influencing seedling abundance, growth, and survival.

Abiotic data such as shrub cover and light are percentage data and were thus transformed in order to meet the assumptions of normality (Dupoy and Chazdon, 2008), using the arc-sine/square-root transformation:

$$p' = \sin^{-1} \sqrt{(p)} \tag{1}$$

where p' denotes the transformation result and p denotes proportion of data. Once transforming the light data, the attribute “canopy openness” is what this defines, suggests that the more open the canopy, light is more likely to penetrate to the ground without interception through the forest canopy.

A number of variables were used in the regression models to predict both the abundance of seedlings, their relative growth rates over the survey period, new recruits entering the plots and survivorship. These variables included:

- Basal area (BA). This was measured by summing all tree and shrub species individual BAs in the permanent vegetation monitoring plots then totalling together for a number representing the BA for the whole plot. The BA of the plot is then divided by 100 to give the measurement in m^2. Basal area is used as a variable to represent the effect of tree biomass on seedling growth in these plots.
- Canopy openness. This was calculated by transforming the light readings (as these were per cent data) from the densiometer. For calculation, see equation 1.
- Slope.

- Aspect. For analyses, aspect was converted so that all plots (permanent vegetation monitoring and temporary survey plots) were expressed relative to north; thus an east and west facing plot both had an aspect of 90°.
- Light index. Light index is a relationship of the height of the forest canopy and light interception through the canopy. Typically, areas in forest patches where trees are small tend to be darker than ones where trees are taller. Light index (LI) was calculated via this equation:

$$LI = Log\ (height)\ x\ canopy\ openness \tag{2}$$

where height denotes forest canopy height at plot centre and canopy openness is derived from the readings of the densiometer.

- Distance from seed source. This was measured in zones (1,2,3) 1 denoting potential seed source trees that are closest to the plots; and 3 denotes seed source trees located at furthest distance away from the plots.
- Shrub cover. This was calculated by transformed mean percentage shrub cover for each plot. Shrub cover was included as an environmental attribute to look for relationships among this together with the other environmental attributes, for seedling growth and survival of tree species, as shrub cover can both reduce forest floor light levels and physically restrict the ability of seedlings to grow.
- Time. Time as a variable was used to assess differences in the abundance of seedlings over time and which environmental attribute(s), over time, affect seedling abundance. Time refers to the two seedling measurement sampling times of 2007 and 2010.

For seedlings of all canopy tree species in the permanent vegetation monitoring plots, relative growth rates (RGRs) were calculated to see how much each seedling had grown over time. The RGR indicates how much each individual plant had grown from the initial measurements (2007) until measurements undertaken in 2010 (growth in terms of rate of increase in size per unit of initial size; Hunt, 1990). Mathematically, the RGR was calculated using the log values from previous measures (2007) and measures made in 2010 (Husheer *et al*. 2006):

$$RGR = \mathrm{Log}_e\,(T2) - \mathrm{Log}_e\,(T1) \tag{3}$$

where,

RGR = relative growth rate for all tree species per plot;

T1 = seedling measurements at 2007;

T2 = seedling measurements at 2010

Relative growth rates were calculated for all seedlings; that is, all seedling heights measured in 2007, but for analysis these were divided into groups (height classes):

- 20 – 49
- 50 – 99
- 100+ cm

where mean RGRs were calculated for each plot.

3.2.2. Temporary Vegetation Survey Plot Analysis

Regression and ordination analyses were used to explore the relationships between environmental attributes and small seedling and large seedling abundance and composition in the temporary vegetation survey plots. More specifically, environmental attributes affect small seedling composition, and hence the number of larger seedlings, so the Detrended Correspondence Analysis (DCA) was conducted, to assess the relationship between seedling composition and environmental attributes (undertaken in CANOCO for Windows, Version 4.5; ter Braak and Smilauer, 2002). The unconstrained version was applied to find the axes with maximum variation in floristic composition at Tiromoana Bush, and to find patterns among species distribution along the gradients (Leps and Smilauer, 2003). The DCA diagram was later passively projected with all environmental variables to show variations across the species data (Kamrani *et al*. 2010). The eigenvalues in the DCA ordination designate the variation accounted for by each gradient, and the gradient lengths depict the amount of species turnover occurring along a gradient (Reay and Norton, 1999a). The Pearson correlation coefficient was used to examine relationships between ordination scores, environmental attributes and species combined (small seedlings and large seedlings) (*sensu* Kamrani *et al*. 2010).

To quantify measures of diversity or biodiversity (known as alpha diversity; α diversity) in all plot sites, Simpson’s index (heterogeneity index; Simpson, 1949) was used to describe the numbers of species present, as well as the abundance of each species (species richness). Simpson’s index (D) is calculated as:

$$D = \Sigma \begin{pmatrix} ni(ni-1) \\ N(N-1) \end{pmatrix} \tag{4}$$

where, D is the probability of 2 individuals belonging to the same species (the sum of all species in the sample); n_i depicts number of individuals of a particular species in plot sites; and N is the total number of organisms of all species. Simpson indices range from 0 (all of the same species) to 1 (myriads of species that are equal in number) where 1 represents infinite diversity and 0 depicts no diversity.

Diversity of the Simpson value can be expressed as the complement:

$$1 - D \tag{5}$$

where this calculates the evenness of species at the sites. The higher value of D, the greater the evenness of species.

To overcome the counter-intuitive nature of the Simpson's index is to take the reciprocal of the index:

$$1/D \tag{6}$$

where the higher reciprocal value indicates higher sample diversity. The reciprocal of the Simpson index was used to assist interpreting the DCA ordination.

For analyses, linear regression was undertaken to assess the effects of environmental attributes on small seedling and large seedling abundance of individual tree species. The environmental attributes listed below were used as predictors in order to test which predictor enabled effects to the response variable, small seedling or large seedling distribution. Similarly to the analyses for the permanent vegetation monitoring plots, variables (predictors) used in the regression included:

- Slope;
- Aspect;
- Canopy openness;
- Light index;
- Distance; and
- Shrub cover

Calculating the above environmental attributes was done as for analyses for permanent vegetation monitoring plot data. Again, shrub cover and canopy openness were transformed for analyses. Regression analyses for both permanent vegetation monitoring plot and temporary vegetation survey plot data were conducted in R 2.11.1. core development team, 2011.

Chapter Four: Results

4.1. Permanent Vegetation Monitoring Plots

4.1.1. General

This section presents the results from the analysis of the permanent vegetation monitoring plots and includes an assessment of both the overall abundance of species based on their current densities, and changes in seedling height over the three years these seedlings have been monitored. Only data on mahoe and fivefinger were analysed. The remaining species, kohuhu (*P. tenuifolium*) and kaikomako (*P. corymbosa*), were not analysed because of too few data. Data are presented and analysed for all seedlings together and for the three height classes seperately.

4.1.2. Commonness of Canopy Tree Species

At Tiromoana Bush, the most common canopy tree species as a seedling is mahoe followed by fivefinger (Figure 11). A total of 265 mahoe seedlings and 88 fivefinger seedlings were counted in all permanent vegetation monitoring plots (Figure 11a). For mahoe, the number of seedlings was similar across the height classes (Table 1). Forty-eight individuals are in the 20-49cm height class (25%), 75 individuals in the 50-99 cm height class (39%) and 69 individuals in the 100 cm or greater height class (36%) (Table 1). In contrast, fivefinger, numbers of individuals decreased throughout the height classes (Figure 11). Twenty-eight per cent of mahoe seedlings are new recruits and 65% of fivefinger seedlings are new recruits (Table 1).

Table 1. Number of seedlings in their characterised height classes, and new seedling recruits (< 20 cm) 2010

Tree species	recruits	20-49cm	50-99cm	100+ cm	Total
Melicytus ramiflorus	73	48	75	69	**265**
Pseudopanax arboreus	57	15	8	8	**88**
Pennantia corymbosa	8	4	3	0	**15**
Pittosporum tenuifolium	4	1	4	2	**11**

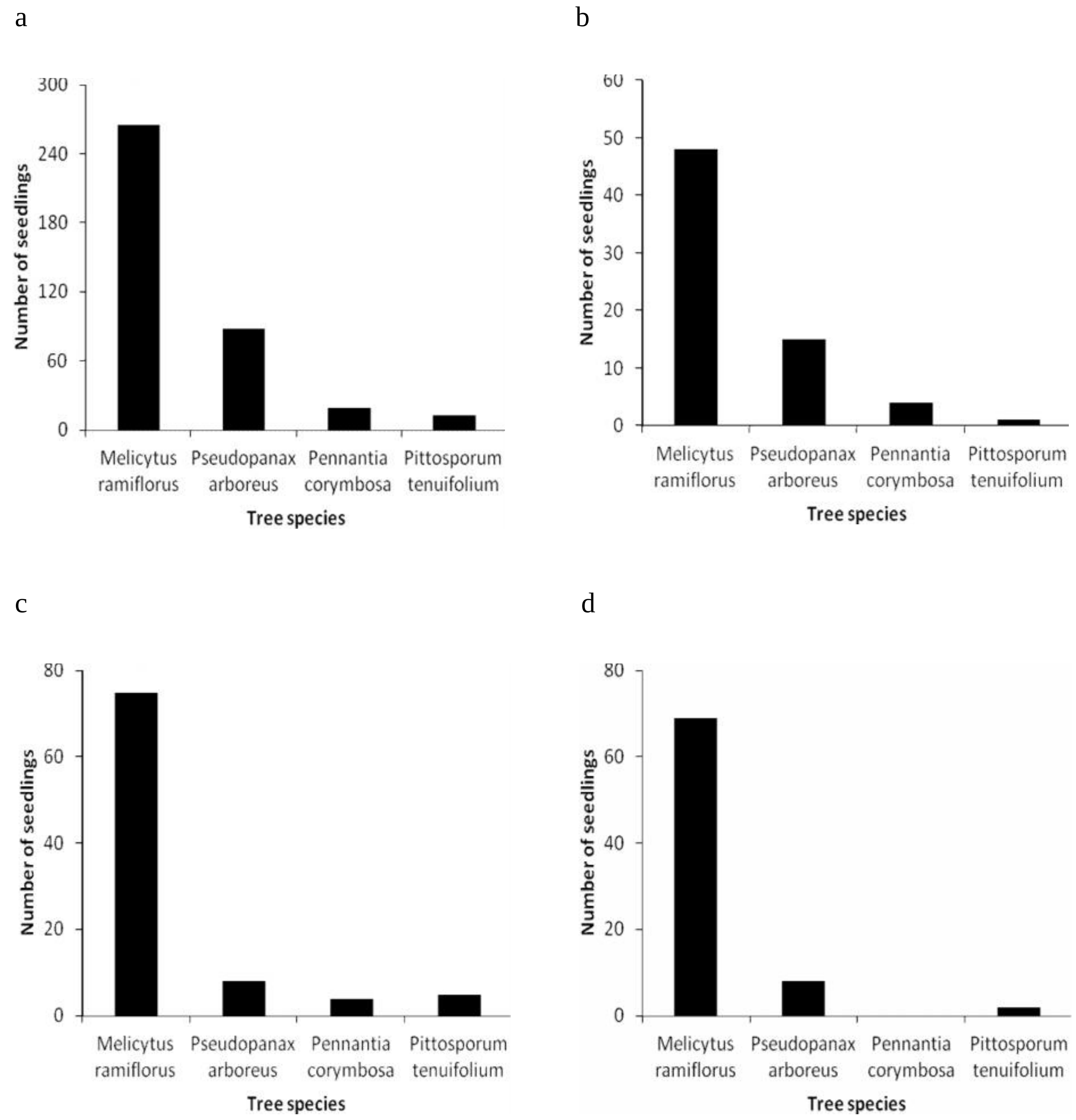

Figure 11. Canopy tree abundance at Tiromoana Bush 2010: (a) all seedlings; (b) 20-49 cm height class; (c) 50-99 cm height class; (d) seedlings 100 cm+ height class

4.1.3. Relative Growth Rates of Canopy Tree Species

i. Mahoe

Figure 12 shows the relationship between seedling relative growth rate and basal area, with plots ranked in order of increasing basal area. Most mahoe seedlings had relative growth rates between 0.3 and 0.4 (Figure 12a). In plot 4B, mahoe had relative growth rates of over 0.8. Most plots with mahoe seedlings had higher relative growth rates where the basal area of canopy trees were 30 m^2/ha or less (Figure 12a). The remaining plots with canopy tree basal area greater than 30 m^2/ha were associated with slower relative growth rates among mahoe seedlings (Figure 12a).

Regression models exploring the influence of environmental variables influencing mahoe seedling relative growth rates showed some associations between canopy cover and relative growth rate. For example, in the regression (response: 20-49 cm; Table 2), the height class in which most of the mahoe seedlings occurred, light index ($a = 1.962$, $P < 0.01$) shrub cover ($a = 7.706$, $P < 0.01$) and canopy openness ($a = -2.700$, $P < 0.05$) significantly affected relative growth rates, although basal area was not a significant attribute ($a = -0.004$, $P > 0.05$), for relative growth rates. Whilst no significant attributes occurred in the models for the taller seedlings, the sample sizes in these size classes were small. Light index was not an important attribute in the regression model developed for seedling survival ($a = -20.301$, $P > 0.05$) although aspect was a significant factor ($a = 0.205$, $P < 0.05$).

ii. Fivefinger

Plots 4A and 5B consisted of fivefinger individuals that grew faster than those in other plots (Figure 13). The regression models developed (response: all seedlings; response: 20-49 cm; Table 3) show that light index and canopy openness respectively show some associations with canopy cover and relative growth rates (a = 2.914 and a = 5.264, $P < 0.05$ for both). Aspect, however, was not a significant factor for the relative growth rates (a = -0.002, $P > 0.05$ for both). Both models are identical because the fivefinger seedling population (all seedlings) is governed only by the 20-49 cm height class (Table 3). Models developed for recruitment and survival of fivefinger show no association between the environmental attributes, as none of the attributes significantly affected both recruitment and survival (Table 3).

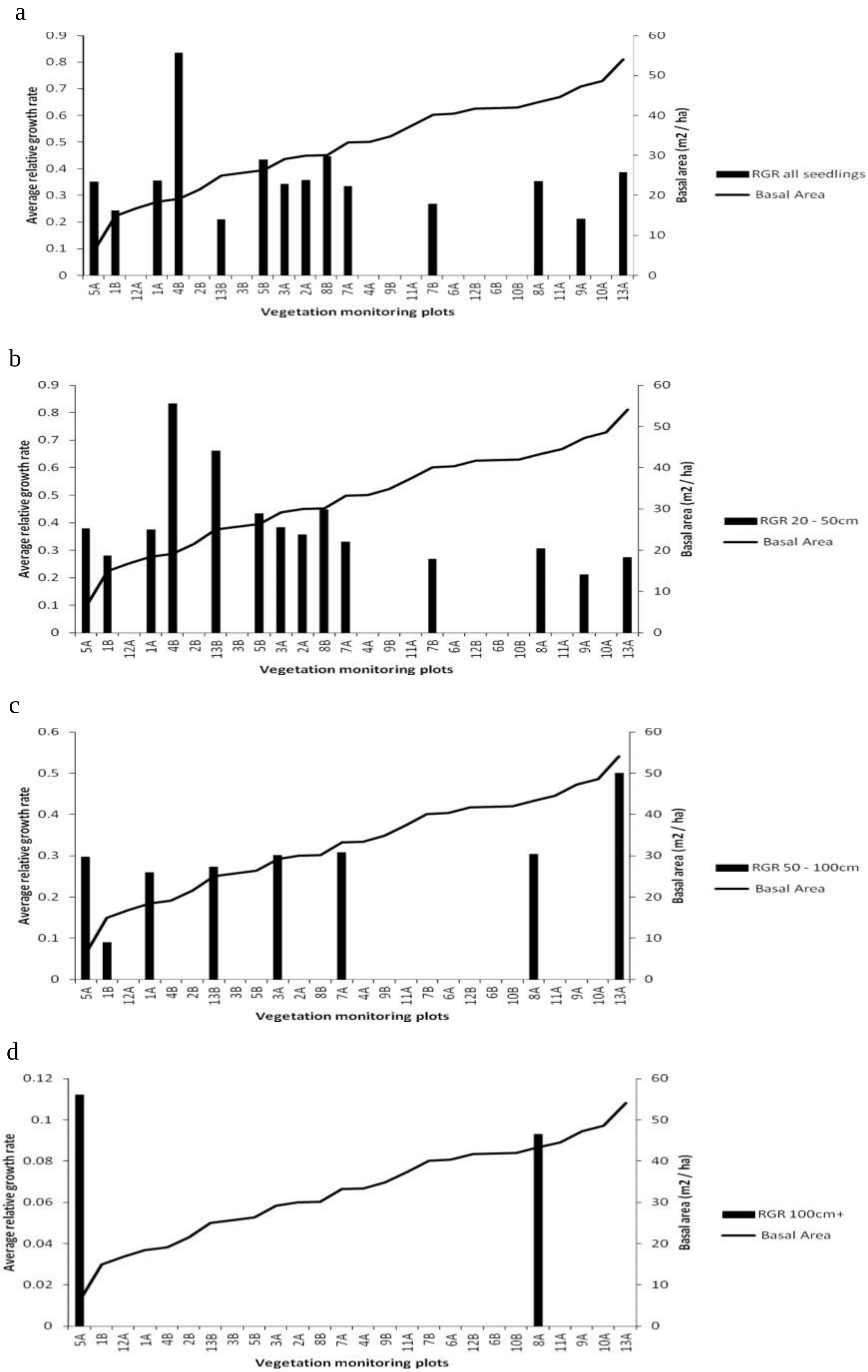

Figure 12. Relative growth rates of mahoe at Tiromoana Bush. (a) all seedlings; (b) 20-49 cm in 2007; (c) 50-99 cm; and (d) > 100 cm

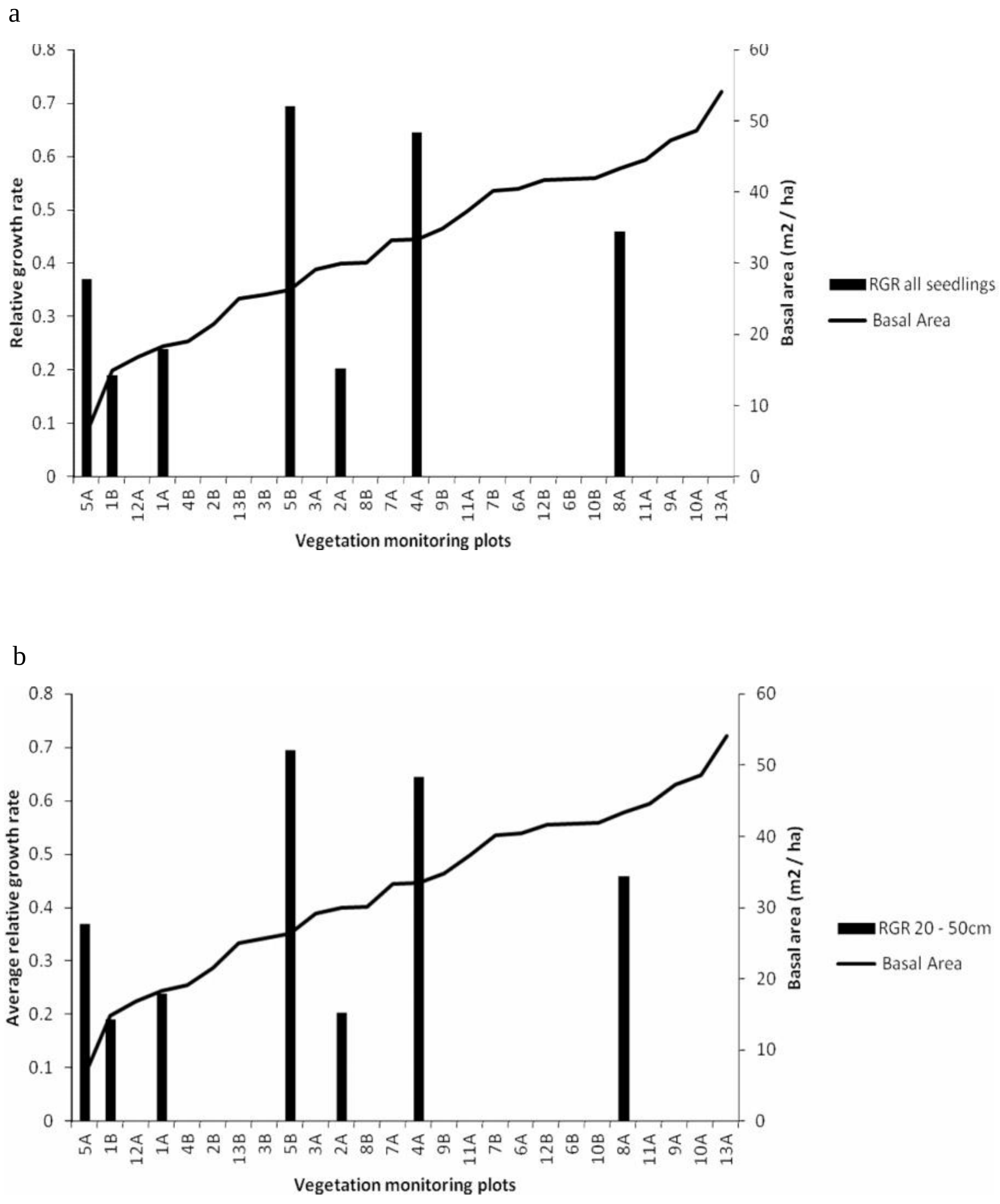

Figure 13. Fivefinger relative growth rates at Tiromoana Bush. (a) RGRs all seedlings; (b) RGRs of individuals 20-49 cm in 2007.

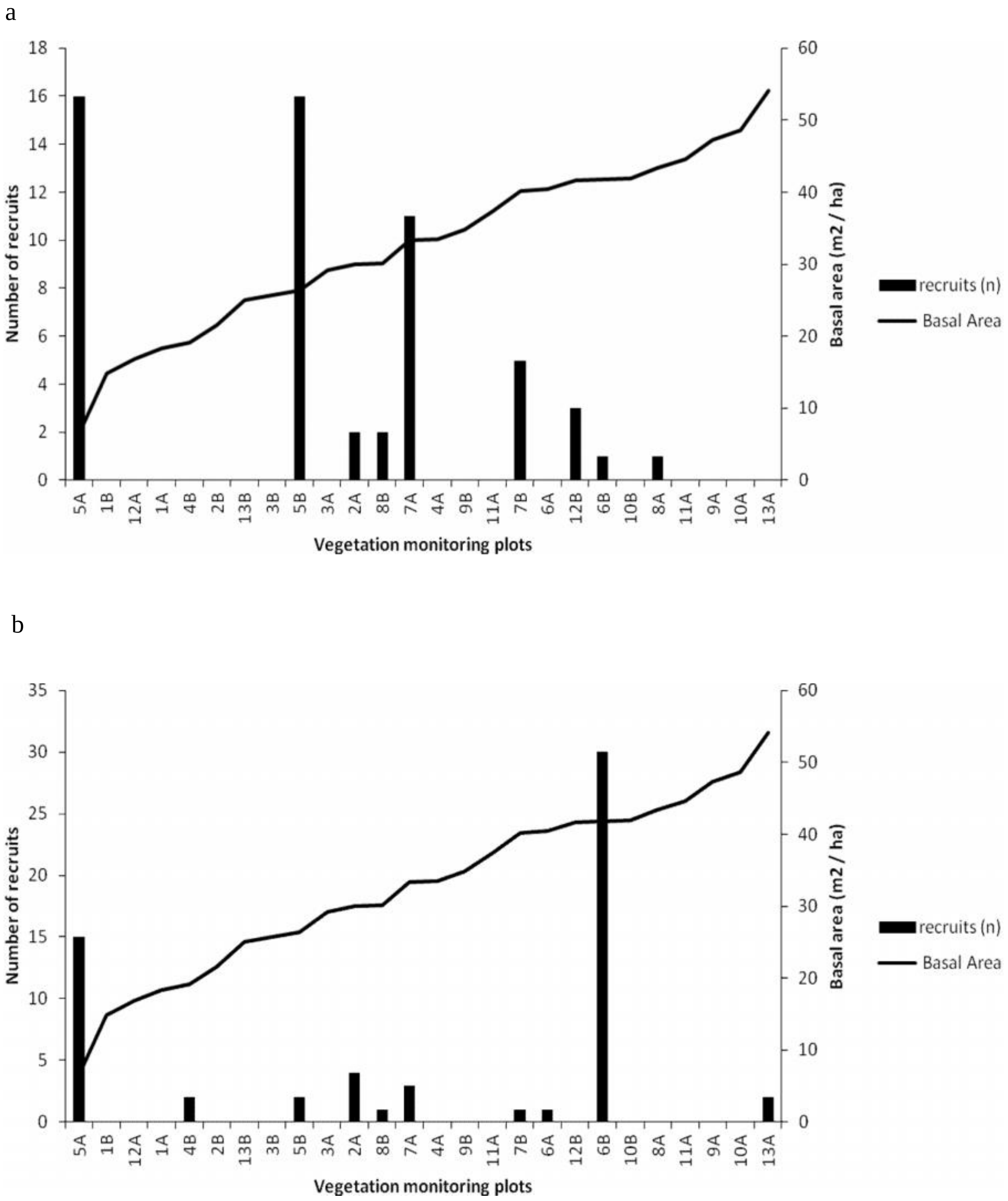

Figure 14. Seedling recruits at Tiromoana Bush. a) Mahoe; b) Fivefinger

4.1.4. New Seedling Recruits

In total, there were 73 new seedling recruits for mahoe and 57 recruits for fivefinger over the 2007-2011 monitored period (Table 1). Figure 14 shows the number of seedling recruits in all permanent vegetation monitoring plots. Plots 5A and 5B had the most recruitment of new mahoe seedlings (Figure 14a). For fivefinger, new seedling recruits were greatest in plot 6B (Figure 14b), while most other plots had fewer than 5 individual recruits (Figure 13b). The number of new mahoe seedling recruits was significantly affected by light index (a = -62.245, P < 0.01) and canopy openness (a = 123.111, P < 0.01) respectively in the regression model (Table 2), again highlighting the relationship between light and mahoe seedlings. Fivefinger seedling recruits showed no association with any of the environmental attributes (Table 3).

Figure 15 shows the number of seedling recruits of both mahoe and fivefinger plotted against canopy openness for all plots. Most seedling recruits of both species were at plots with moderate levels of canopy openness, while plots with low openness or complete openness had fewer or no seedling recruits at all (Figure 15).

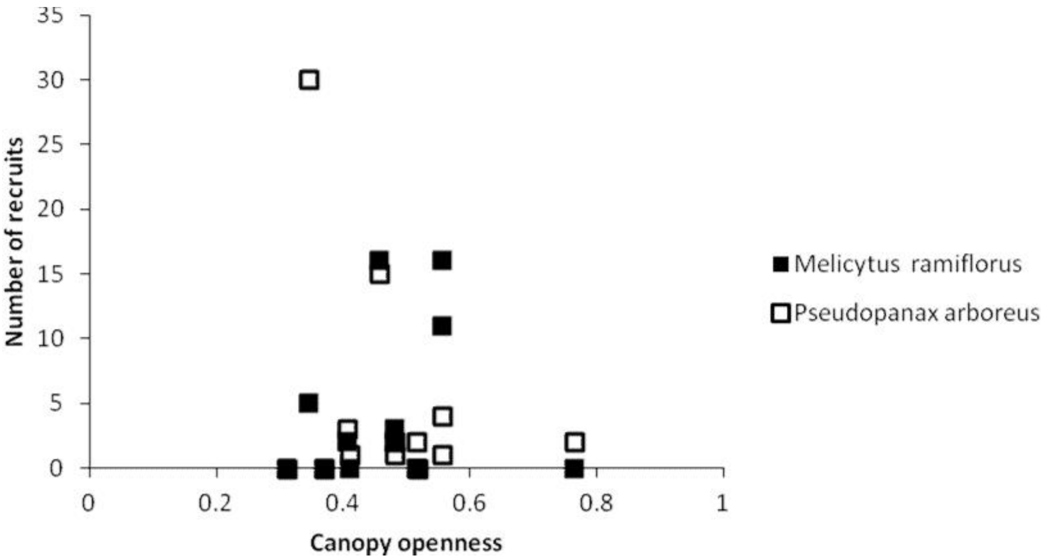

Figure 15. Light levels (canopy openness) and seedling recruits of mahoe and fivefinger at Tiromoana Bush. 0 on the horizontal axis defines complete closure; 1 depicts complete openness

Table 2. Regression coefficients for the different environmental variables used to predict mahoe seedling relative growth rate for all seedlings, survival and number of recruits

	All	**20-49**	**50-99**	**100+**	**survival**	**recruits**
r^2	0.29	0.73	-0.24	0.00	0.27	0.48
Variable						
Shrub cover	8.999*	7.706**	-0.945	-1.111	406.932	-138.304
Light index	1.284	1.962**	-0.366	-0.159	-20.301	-62.245**
Slope	< 0.001	0.006	-0.008	0.001	-1.516	-0.012
Canopy openness	-1.773	-2.700*	1.301	0.213	27.201	123.111**
BA	< 0.001	-0.004	0.002	-0.002	0.232	-0.111
Aspect	< 0.001	0.074	0.000	-0.000	0.205*	0.011

Level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 3. Regression coefficients for the different environmental variables used to predict fivefinger seedling relative growth rate for all seedlings, survival and number of recruits

	All	**20-49**	**survival**	**recruits**
r^2	0.48	0.48	0.03	-0.45
Variable				
Shrub cover	3.025	3.025	-389.366	-141.943
Light index	-2.914*	-2.914*	-182.561	-21.340
Slope	-0.001	-0.001	-1.226	0.113
Canopy openness	5.264*	5.264*	225.504	-2.801
BA	0.007	0.007	-2.176	-0.122
Aspect	-0.002	-0.002	-0.193	0.022

Level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 4. Regression coefficients for the different environmental variables used to predict mahoe seedling abundance. Differences are between 2007 to 2010

	All	**20-49**	**50-99**	**100+**
r^2	0.40	0.21	0.15	0.35
Variable				
Canopy openness	1.850*	71.291*	5.745	0.792
Light index	-7.413*	-34.875*	-3.509	-4.248
Shrub cover	-2.878*	-130.774*	-1.822	-1.269*
Distance	-6.908*			
Slope	-6.325*	-0.234	-0.146	0.174
Aspect	0.016	0.009	-0.005	-0.029
BA	-0.092	-0.046	-0.014	-0.113
Time	1.490	-1.214	1.455*	1.615**

Level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 5. Regression coefficients for the different environmental variables used to predict fivefinger seedling abundance. Differences are between 2007 to 2010. Distance coefficient for 20-49 cm height class excluded.

	All	**20-49**
r^2	0.02	0.72
Variable		
Canopy openness	0.952	-16.253
Light index	-1.615	-12.834
Shrub cover	-3.582	1.019
Distance	0.124	
Slope	0.035	0.112
Aspect	-0.002	-0.027
BA	-0.126	-0.072
Time	1.718	-0.083

Level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

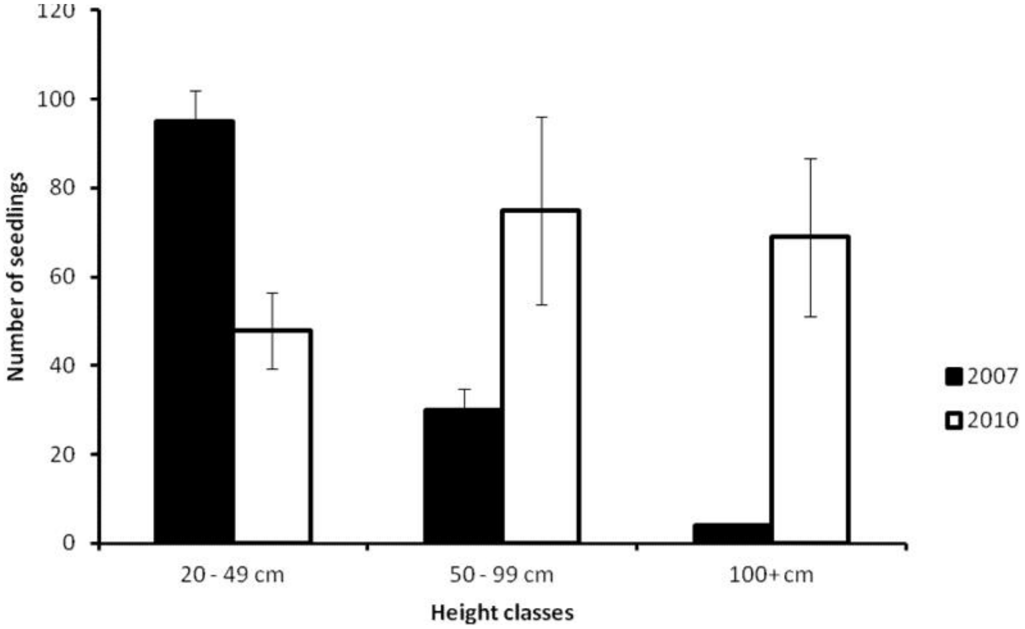

Figure 16. Mahoe abundance at Tiromoana Bush by height classes with ± standard deviation bars

4.1.5. Abundance of Seedlings of Canopy Tree Species at Tiromoana Bush

Concerning abundance, for mahoe, all seedlings increased from 188 in 2007 to 265 in 2010 (Figure 11, Table 1, 2010 data only). The differences in abundance of mahoe seedlings of all classes from 2007 to 2010 were associated with canopy openness ($a = 1.850$, $P < 0.05$), distance ($a = -6.908$, $P < 0.05$), light index ($a = -7.413$, $P < 0.05$), shrub cover ($a = -2.878$, $P < 0.05$) and slope ($a = -6.325$, $P < 0.05$). Aspect, basal area and time were not significant factors governing all seedling abundance changes (Table 4).

Mahoe is the most abundant seedling of any tree species at Tiromoana Bush. In 2007, mahoe individuals in height class 20-49 cm outnumbered all other height classes in the same year (Figure 16). Counts of individuals in this height class outnumbered counts in 2010 for the same height class (Figure 16). The number of individual mahoe seedlings in this height class was significantly affected (Table 4) by light index ($a = -34.875$, $P < 0.05$), canopy openness ($a = 71.291$, $P < 0.05$) and shrub cover ($a = -130.774$, $P < 0.05$), but there was no time effect ($a = -1.214$, $P > 0.05$). Time was however a significant factor affecting individual numbers of mahoe seedlings in height class 50-99 cm ($a = 1.455$, $P < 0.05$), and 100 + ($a = 1.615$, $P < 0.01$; Table 4) which highlights the differences in individual numbers between the two time periods. Shrub cover was also a significant factor ($a = -1.269$, $P < 0.05$) for 100 +. For fivefinger, there was no association between any of the environmental attributes, nor time, with abundance differences in 2007 to 2010 (Table 5).

4.2. Temporary Vegetation Survey Plots

4.2.1. General

This section presents the results from the analysis of the temporary vegetation survey plots and includes an assessment of both the overall diversity of broadleaved tree species seedlings surveyed and the floristic composition of canopy tree species seedlings at Tiromoana Bush. Data are presented and analysed for small seedling and large seedling composition of all broadleaved tree species identified.

4.2.2. Species Composition at Tiromoana Bush

The temporary vegetation survey plots were undertaken in three major forest patches at Tiromoana Bush (Figure 9). The three forest patches were dominated mostly by kanuka but in some areas, parts of the canopy were mixed with other broadleaved tree species. Eighty-seven percent of plots had a pure kanuka canopy and 13% of plots had a mixed canopy of kanuka and other broadleaved tree species.

Overall, ten tree species were recorded as small seedlings or large seedlings. Mahoe dominated the tree species seedlings found at Tiromoana Bush (Figure 17), in both small seedling and large seedling counts combined. Fivefinger and kohuhu are second and third respective tree species in commonness at Tiromoana Bush (Figure 17; Table 6).

Table 6. Small and large seedling counts for all tree species at Tiromoana Bush and their associated small seedling/large seedling ratios. Species are ordered by the number of small seedlings

Species	Total number of small seedlings	Total number of large seedlings	Small seedling / large seedling ratio
Melicytus ramiflorus	609	635	1.04
Pseudopanax arboreus	259	118	0.45
Pittosporum tenuifolium	85	58	0.68
Pseudopanax crassifolius	65	1	0.02
Pennantia corymbosa	35	31	0.88
Myrsine australis	13	4	0.30
Olearia paniculata	13	19	1.40
Carpodetus serratus	10	6	0.60
Myoporum laetum	10	7	0.70
Pittosporum eugenioides	9	1	0.11

Comparing canopy tree seedling counts in both permanent vegetation monitoring plots and the temporary vegetation survey plots, mahoe, and fivefinger are most common canopy trees as seedlings. Kaikomako seedlings in the permanent vegetation monitoring plots slightly outnumber kohuhu seedlings (Table 1). In the temporary vegetation survey plots, however, kohuhu (total count = 143) is twice the number of kaikomako seedlings counted (Table 6).

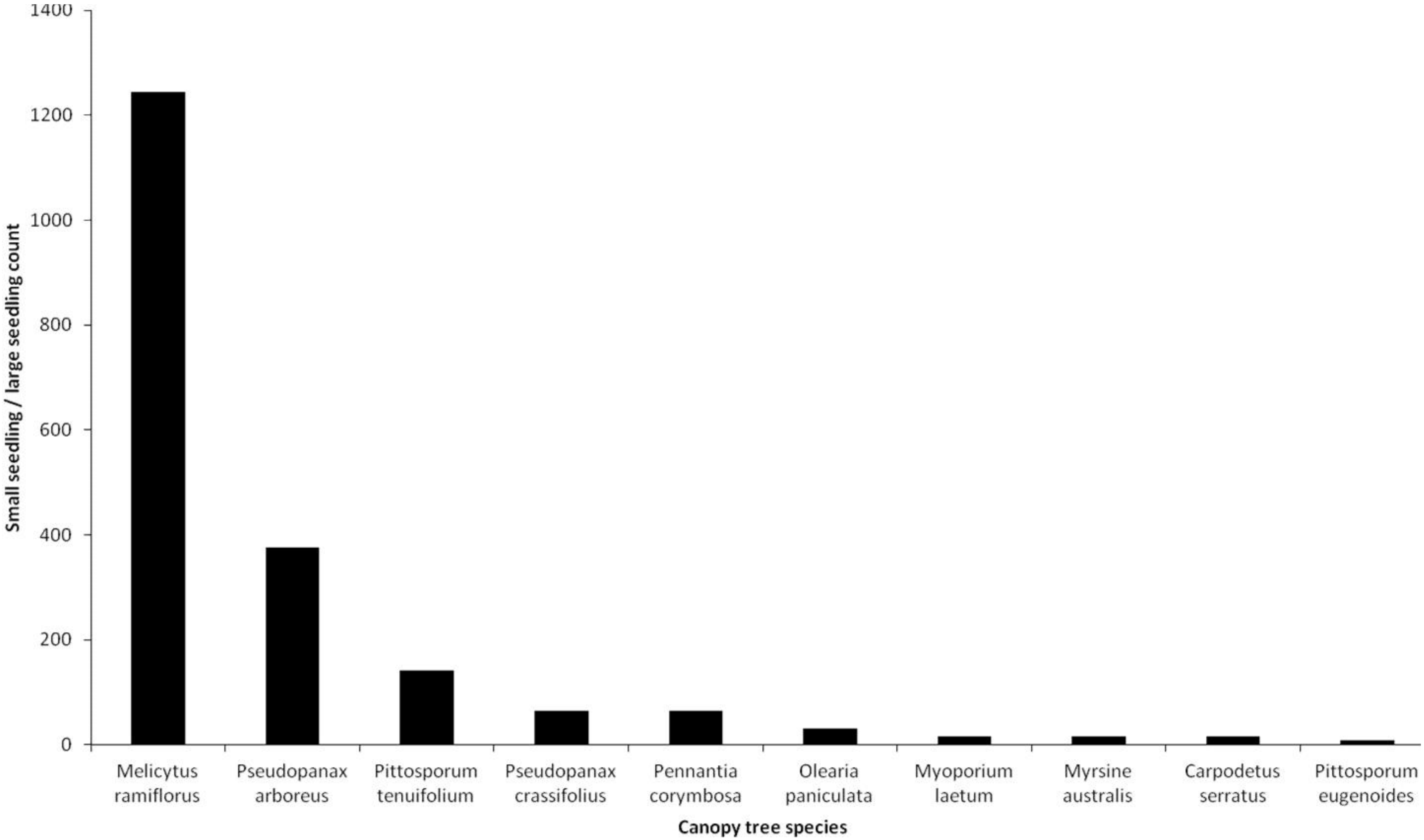

Figure 17. Counts of individual canopy tree species at Tiromoana Bush 2010

4.2.3. Small Seedling and Large Seedling Composition for all Species

For small seedlings and large seedlings of all ten tree species identified at Tiromoana Bush, there were a total of 1244 combined individuals for mahoe, 377 individuals for fivefinger, 143 for kohuhu, 66 individuals for lancewood and kaikomako, 32 individuals for golden akeake, 17 individuals for red matipou (*Myrsine australis*) and ngaio, 16 individuals for marbleleaf and 10 individuals for lemonwood (Figure 17), where these numbers were divided into small seedling and large seedling categories (Table 6). These numbers in comparison, particularly for mahoe and fivefinger relate to their abundance also in the permanent vegetation monitoring plots (see Table 1).

For both mahoe and golden akeake there were more larger seedling individuals than small seedlings (Figures 18, 23 and 24; Table 6). However, for fivefinger and lancewood there were fewer large seedlings than small (Figures 19, 21 and 24) as was also the case for lemonwood (Figure 24; Table 6). Kaikomako and kohuhu small seedling and large seedling counts were similar (Figures 20, 22 and 24). Ngaio and marbleleaf both consisted of similar counts of small and large seedlings (Table 6). Mahoe is the most dominant broadleaved tree species found at Tiromoana Bush, followed by fivefinger, based on both the permanent vegetation monitoring plots and the temporary survey plot data. Kohuhu was the least dominant canopy tree species in the permanent vegetation monitoring plots in the monitoring period of 2010-2011 (Table 1), but was the third dominant canopy tree species in the temporary vegetation survey plots (Table 6).

The regression models developed for all ten tree species show limited associations with the environmental attributes (Tables 9 and 10). For example, fivefinger small seedling densities are significantly affected by distance (a = 2.368, P < 0.05), golden akeake small seedling distribution is affected by canopy openness (a = 0.017, P < 0.05) and light index (a = 2.165, P < 0.001) and red matipou small seedling distribution is significantly affected with slope (a = 0.018, P < 0.05). For large seedling densities (Table 10), kohuhu distribution is significantly affected by aspect (a = 0.009, P < 0.05) and ngaio large seedling density is associated with light index (a = 1.804, P < 0.05).

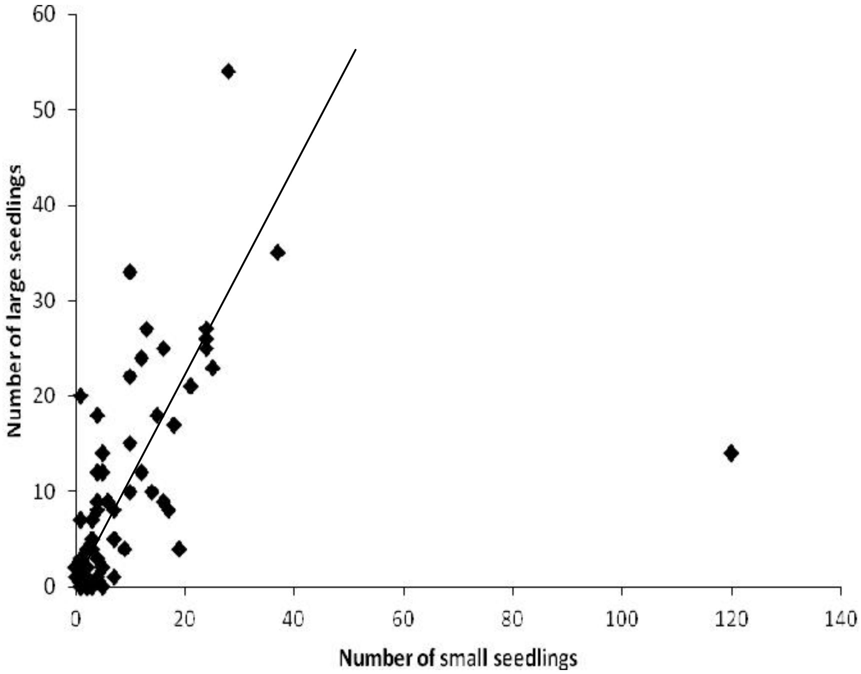

Figure 18. Mahoe small and large seedling distribution at Tiromoana Bush

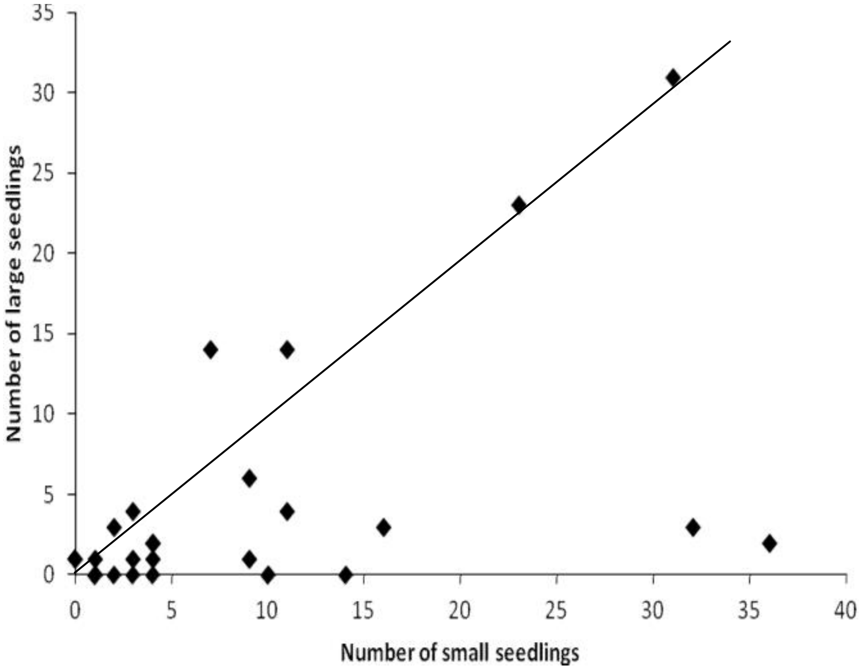

Figure 19. Fivefinger small and large seedling distribution at Tiromoana Bush

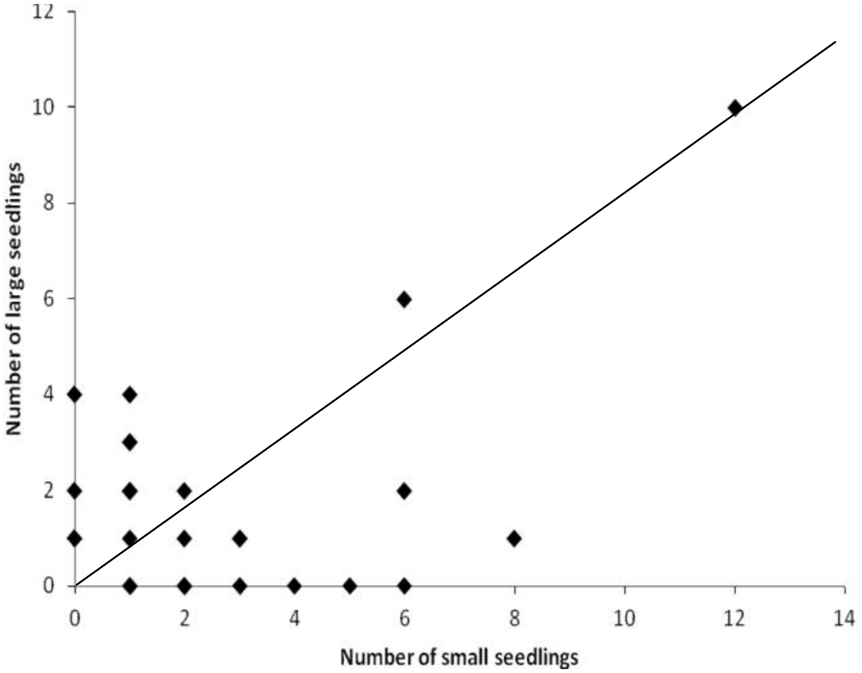

Figure 20. Kohuhu small and large seedling distribution at Tiromoana Bush

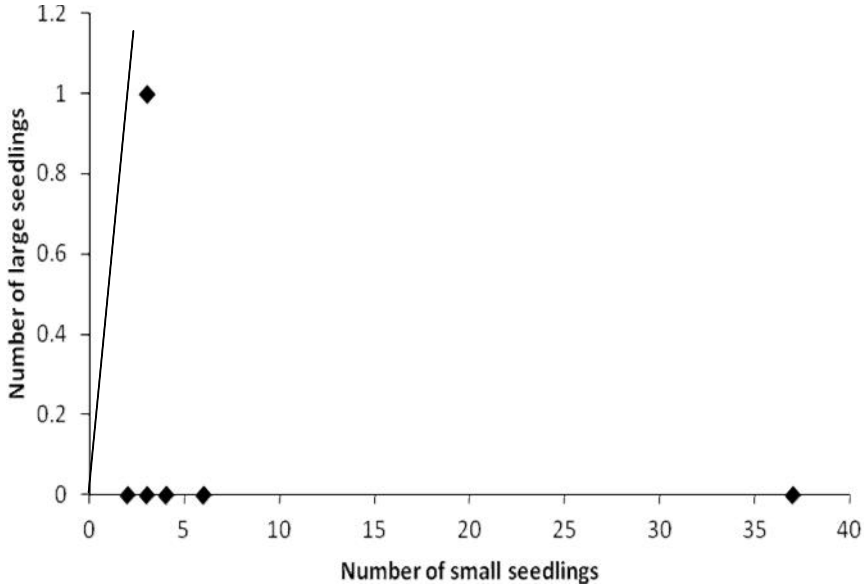

Figure 21. Lancewood small and large seedling distribution at Tiromoana Bush

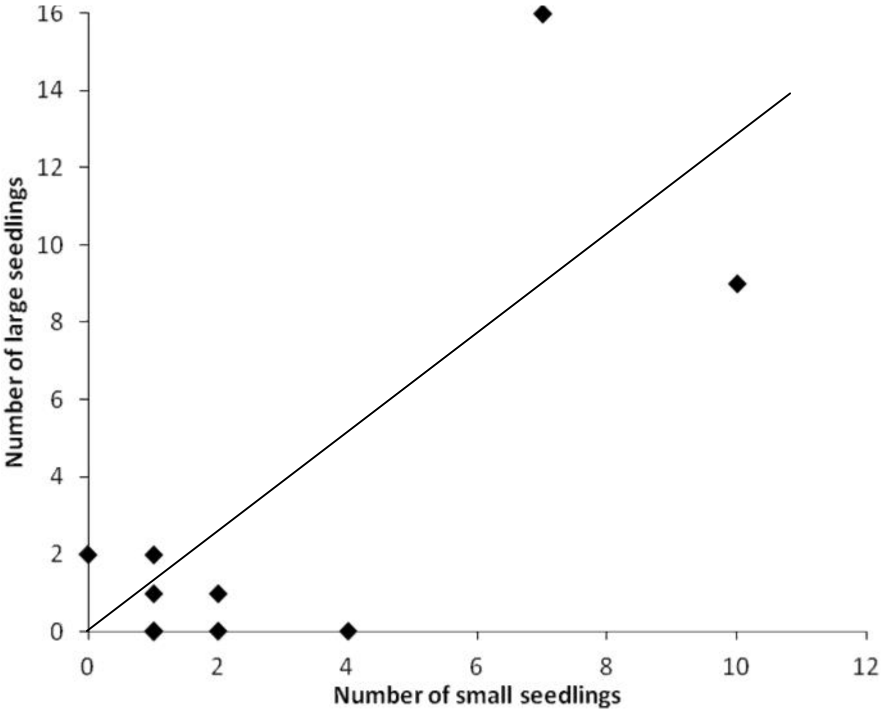

Figure 22. Kaikomako small and large seedling distribution at Tiromoana Bush

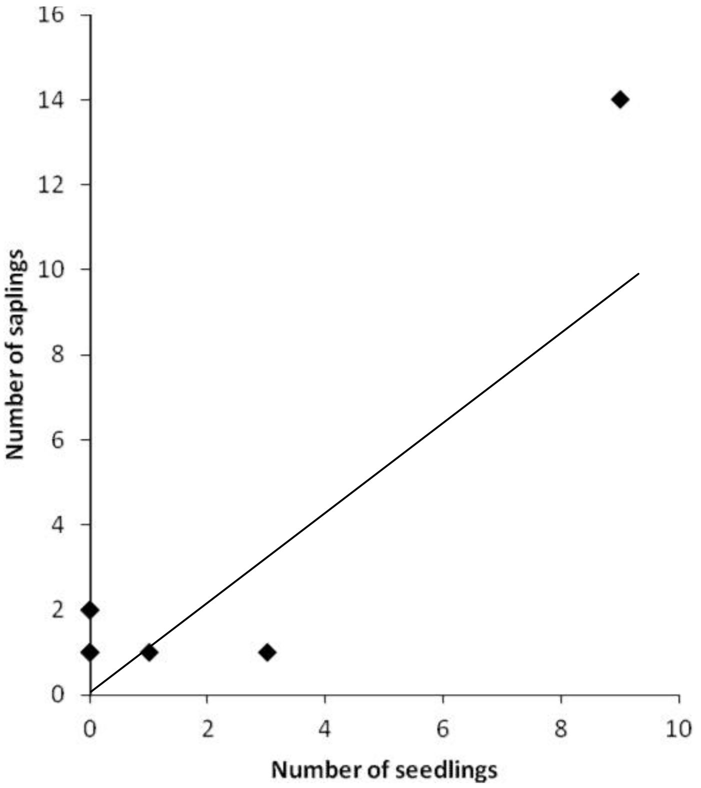

Figure 23. Golden akeake small and large seedling distribution at Tiromoana Bush

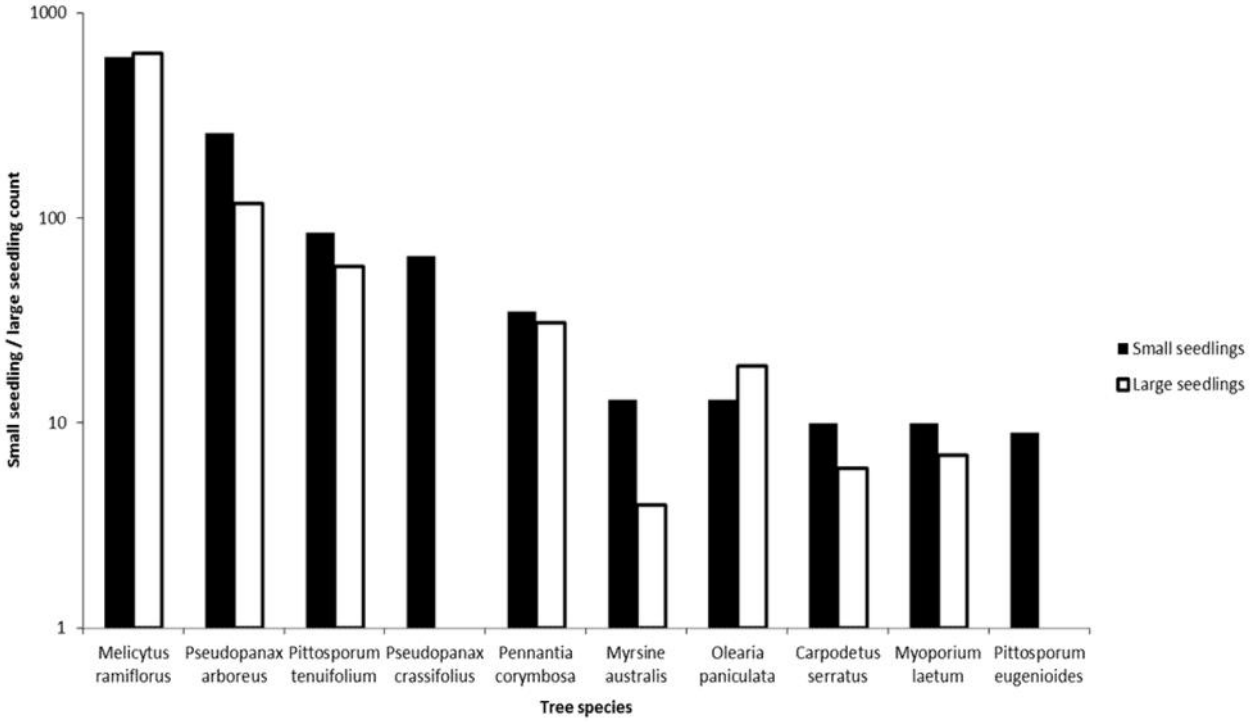

Figure 24. Canopy tree species at Tiromoana Bush. Small seedlings with large seedlings log scaled

4.2.4. Species Composition at Tiromoana Bush – Ordinations

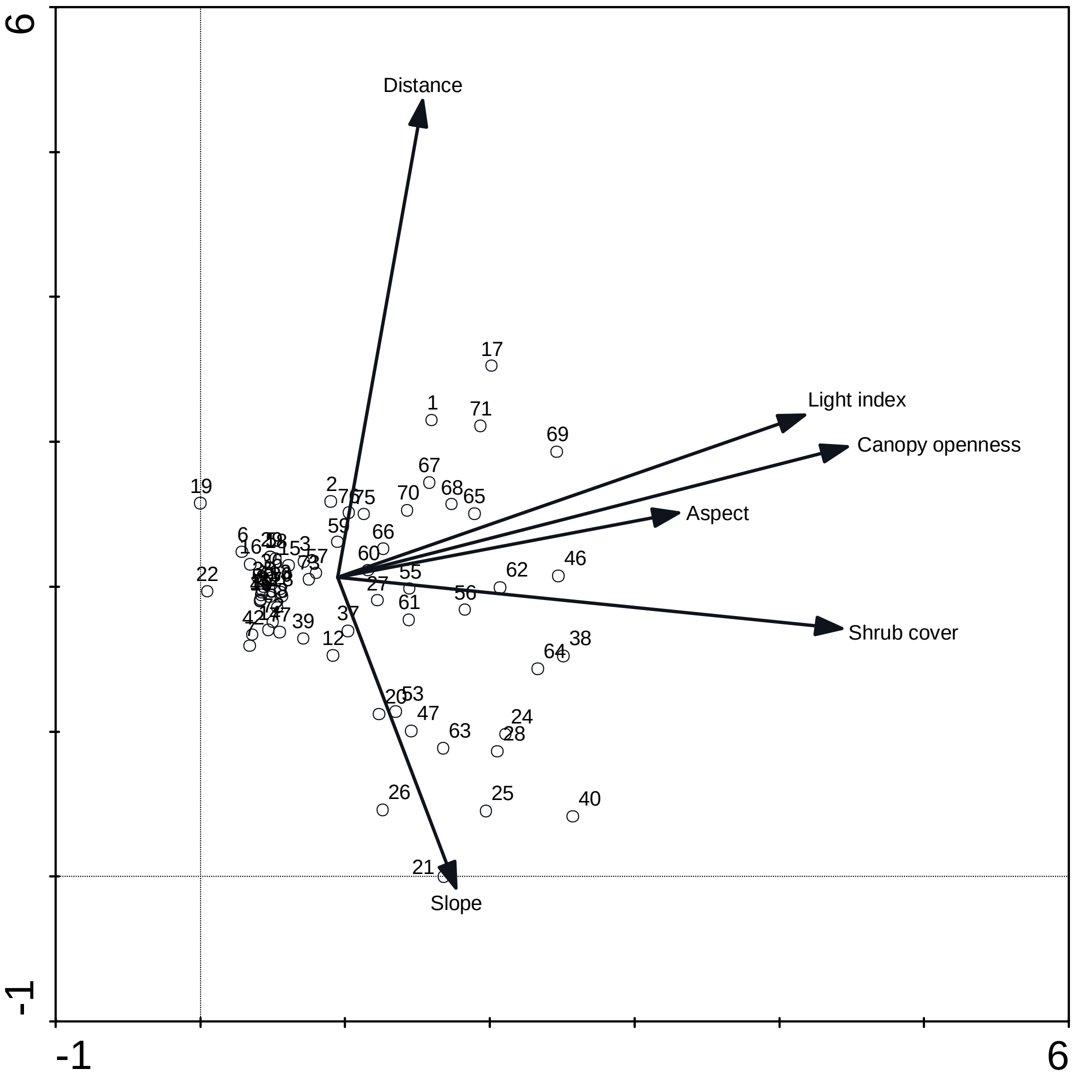

Figure 25. DCA ordination of plots (64) and environmental attributes at Tiromoana Bush where plots with nil tree species omitted (14)

The temporary vegetation survey data were ordinated by Detrended Correspondence Analysis (DCA; Figure 25). The first two axes of the DCA ordination of the temporary vegetation survey data (Figure 25) explained 19.6% and 13.5% of the total variation in the floristic data (Table 7). Gradient lengths of 2.573 and 3.525 (Table 7) respectively for axes one and two suggests that there is reasonable species turnover along both axes. The ordination had highlighted one group of plots (26/64 plots) that are tightly clustered on the left-hand side of the first DCA axis, which has a similar floristic composition. In these plots, mahoe dominated the small seedling and large seedling vegetation (46% of species composition), followed by fivefinger at 16% and kohuhu at 14%. These plots also had high kanuka canopy cover. The first axis of the plot DCA is correlated with canopy openness, which denotes variation in light entering the canopy. The vertical axis (axis two of the ordination) is correlated with slope and distance (distance from seed sources). Distance refers to how far away potential seed source trees are from the temporary vegetation survey plots. To the left of the ordination, are plots that are clustered together (Figure 25).

Plots with good light index levels, canopy openness, and shrub cover occur toward the right of the DCA (axis one; Figure 25), whilst plots with poor light index levels, limited openness of the canopy and little slope occurred to the left. The remaining plots are spread out along axis one and are also well separated on the second DCA axis (plots governing more heterogeneous floristic composition).

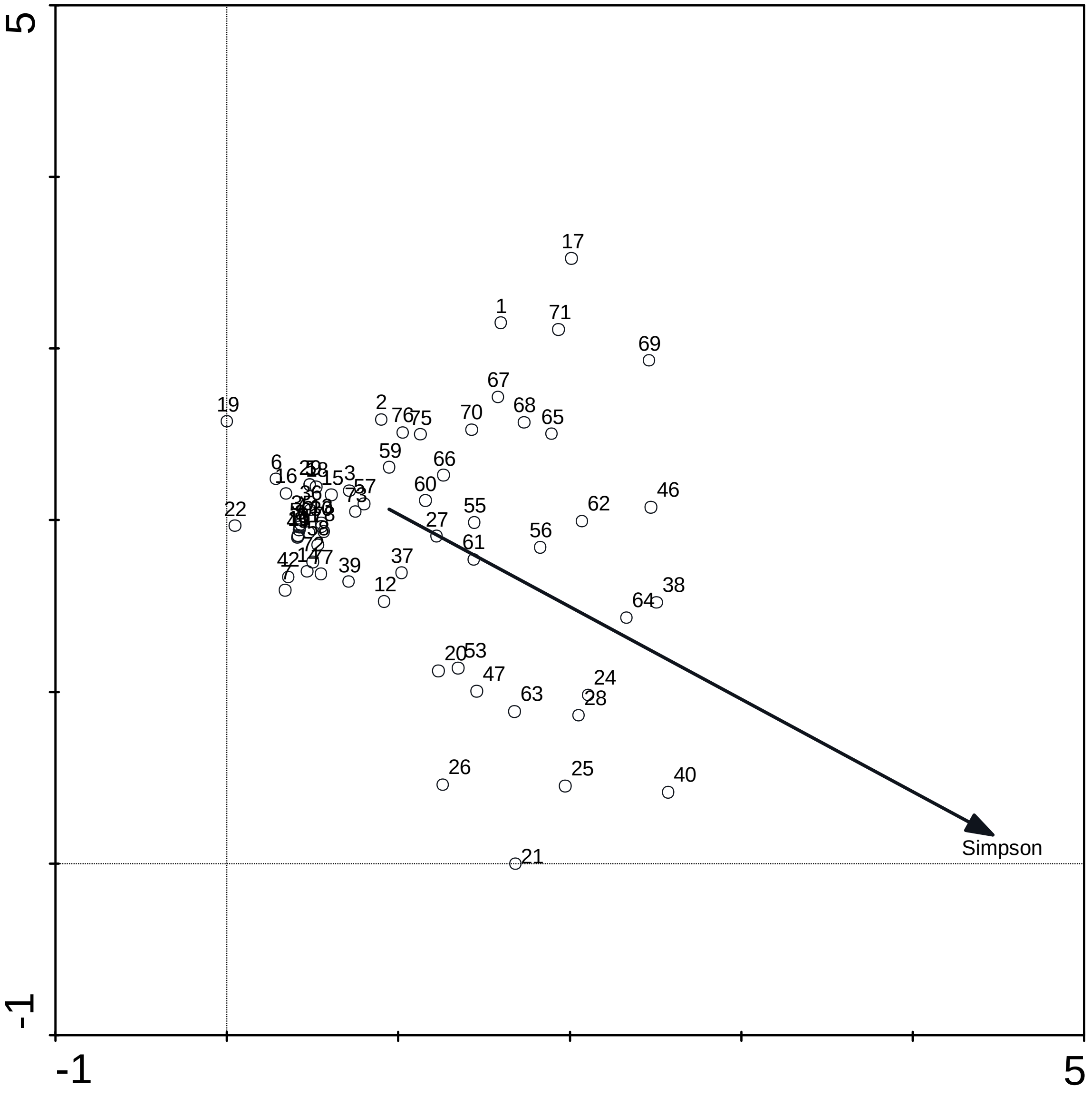

Figure 26. Sites DCA ordination with Simpson's diversity index. Plots on the DCA ordination with a higher Simpson Index value depict higher floristic diversity (plots to the right)

Figure 26 assists in the interpretation concerning temporary vegetation survey plots and their diversity regarding the number of canopy tree species that are present in each plot. Most of the temporary vegetation survey plots consisted of mahoe and fivefinger seedlings, although others consisted of seedlings of three or more canopy tree species. Plot 40 (Figure 26) was the most diverse plot regarding the number of tree species seedlings present there during the survey period of 2010-2011.

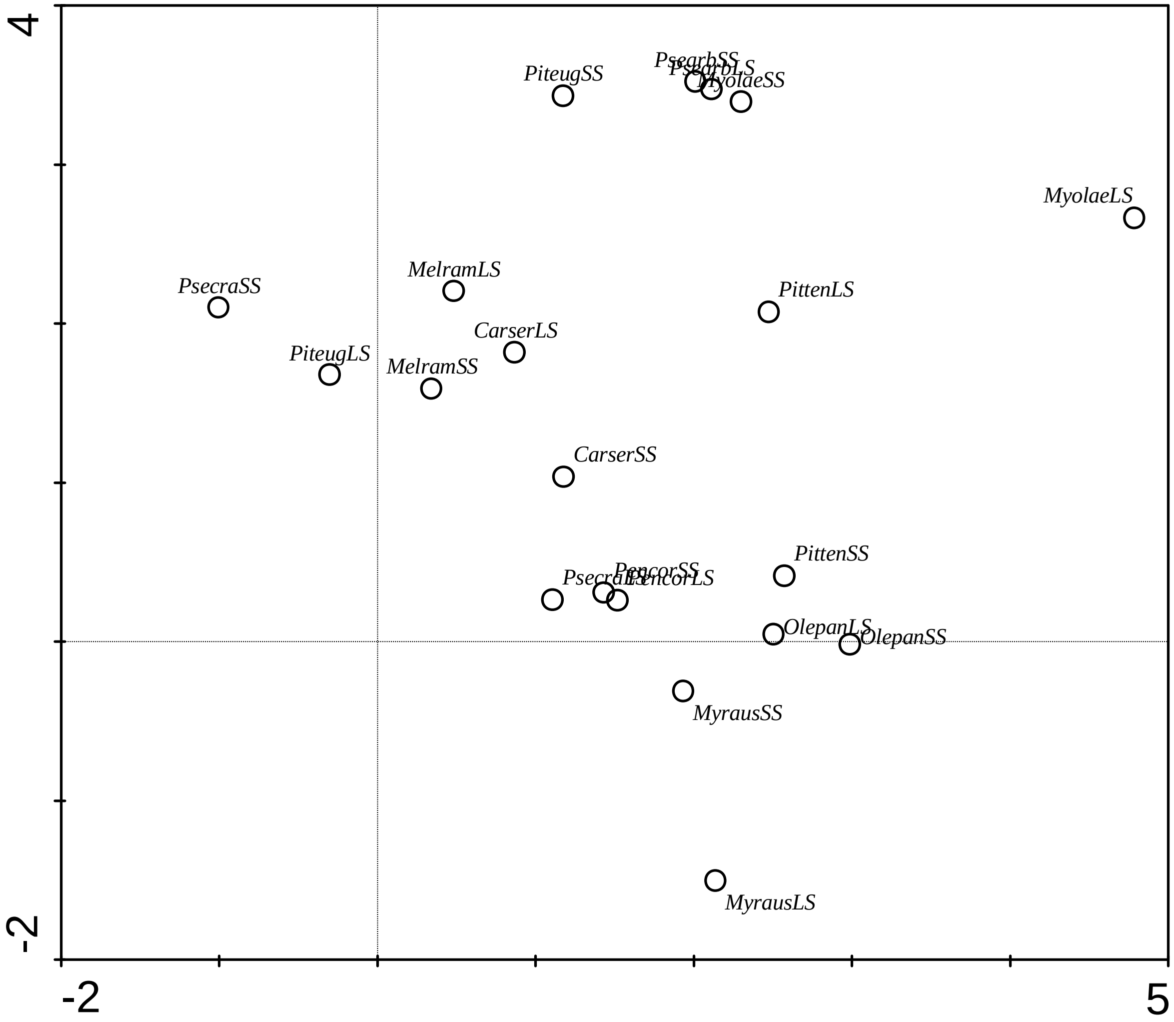

Figure 27. Species composition at Tiromoana Bush DCA ordination. The ordination represents small seedlings (SS) and large seedlings (LS) combined. First three letters define the Genus; second three letters define the species. Tree species names in full are provided in Table 6

The species DCA ordination (Figure 27) highlights the small and large seedling species that are typical of plots with different locations in the plot DCA ordination. For example, large seedlings of ngaio, small and large seedlings of kohuhu, and golden akeake small and large seedlings are more likely to be associated with plots with high values on axis one of the ordination (Figures 25 and 27). However, small and large seedlings of red matipou are more likely to be associated with slope, and small seedlings of lemonwood, fivefinger and ngaio are likely to be associated with high values on axis two of the ordination (Figures 25 and 27). Species predominantly in plots with lower light index levels are to the left of the species DCA (Figure 27). Widely dispersed species such as mahoe and kaikomako occur in the centre of the species DCA ordination (Figure 27).

Comparison of plot scores from the unconstrained DCA ordination with those obtained from a Detrended Canonical Correspondence Analysis (DCCA) ordination assists interpretation of the influence of environmental attributes in explaining the observed floristic gradients. The order of plots is also constrained by the environmental attributes which shows a good agreement between both the order of axes one and axes two scores in the two ordinations (Table 7). This suggests that the environmental variables used in the DCA ordination are likely to be important drivers of the observed floristic variation.

Table 7. Gradient lengths, cumulative variances and correlations of both axes of DCA and DCCA ordinations for canopy tree species combined – small seedlings and large seedlings with environmental attribute

Item	Ordination method	Axis 1	Axis 2
Gradient length	DCA	2.573	3.525
Cumulative percent variance (Variance explained)		19.6	13.5
Gradient length	DCCA	1.918	1.422
Cumulative percent variance (Variance explained)		7.6	4.9
Correlations of DCA and DCCA axes relationships		0.777	0.740

Table 8. Weighted correlation matrices (3 dp) derived from the DCA ordination of canopy tree small seedlings and large seedlings combined

Environmental drivers for species turnover (DCA ordination)	Weighted correlation matrix axis one	Weighted correlation matrix axis two
Slope	0.043	-0.228
Aspect	0.243	0.100
Light index	0.342	0.195
Distance	0.119	0.388
Shrub cover	0.341	0.032
Canopy openness	0.368	0.176

Table 9. Regression coefficients for the different environmental variables used to predict canopy tree small seedling distribution at Tiromoana Bush

	Mahoe	Fivefinger	Kohuhu	Lancewood	Lemonwood	Kaikomako	Ngaio	Golden akeake	Red matipou	Marbleleaf
r^2	0.02	0.08	0.04	0.002	0.02	0.04	0.04	0.32	0.03	0.01
Variable										
Canopy openness	10.227	-2.026	0.074	-25.707	-2.056	-3.946	0.960	0.017*	0.403	-2.041
Light index	-5.947	12.208	1.317	9.801	1.196	1.489	-0.649	2.165***	-0.141	1.225
Shrub cover	-39.388	-53.301	-2.822	19.726	-0.360	-2.116	3.718	0.374	0.506	-1.181
Distance	-1.545	2.368*	-0.209	-0.297	0.088	-0.242	0.022	-0.004	0.056	-0.089
Slope	0.065	-0.014	-0.001	0.078	-0.000	0.004	0.004	0.007	0.018*	0.004
Aspect	0.021	0.034	0.005	0.003	0.001	0.000	0.000	0.001	0.000	-0.000

Level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table 10. Regression coefficients for the different environmental variables used to predict canopy tree large seedling distribution at Tiromoana Bush

	Mahoe	Fivefinger	Kohuhu	Lancewood	Lemonwood	Kaikomako	Ngaio	Golden akeake	Red matipou	Marbleleaf
r^2	0.005	0.03	0.02	0.03	0.02	0.02	0.19	0.07	0.002	0.02
Variable										
Canopy openness	-3.712	8.028	3.909	-0.434	0.424	-6.303	-2.098	-0.693	-0.464	-1.588
Light index	1.728	-1.861	-2.428	0.192	0.148	2.993	1.804*	0.782	0.197	0.623
Shrub cover	-8.895	-24.945	8.873	-0.323	0.789	-7.705	3.380	-0.476	1.926	-0.735
Slope	0.135	0.102	-0.012	0.000	0.001	0.016	0.004	0.008	0.008	-0.004
Aspect	0.044	0.009	0.009*	0.000	0.000	-0.001	0.002	0.001	-0.000	-0.000

Level of significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Chapter Five: Discussion

5.1. General

This study clearly demonstrates that there is a wide range of spatial and temporal compositional variation in the small and large seedling vegetation in the secondary vegetation of Tiromoana Bush. The research provides insight into what broadleaved tree species are regenerating beneath the seral kanuka canopy and the implications this has for restoration at Tiromoana Bush.

5.2. Current Canopy Tree Seedling Composition

The most common canopy tree species in the regenerating layer at Tiromoana Bush are, in descending order of abundance, mahoe, fivefinger and kohuhu. This is supported by both the permanent vegetation monitoring plots (Figure 11) and the temporary vegetation survey plots (Figures 17 and 24).

The dominance of mahoe in the seedling stratum (where 2/3 of all seedlings are mahoe), and also that (based on the permanent vegetation monitoring plots) mahoe are rapidly moving up into larger height classes, highlighting the likely importance of mahoe in the future forest. In contrast, other tree species present are much more scarce and do not appear to be putting on height growth as rapidly. Implications of this are that mahoe is likely to form the next canopy cohort once the kanuka canopy begins to open-out and subsequently dies out. Estler and Astridge (1974) stated that mature kanuka stands (over

15 years) go through episodes of natural thinning hence increasing gaps in the canopy, initiating mahoe and other broadleaved vegetation to regenerate.

The occurrence of mahoe and its dominance over other broadleaved canopy tree species could be due to its superior colonisation potential post disturbances (Reay and Norton, 1999a). Another possible reason could be that phosphorus concentrations in the ground post aerial fertiliser application in the past, and also from wastes of grazing animals may be initiating a shift in tree species composition from less fertile-demanding species to more fertile-demanding species such as mahoe (Wardle, 1991), and this reflects upon the results that mahoe is the most common tree species at Tiromoana Bush (*sensu* Burns *et al*. 2011), even though agricultural activities have now ceased. But perhaps most importantly, mahoe produces abundant seed surrounded by flesh (in small fruits) where these contain up to six small seeds per fruit (Partridge and Wilson, 1990; Burrows 1994, 1997), and adult mahoe trees at Tiromoana Bush are rather common in the gullies. Open (post grazing) site conditions were favourable for mahoe, and also elevated levels of phosphorus may have also helped. Mahoe occurs frequently in dry forests, but seedlings are more vulnerable to drought than those of the xeric species associated with mahoe, such as kanuka (Partridge and Wilson, 1990; Innes and Kelly, 1992).

The effect of domestic grazing removal at Tiromoana Bush led to increases in canopy tree seedling abundance. The abundant regeneration of mahoe at Tiromoana Bush is most likely due to the removal of grazing animals as much as anything else.

5.3. Factors Affecting Broadleaved Tree Seedling Regeneration

Concerning seedling regeneration and establishment in any forest ecosystems worldwide, light has been hypothesised as the most important abiotic factor in order for plant growth and hence forest recovery. In this study, the main abiotic factor influencing canopy tree seedling regeneration was found to be light index. Many studies have shown that light is an important determinant for seedling regeneration, growth and survival, and hence forest turnover (Pacala *et al*. 1996; Finzi and Canham, 2000; Gilman and Ogden, 2005) in temperate forests. At low or high light levels however, there were fewer mahoe and fivefinger seedlings (Figure 15). This occurred even though mahoe, is known to be shade tolerant (Williams and Buxton, 1989). The relationship observed is that most individual seedling recruits (mahoe and fivefinger) were found in plots where light levels are moderate, as plots with low or high light levels limited seedling recruits.

Figure 28 is a conceptual view regarding the relationship between mahoe seedling densities with shrub cover in response to light levels. A number of suggested reasons for the non-linear relationships among light index levels and mahoe seedlings exist. At higher light levels, shrub cover abundance increases taking up more available space which suppresses mahoe and other broadleaved tree seedling regeneration whilst lower light levels are less conducive to regeneration. Based on what is shown by this bimodal relationship is that seedling densities, albeit mahoe or other broadleaved tree species, tend to be higher in places where enough light penetrates through the canopy to the extent that shrub cover expansion is less than for areas where light is more intense.

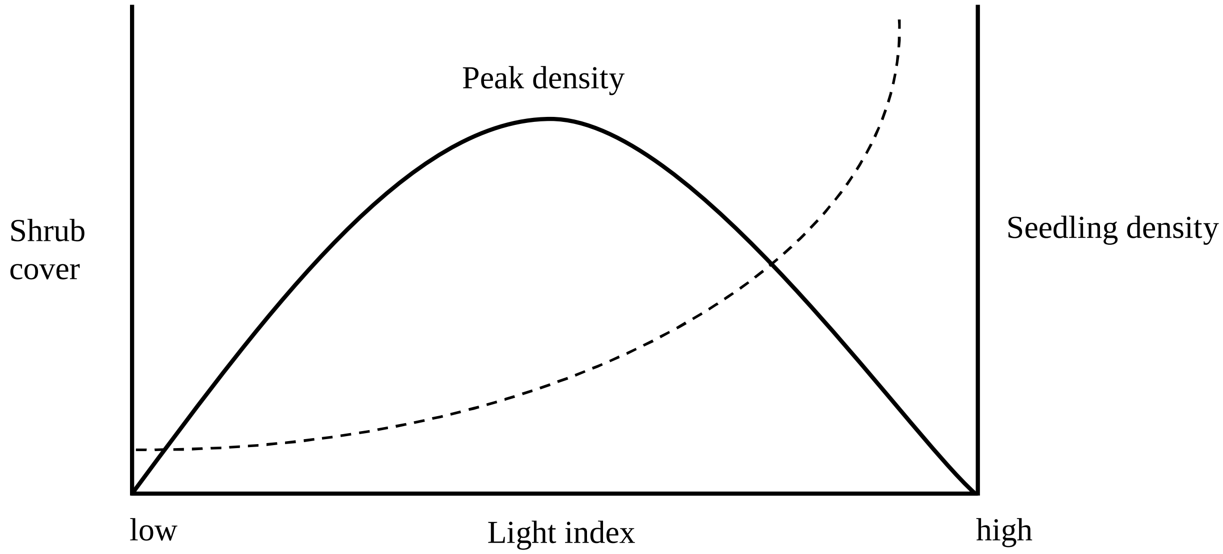

Figure 28. Bimodal relationship of mahoe seedlings and shrub cover with light. The solid line denotes seedling density; broken line represents shrub cover

The three forest patches surveyed for seedling abundance and seedling composition indicated that distance from local seed source trees, a biotic influence, was not an important factor in the regression models developed for canopy tree seedling distribution (both small seedlings and large seedlings). The three forest patches comprised major gullies which harboured adult canopy trees that were generally near the temporary vegetation survey plots (< 500 m), which suggests that in all three forest patches, the plots sampled were within bird dispersal distances. If distance to seed source trees were to be important for seedling regeneration, the consideration of perch preferences may be a factor in which birds defecate the seeds beneath the perches (Dungan et al. 2001), at greater (> 1 km) distances away from the natal site (a major remnant consistent of parent trees).

5.4. Seedling Community Patterns at Tiromoana Bush

The DCA ordination plot (Figure 25) presents floristic similarities and dissimilarities at Tiromoana Bush. With respect to light index levels, increasing tree species heterogeneity is inevitable. The data collected for this indicated that light index is the most important driver as has been observed in other studies (Pacala *et al*. 1996; Finzi and Canham, 2000; Gilman and Ogden, 2005). This is especially evident in the plot DCA ordination (Figure 26) with the Simpson's diversity index included. The plot DCA with environmental attributes (Figure 25) indicates that the plots with higher diversity also have higher light index levels. Beneath the existing canopy of young- or old-growth forests, light intensity and availability often lead to increasing tree species richness and diversity (Brockerhoff *et al*. 2003).

5.5. Future Canopy Composition at Tiromoana Bush

Based on the results gathered from the permanent vegetation monitoring plots and the temporary vegetation survey plots, mahoe, fivefinger and kohuhu respectively are likely to dominate the future canopy composition of Tiromoana Bush. More specifically, the small seedling/large seedling ratio of these tree species, 6 : 1 : 0.5, suggests that for mahoe, there is approximately six times the number of large seedlings than for fivefinger, and there is approximately half more of the number of large seedling individuals of fivefinger than for kohuhu. This could indicate that mahoe will be the dominating broadleaved tree species at Tiromoana Bush once the kanuka canopy opens out and dies. Large seedling counts over small seedlings for golden akeake suggest that this tree species may also be part of the future canopy although counts of this tree species were small compared to the other three tree species. The continued nursing effects of kanuka for other broadleaved species regeneration in the future will allow for these tree species to grow through and also form part of the next forest canopy.

Previous studies found that not only does kanuka provide a nursing environment for broadleaved tree species other species can also act as nurses as well. Gorse, an invasive prickly shrub is known to support young, vulnerable canopy tree seedlings beneath its canopy and also, gorse provides nitrogen for plant growth (Wilson, 1994; Williams and Karl, 2002). However, gorse is an invasive species and may not be desirable in some areas, as gorse can displace other native vegetation. A more attractive alternative to gorse could be flax (*Phormium tenax*; Reay and Norton 1999b), particularly in grass pastures. Flax readily reduces grassland and provides food (nectar) for bellbirds, which also play an important role in seed dispersal of broadleaved tree species. The addition of flaxes for nectar among fleshy fruits of indigenous canopy trees as alternative food sources will attract bellbirds aiding in dispersal of broadleaved tree species within Tiromoana Bush in the future.

5.6. Implications for Restoration

The removal of domestic grazing livestock has allowed regeneration of woody canopy tree species to occur (Figure 29), which reinforces the importance of removing sheep and cattle away from forest remnants. The study conducted by Burns *et al*. (2011) points out that fencing off forest patches from grazing livestock has allowed seedling regeneration to occur as opposed to patches without any form of protection from grazing.

Figure 29. Mahoe regeneration beneath a kanuka canopy (permanent vegetation monitoring plot VP7a) five years after grazing removal. The removal of grazing stock from this site has allowed rapid regeneration to occur

Given that light index is the most important abiotic factor initiating tree regeneration, natural (or mechanical) openings of the seral kanuka canopy has been suggested to benefit other broadleaved canopy tree species regeneration (*sensu* Grubb, 1977; McAlpine and Drake, 2003). This has important implications concerning restoration management particularly in order to promote the establishment of target species (McAlpine and Drake, 2003). For example, exposure to open sky promotes germination of alien weeds, such as broom (*Cytisus scoparius*; McAlpine and Drake, 2003). Therefore any canopy openings should be done over many years rather than clear-felling a large number of trees (McAlpine and Drake, 2003), but could be a useful strategy at Tiromoana Bush to facilitate regeneration.

Other restoration implications include the absence of the podocarps in the regenerating forest at Tiromoana Bush. Currently at Tiromoana Bush, the indigenous conifers (podocarps) are absent, but prior to human disturbance, podocarp tree species would have been dominant, especially totara and matai occurring as emergent trees (Norton, 2005). The primary reason for the absence of the podocarps is that there are no podocarp seed source trees at Tiromoana Bush. While the kanuka canopy will most likely be replaced by mahoe forest in future, planting of podocarp tree species is likely to be necessary to speed up their return to the forest. Growing canopy tree seedlings from local seeds is paramount for restoration as local seedlings are physiologically acclimated to where their natal parents come from. This will certainly aid in forest recovery as most seedlings will survive in their habitats provided their acclimation potential. A possible seed source area for podocarps close to Tiromoana Bush could be the southeast facing slopes beneath the Mount Cass-Totara Ridge, approximately 2 km northwest of Tiromoana Bush (Norton 2005). This area today (and pre-disturbance times) consists of extant totara and matai forest. The substrate of the Mount Cass-Totara Ridge is dominated with limestone and loess, meaning that totara and matai sourced from the Mount Cass-Totara Ridge are likely to be acclimated to the environmental conditions at Tiromoana Bush.

5.7. Study Limitations

These are two-fold.

5.7.1. Restriction of study sites:

This study was focused at Tiromoana Bush. A possible limitation could be the restriction of study sites. This being the case of significance especially when needing to understand fully the processes and dynamics of seedling recruitment and determining future canopy composition. Other areas, especially the Port Hills (Reay and Norton, 1999a) and Hinewai Reserve (Wilson, 1994) go through similar processes regarding future forest composition and canopy tree seedling recruitment. Including data from these sites together with Tiromoana Bush would have potentially, aided in developing a more sound and complete coverage of forest regeneration overall.

5.7.2. Environmental Attributes:

Soil moisture: At any one site and at different times, soil moisture levels always change. Soil moisture, an abiotic influence affecting plant growth and survival may well be a limiting factor in the study area. During the summer, most areas in the three sampled forest patches were rather dry and this could have limited seedling distribution in places. However, soil moisture as a variable was not assessed.

Browsing: A biotic factor especially in the permanent vegetation monitoring plots. This was a limiting factor because numerous seedling individuals in the permanent vegetation monitoring plots (particularly mahoe) experienced browsing as their tops were removed. Measuring height thus was impacted negatively for these seedling individuals. Seedling mortalities following mammal clipping behaviour also limited this study as the loss of individuals through mortality affected data collection, in particular height data and counts of individuals within these heights. Browsing is most likely due to deer and possibly hares.

5.8. Areas for further research

Further research aimed for restoration of indigenous forests should primarily focus on seed dispersal, seedling recruitment and an assessment of restoration success.

5.8.1. Seed dispersal:

Seed dispersal is a fundamental process in order for new seedlings to establish in new areas away from their natal parent trees. Seed dispersal in this manner avoids potential in-breeding (Wenny, 2001). Seed dispersal dynamics in forests including the processes of avian and mammalian dispersers initiating dispersal is a large area of research ultimately relating to forest development over time and promoting restoration in the long-term.

5.8.2. Seedling recruitment:

Seedling recruitment determines the overall health of the forest. Whilst seedling recruitment takes place at any seasonal times, seedling recruitment is a prerequisite in order for evident forest restoration taking place. Further study on this should focus on recruitment potential of particular tree species and what this means for forest restoration, and also for overall forest health both florally and faunally.

5.8.3. Restoration success:

This particularly refers to forest development over time through the processes of seed dispersal and seedling recruitment. Restoration success also encompasses non-human mediated processes partaking in natural dynamical processes. Further research on this broad topic is likely to focus on tree species composition and abundance, together with native bird population dynamics (as birds are primary seed dispersers in forests), as the regenerating forests at Tiromoana Bush continue to develop.

Chapter Six: Conclusion

This study aimed to predict and thus understand the likely environmental factors affecting future forest composition at Tiromoana Bush. The future composition of Tiromoana Bush is related to what canopy tree species are currently most numerous in the seedling stratum. Based on the results presented here, both the absolute numbers and the ratios of canopy tree small seedlings and larger seedlings, mahoe, fivefinger and kohuhu are likely to dominate the broadleaved canopy of Tiromoana Bush in the future (50-100 years time), but with mahoe the most dominant broadleaved canopy tree species.

The abundance of mahoe as a seedling is most likely due to adults of this species dominating the gullies running through the regenerating kanuka stands; adult mahoe produce numerous fruits each consisting of up to six seeds, as well as being persistent (as seedlings) in areas that are shady as well as with moderate light index levels. The rapid relative growth rates and number of mahoe seedling individuals over the other canopy tree species suggest that mahoe will persist as seedlings more so than the other canopy tree seedlings.

It is likely that the kanuka canopy will soon die out and thus be replaced by a mahoe forest with fivefinger and kohuhu, the main associated broadleaved canopy tree species. While kanuka will be naturally replaced by mahoe, fivefinger and kohuhu, the replanting of podocarp species is likely to be required to ensure their return as part of the forest composition in the near future because seed sources are not locally available.

This study and other research shows that kanuka provides environmental conditions suitable for broadleaved tree seedling development in the understorey. The removal of domestic livestock has led to the first signs of restoration success, through seed dispersal and seedling recruitment, thus individual canopy tree seedlings are able to colonise new areas without the pressures of grazing by domestic stock. However, the presence of animal pests (e.g. deer) and their negative consequences upon the broadleaved seedlings needs further study in order to develop long-term management strategies for this and other restoration projects.

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