

Restoration of Canopy Tree Species in Degraded Eastern South Island Ecosystems

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Degree of

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By

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Please detail the nature and extent (%) of contribution by the candidate:

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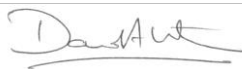
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ABSTRACT

The history of ecosystem disturbances has altered most of the original forest ecosystems in New Zealand especially those associated with the eastern zone of the South Island where fire and pastoral farming have transformed much of the forestlands into degraded grasslands and shrublands. While these communities are viable conservation areas for biodiversity in restoration schemes, they require active human intervention to facilitate natural regeneration and the success of restoration planting project. Thus, in the context of managing early-successional communities for forest restoration, understanding the effects of any intervention will have important implications to the sustainability of any restoration measure as restoration outcomes may vary with target species, vegetation, and disturbance regimes involved.

This research addresses three key research questions: (1) Whether long-term protection alone (e.g. grazing exclusion) is sufficient to facilitate the establishment of canopy trees and other native woody species in regenerating communities; (2) Whether canopy disturbance regime can be a viable intervention to accelerate forest succession and/or establishment of canopy species in degraded early-successional communities; and (3) Whether early-successional communities can be managed as nurse vegetation for canopy species restoration in degraded and stressful environment. To answer these questions, I examined the succession in an intact canopy of regenerating kānuka (*Kunzea robusta*, Myrtaceae) forest in abandoned pastureland by utilizing long-term data from permanent vegetation plots to describe the changes in species composition, density, and growth of native woody species over time. Two separate restoration trials were then established within the regenerating kānuka forest to examine respectively the succession of native woody species in response to artificial canopy gaps and the establishment of canopy species in response to different canopy manipulation methods. Nurse-protégé or plant-to-plant interaction between canopy species and early-successional shrubland communities with different canopy interventions were also assessed in a degraded high-country environment to determine whether regenerating shrub communities can be managed to serve as nurse plants to restoration planting in post-disturbance grasslands.

The findings of this research demonstrate that canopy intervention, particularly small-scale canopy gaps, is a viable management option to facilitate the regeneration and establishment of canopy species within degraded and dense early-successional communities.

Small-scale canopy gaps can provide favourable growing conditions for canopy species including the mitigation of the intensity of competition, improvement of species tolerance to the impacts of herbivory by ungulates, and the provision of opportunities for co-existence with other regenerating native woody species with different shade tolerance traits. The findings, however, show that while succession can benefit from canopy intervention, regeneration can be slow even in gap environments especially in degraded seral communities with inadequate seed sources or with seed dispersal limitation. Moreover, results from the nurse-protégé interactions between canopy species and shrub communities in post-disturbance grasslands indicated that dense early-successional communities can be managed to serve as a nurse vegetation to facilitate the initial growth and survival of canopy species in stressful environment.

These restoration benefits from canopy interventions are relevant to the management goals in New Zealand Canterbury region that include conservation of native biodiversity and restoration of representative habitats and ecosystems that have been lost or severely degraded. While the focus of this research was the eastern South Island, the findings are likely to be relevant as well to other areas in New Zealand and in many parts of the world as the dominance of early-successional communities such as grassland and shrubland in stressful or degraded conditions are typical over large areas especially in tropical and subtropical environments.

1. CHAPTER ONE

INTRODUCTION

1.1. CHANGES IN NEW ZEALAND'S NATIVE FORESTS

New Zealand is considered one of the last landmasses in the world to be inhabited by humans. Prior to Polynesians arrival in the late 13th century, most of the landmass is believed to have been covered by forest extending about 75-80% of the total land surface area (Graham et al., 2012; Perry et al., 2014). Since human settlement, however, New Zealand forests have been exposed to a range of disturbances operating at different spatial and temporal scales (Norton & Miller, 2000). The most significant of these have been fire (Burrows, 1996; Guild & Dudfield, 2009; Perry et al., 2014; Rogers et al., 2007; Williams, 2009), logging/felling (Carswell et al., 2012), and the impacts of invasive animals and plants (Halkett, 1991; Norton, 2009). Fire, both deliberate and accidental, has been an important agent in the changes and development of New Zealand many ecosystems, especially in the reduction of native forest cover to only about 23-25% of the land area (Burrows, 1996; Perry et al., 2014). Although fires occurred in New Zealand millions of years ago mainly from volcanic eruptions (Guild & Dudfield, 2009), historical evidence suggests that the frequency and severity of fires have dramatically increased since the time the first Polynesian settlers inhabited the pristine forests of New Zealand (Burrows, 1996; Halkett, 1991).

Deforestation mainly by fire occurred with Polynesian settlement and continued throughout centuries until much of the more fire-susceptible forest had been razed (Halkett, 1991). Since the time of European colonization in the first half of the 19th century, uncontrolled fires together with destructive logging have destroyed more than eight million hectares of remaining forest cover in less than a century-and-a-half (Guild & Dudfield, 2009). It was during this period where extensive conversion of forestlands to agricultural was initiated since much of the timbers extracted (such as *Agathis australis*, *Dacrycarpus dacrydioides*, and *Podocarpus totara*) in forest clearances were of significant economic resource for the growing colony (Graham et al., 2012). With the perception that native tree species were slow growing, exotic tree species were eventually introduced and favored (that include *Pinus radiata*, *P. sylvestris*, *Cupressus macrocarpa*, and 47 other important timber species) to sustain the

country's growing timber requirements (Graham et al., 2012; Williams & Cameron, 2006). With large areas degraded to scrub or tussock grassland, pastoralists began to realize the grazing value of inland grasslands and consequently the use of fire as a good practice by burning one-quarter of the land each year mainly to eradicate the unpalatable plants, facilitate access, and promote fresh regrowth palatable to stock (Ledgard & Baker, 1988).

Thus, cultivation and pastoralism intensified since then which further altered the native vegetation, accelerated the erosion rates, and increased the opportunities for introductions, naturalizations and spread of exotic plants and animals (Ledgard & Baker, 1988; Walker et al., 2009b; Williams & Cameron, 2006). All introduced species are now a key concern in New Zealand as they continue to exert substantial pressure on native biodiversity (Norton, 2009). Many of these exotic plant species (particularly *Pinus* spp., *Acacia* spp., *Hakea* spp., *Ulex europaeus*) along with invasive mammalian species (that act as predators of plants and seed-dispersing birds) now co-exist with the remaining native flora in communities whose long-term successional trajectory and composition are still poorly understood (Perry et al., 2014). Norton (2009), however, stressed that even with the elimination of invasive species, the future composition of New Zealand forests will not be the same as that prior to invasion, thus, posing long-term challenges to forest restoration efforts.

The recent review on forests dynamics by Wyse et al. (2018) highlights the unpredictability of the New Zealand forest successions, with many of its ecosystems have been transformed into new, non-historical configurations or novel assemblages of native and exotic species owing to past and present disturbances of different types, frequencies, and magnitudes. The authors stressed that further alterations to disturbance regimes or to species interactions by invasive species, introduced plant pests and diseases, and climate change have wide-ranging consequences for New Zealand ecosystems including trajectory of community change and species diversity.

The history of ecosystem disturbances in New Zealand has therefore altered most of the original woody ecosystems including those associated with the eastern 'drylands' zone of the South Island where much of the forest was destroyed by fire and transformed rapidly to grasslands, fernlands, and successional shrublands (McGlone, 2001; Walker et al., 2009b). This zone has one of the longest human disturbance and weed invasion histories in New Zealand (Lee et al., 2006) and the most pronounced forest loss; hence issues arise on the long-

term stability of the existing grasslands and to what extent the remaining woody components within them will persist (McGlone, 2001). Ecological restoration in this zone is even more challenging because the eastern regions are considerably drier than western regions (which is caused by the dominance of desiccating westerly winds and low rainfall), hence, referred to as the ‘eastern New Zealand drylands zone’ (Rogers et al., 2005). The dryland condition is largely due to the unbroken axial chain of mountains (the Southern Alps) in the South Island, thus, creating a distinct physical barrier and causing more moisture to be precipitated in the west where mean annual totals can exceed 10,000 mm in the westernmost ranges (Wardle, 2002). The ‘eastern drylands’ zone has an average Penman annual water deficits of ≥ 270 mm (Rogers et al., 2005) with periodic summer drought and frequent dry north-west winds, conditions which favor fires and restrict the growth of a protective vegetative cover (Ledgard & Baker, 1988). The extremes of 42°C and -20°C temperatures were also recorded in eastern South Island since the area is subject to föhn (or foehn) winds and severe frost (Wardle, 2002).

1.1.1. Why restoration is required in New Zealand Dryland Zone

Restoration of indigenous habitats in dryland environments is indispensable for ecological and economic reasons. Dryland represents 41 percent of the earth’s land area with around two billion people being dependent on environmental services that dryland forest ecosystems provide (EMG-UN, 2011). However, an increasing area (ca. 6 million km² or 10%) of dryland ecosystems are classified as highly degraded or with high desertification risk (EMG-UN, 2011). Thus, active interventions to reinitiate forest recovery in dryland environment at a local scale will have sustainable implications or would provide empirical data on dryland ecosystems management around the world especially in reversing the processes of dryland degradation and desertification at these times of climate change.

Similar to other highly modified dryland habitats elsewhere (EMG-UN, 2011), the New Zealand dryland zone is an important and viable resource of native biodiversity in restoration schemes (Norton et al., 2018). It still represents all that remains of a unique and diverse ecological zone that covers about 19% (53,000 km²) of the New Zealand land area (Walker et al., 2009a). However, the dryland zone contains some of the country’s least well protected native habitats as well as the most transformed and endangered ecosystems (Walker et al., 2009a). It is also projected to change towards a highly degraded state as species invasion by competitive grass (e.g. *Dactylis glomerata*), woody species (e.g. *Crataegus monogyna*,

Sambucus nigra, *Salix elaeagnos*, *Prunus cerasifera*, *Rubus fruticosus*, and *Clematis vitalba*) and animal predators (such as exotic mammals, birds or invertebrates) that now co-exist with native vegetation communities can impose key biotic thresholds limiting the success of ecological restoration projects (Norton, 2009, 2012). While the ecology, impacts, and control of invasive species have been dominant research subjects in New Zealand for more than a century (Lee et al., 2006), continued extinction of native biodiversity in the dryland zone seem inevitable unless active restoration and management of invasive species are undertaken (Norton, 2009). At present, the dryland environment is still poorly represented in public conservation lands in New Zealand with only about 1.9% of the total land area of the dryland zone is under legal protection (Rogers et al., 2005; Walker et al., 2009a).

Although the processes of vegetation recovery of degraded ecosystems are unpredictable even following restoration projects, some generalizations can be made. Active restoration of drylands (either through restoration plantings of woody species or assisting successional trajectory) to initiate and speed up assemblages of native woody communities is likely to support significant local biodiversity while delivering ecosystem services that these forests are known to provide such as carbon sequestration, soil and water conservation, atmospheric regulation and pollination (Bullock et al., 2011; Harrison et al., 2014; Rey-Benayas et al., 2009). A meta-analysis by Rey-Benayas et al. (2009) of 89 restoration assessments in a wide range of degraded and disturbed ecosystems across the globe, showed that ecological restoration can increase both the provision of biodiversity and ecosystem services by 44 and 25%, respectively. Once an ecosystem is restored, woody communities can continue to modify ecosystem thresholds that limit natural succession and eventually catalyse the establishment of more mature and diverse communities and quality ecosystem functionality (Cortina et al., 2011; Zhang et al., 2005). This improved functionality will, in turn, boosts the resilience of the ecosystem especially against biological invasion, which otherwise could be too expensive to manage (Ramsey & Norbury, 2009), by acting as a filter thus constraining invasive species while allowing colonization by native species (Bakker & Wilson, 2004). Such resilience is supported well by community ecology theory that invasive species will be unlikely to establish if available niches are filled (Funk et al., 2008). In a recent experiment in dryland environment, for instance, Cieraad et al. (2015) observed that exotic woody species are not significantly superior in growth rates than native species along the nutrient and moisture gradients indicating the potential of creating native-dominated woody vegetation cover in drylands. Moreover, Thompson (2011) noted strong evidence that forest resilience is strongly

tioned to biodiversity as each species or groups of species perform key functions in forest critical to sustaining ecosystems functional processes. A key function like pollination is known to support plant reproductive sustainability especially in restored ecosystems and is responsible for most biological and genetic diversity (Dixon, 2009; Friedman & Barrett, 2009; Menz et al., 2011).

However, because of habitat fragmentation along with changes in land-use, use of chemicals such as pesticides and herbicides, and invasions of exotic plants and animals, pollination systems have become increasingly endangered (Kearns et al., 1998). One important consequence of disruptions in plant-pollinator mutualisms is a reduction of seed production, which in turn can negatively influence the sustainability of successional processes and recruitment (Harris & Johnson, 2004). This relationship along with other kinds of mutualisms that normally occur in ecosystems such as plant-insect mutualism (Bronstein et al., 2006) and plant-fungi symbiosis (Bidartondo et al., 2011) is a microcosm that highlights the importance of forest restoration, either artificial or natural, in degraded dryland ecosystems.

On the other hand, since many farmers remain dependent on New Zealand dryland ecosystems to sustain farm productions (Hunter & Collins, 2008), they will be the most vulnerable to future drought (Burton & Peoples, 2014). For years, pastoral farmers in New Zealand drylands usually have to cope with drought by measures such as de-stocking, but the long-term impact has been economic hardship and only fewer farmers were able to adapt to drier condition (Ogle, 2008). Thus, restoration of native forest cover in the dryland zone at these times of changing climate will not only improve ecological services (e.g. soil and water conservation) but will have sustainable development implications that can translate to increase economic benefits and invigorate farming practices of local farmers (Ffolliott et al., 1995).

1.1.2. Factors affecting forest restoration in New Zealand dryland zone

Restoration plantings and facilitating natural regeneration to occur are common strategies for forest restoration in degraded environments (Cortina et al., 2011). However, these strategies are often confronted, especially successional-based restoration efforts, by a number of biotic and abiotic factors that act as barriers or filters to restoration success, and failure to recognize them can be costly to restoration projects (Hobbs, 2007; Hobbs & Norton, 1996, 2004; Suding et al., 2004; Tambosi et al., 2014; Young et al., 2005). Similar to many restoration

constraints in degraded landscapes elsewhere (Hobbs & Norton, 1996; Suding et al., 2004), the following barriers could be significantly at play in degraded New Zealand dryland zone that can influence the success or sustainability of its restoration programs:

1.1.2.1. Altered environmental conditions

With the long history of degradation in New Zealand landscapes as a result of sustained pressures from fire, felling and species invasions, it is possible that some of the present ecosystems (e.g. grasslands and shrublands) have crossed ecological thresholds or have developed into novel states or assemblages that are difficult to reverse (Cieraad et al., 2015; Hobbs et al., 2006; Hobbs & Norton, 2004; Norton, 2009). An ecological threshold is described as “the point at which there is an abrupt change in an ecosystem quality, property or phenomenon, or where small changes in an environmental driver produce large responses in the ecosystem” (Groffman et al., 2006). When critical thresholds are crossed, new ecosystem states are formed that are completely different from their original configurations and functions hence described as ‘novel ecosystems’ (Hobbs et al., 2009).

Other authors argued against the use of the term ‘novel ecosystem’ and the absence of evidence to demonstrate that ecological thresholds would prevent the ecological restoration of an ecosystem (Murcia et al., 2014). Yet some ecosystems subjected to a range of disturbances or degradations could barely recover their structure and ecological functions even after abandonment or management interventions (Chapman & Chapman, 1999; Lockwood & Pimm, 1999; Zedler & Callaway, 1999), and there are those that have recovered unaided to become native species-rich ecosystems (Hölzel et al., 2002; Lamb et al., 2005; Rosales et al., 1997). These may suggest that degraded lands can vary in their capacity to recover or can respond differently to management interventions depending on the history and age of disturbance (years vs decades), magnitude of degradation, identity of residual vegetation, seed banks, seed sources availability, among other factors (Guariguata & Ostertag, 2001; Hobbs & Norton, 1996; Lamb et al., 2005). Thus, whether in novel state or not, ecosystems with altered, transformed, or degraded environment such as the degraded tussock grasslands in New Zealand and other degraded ecosystems elsewhere (cf. Hobbs et al., 2006; Jäger & Kowarik, 2010; Jimenez et al., 2013; Venton, 2013) present a serious and long-term challenge to restoration.

In New Zealand, the observed decline or changes in species configurations of many early-successional communities such as grassland (Duncan et al., 2001; Norton & Young, 2016b) only indicate the need for a comprehensive and active restoration measures besides the removal of degrading factors and/or re-introducing lost species to improve the systems conservation values and overcome restoration thresholds that exist (Hobbs & Norton, 2004; Norton et al., 2018). Removal of degrading factors (e.g. grazing, herbivory) and allowing degraded lands to naturally regenerate are important themes in New Zealand forest restoration programs (Dodd & Power, 2007; Ewans, 2004; Norton & Young, 2016a, 2016b), but the slow forest recovery from such interventions further validates the idea that restoring degraded ecosystems may depend strongly on the site-specific conditions (cf. Hobbs & Norton, 1996; Lamb et al., 2005). There is already a good body of information available on the succession dynamics of New Zealand indigenous flora in disturbed environments (e.g. Baxter & Norton, 1989; Duncan et al., 1990; Miller & Wells, 2003; Nancy, 1999; Reay & Norton, 1999a; Stewart & Veblen, 1982; Walker et al., 2014; Wardle, 1980) including an intensive review of substrate requirements for regeneration of dominant native tree species (Stewart, 2002) that could provide viable options for re-establishing later-successional forests. However, Hobbs and Norton (2004) suggested that the approach is to consider factors that are likely to be important in the restoration success in a given situation as each system is likely to be different. The restoration priorities do not need to dwell only on the restoration of degraded ecosystems to their historical analogs, but the improvement of their current condition or function to build resilient systems that can withstand the impacts of climate change, habitat fragmentation, and other anthropogenic induced stresses (Chazdon, 2008; Harris et al., 2006; Hobbs & Cramer, 2008).

1.1.2.2. Dispersal constraints

Dispersal of seeds is identified as one of the most significant factors influencing regeneration or recruitment in many degraded fragmented landscapes and successional areas such as reforestation sites (Gonzales & Nakashizuka, 2010; Hérault et al., 2004; Koonkhunthod et al., 2007; Nagaike et al., 2012; Parrotta et al., 1997) and grasslands (Duncan & Duncan, 2000; Matsumura & Takeda, 2010; Zanne & Chapman, 2001) where a significant decrease in species richness or regeneration density with increasing distance from seed sources is a common concern. Zanne and Chapman (2001), however, observed that not all sites adjacent to a seed source had equal amount of regeneration (i.e. in terms of species richness and stem

density) as variability in site characteristics (e.g. percent herb, grass/fern, and seedling cover, degrading factors) exists even among similar vegetation types at the same sites. Thus, for successful regeneration or recruitment to occur, it is both critical that local seed sources are available and successional sites are able to support early stages of plant development from seed germination to seedling establishment and survival (Caspersen & Saprunoff, 2005).

In highly fragmented dry habitat, availability of seed sources is a key limitation to regeneration success since many native trees growing in dry condition often lack adaptations for long-distance dispersal (Thompson et al., 2014). Such situation highlights the important role of different dispersal syndromes like anemochory, zoochory, ornithochory, among others (Van der Pijl, 1982) in facilitating seed dispersal and species distribution. However, in New Zealand, while seed rain (including seed bank) is a potential source of recruits for many native woody species, the regeneration of native forest is not guaranteed as some species do not establish in dense stands and are sensitive to competition, and would require some active human intervention such as reintroduction of some native species, canopy manipulation, and removal of exotic species (Moles & Drake, 1999).

Moreover, the decline in the abundance of seed sources and dispersal agents especially bird species after forest degradations have been recognized to limit mutualistic relationships that are critical to seed dispersal (Kelly et al., 2010; Norton, 2009) as significant numbers of native species in New Zealand are bird dispersed (Beveridge, 1973; Canham et al., 2014; Norton & Kelly, 1988). The incidence of mast seeding of many New Zealand flora including beech and podocarp species (Beveridge, 1973; Smale et al., 2012) are also presumed to have cascading effects on seed consumers (especially avifauna) and consequently on seedling recruitment and migration as these are all dependent on dispersal (Canham et al., 2014; Norton & Kelly, 1988; Sullivan & Kelly, 2000). For instance, the incidence of years with poor seed production in podocarps was observed to be more apparent than the incidence of years in which all species fruit well (Beveridge, 1973). Even the ripening and quality of seed borne by individual podocarp trees can vary considerably within areas of similar forest type, aspect and altitude (Beveridge, 1964) suggesting that a great number of seeds would be needed to get a reliable number of propagules for dispersal, planting and/or effective regeneration. Canham et al. (2014), for instance, reported that local seed rain of some native canopy species in New Zealand temperate rainforest may decline steeply with increasing distance from local seed sources, with highest local dispersal within 6 m from parent trees. Even the lightest seed among the New Zealand podocarps, which is produced by rimu (*Dacrydium cupressinum* Lamb.), the

sound seeds usually fall attached to well-developed fleshy receptacles which can only be removed by birds (Beveridge, 1973). Hence, many seeds especially podocarps are hardly dispersed more than 20 m from their parent tree in the absence of seed-dispersing birds (Beveridge, 1973; Norton & Kelly, 1988).

Interestingly, the study of Young and Kelly (2014) in the fragmented landscape of Canterbury Region, South Island, has provided no evidence for large-scale dispersal failure despite changes to dispersing animals, suggesting that some mutualisms could be resilient to disturbance or forest degradation (Dick, 2001).

1.1.2.3. Mammalian herbivory/predation

Increased abundance of ungulates is identified as one of the major drivers of change in the structure and configurations of many temperate forests worldwide (Rackham, 2008). For instance, studies in North America that have examined the influence of white-tailed deer have reported that deer density is frequently positively and significantly correlated with the magnitude (spatial and temporal) of herbivory effects on vegetation (reviewed in Russell et al., 2001). Most of the studies reviewed have linked herbivory effects to a reduction in growth rates and survival of tree seedling and saplings and decreased in size distributions of populations of preferred palatable species by preventing recruitment to sapling or adult sizes, which consequently affected species diversity and identity of dominant species. In a temperate forest in Europe, high ungulate densities (e.g. deer, moose, mouflon, and wild boar) have substantially caused shifts in population dominance by hindering woody species regeneration and increasing species-richness and dominance of ruderal herbs, which was highly facilitated by ungulate-mediated dispersal (Vild et al., 2017). Although experimental measures to address the effects of herbivory through ungulates exclusion have indicated significant positive gains in terms of species diversity, plant growth, and abundance in woody species recruitment, some preferred herbaceous forage species still appear to dominate forest understories in the presence of ungulates (Habeck & Schultz, 2015; Kuijper et al., 2010). These negative effects of herbivores, however, is not ubiquitous on temperate ecosystems as some studies revealed insignificant impacts of herbivory on tree regeneration and establishment even following canopy disturbance, (Forrester et al., 2014; Holladay et al., 2006; Naaf & Wulf, 2007) perhaps

because herbivory effects may vary among habitats or could be due to a lower density of herbivores in the area.

In New Zealand, the adverse impacts of different mammalian herbivores (such as *Cervus elaphus*; *Trichosurus vulpecula*, *Oryctolagus cuniculus*, *Mus musculus*, *Rattus rattus*) on native vegetation or species have been extensively documented (e.g. Atkinson, 2001; Gillman & Ogden, 2003; Glen et al., 2012; Grüner & Norton, 2006; Husheer et al., 2006a; Husheer et al., 2006b; Nugent et al., 2001; Wardle et al., 2001; Wilson et al., 2003; Wilson et al., 2006; Wilson et al., 2007). Although some forest fragments under conservation management can be resilient to ungulate browsing or predation (Dodd et al., 2011), some herbivores (e.g. *Trichosurus vulpecula*) are also acting as seed vectors for some highly invasive exotic weed species (Glen et al., 2012), which can aggravate biological invasions in New Zealand degraded landscapes in the absence of a long-term resource commitment to invasive species management (Norton, 2009). Mammalian herbivores have indeed greatly modified the structure, functioning and species configurations of many New Zealand native forest ecosystems since their introductions in the 19th Century and still a considerable threat to remaining indigenous species of flora and fauna (Glen et al., 2012; Grüner & Norton, 2006; Husheer et al., 2006a; Husheer et al., 2006b; Norton, 2009; Wardle et al., 2001; Wilson et al., 2003; Wilson et al., 2006) despite intensive efforts to control them (Coomes et al., 2003; Norton, 2009; Nugent et al., 2011). Although the current presence of mammalian ungulates in New Zealand ecosystems are presumably in lower density since their introductions, they remain a serious limitation to forest restoration success as they have been observed to browse heavily on planted trees and restricting canopy species regeneration and establishment (Dodd et al., 2011; Forbes et al., 2016a; Wardle et al., 2001). Thus, Norton (2009) stressed that any letup to species invasion management is detrimental to restored ecosystems' sustainability as conservation gains can be quickly lost.

1.1.2.4. Competition

Similar to above mentioned factors, competition also plays a significant role in plant community structure and dynamics. Ecologists viewed this phenomenon as part of the post-disturbance forest development process, which recognizes four distinct phases: the establishment phase, the thinning phase, the transition phase, and steady-state phase (reviewed in Peet & Christensen, 1987). According to this review, competition is more intense during the

thinning phase since seedlings and saplings that are suppressed by initial cohorts would intensely compete for space and available resources. The thinning phase continues until most individuals which are slow growing, less vigorous, or shade-intolerant are unable to survive, thus creating a more open canopy structure where new seedlings become established or previously established cohorts increase in size with the final state being dominated by hardwood species of varying age and sizes. This model of succession has been viewed as an orderly straightforward ecosystem development, and therefore predictable, instead of complex interacting processes with some of which may counteract one another (Odum, 1970).

For instance, spontaneous succession in many abandoned fields in temperate region is expected to proceed like that of secondary succession seres with annual plants and perennial grasses and shrubs in the early stages, followed by tree species forming the climax stage of succession (Prach et al., 2001; Prach et al., 2014; Sojneková & Chytrý, 2015). However, in other instances, some early-successional communities (e.g. grass and shrubs) in degraded environment tend to exert control of successional sites conditions (e.g. light, nutrients, soil moisture) and eventually arrest succession for extended periods or indefinitely (Reynolds & Pacala, 1993). Evidence of arrested successions including in New Zealand have been documented in many areas including abandoned fields disturbed heavily by fire, farming, logging, among others (e.g. Acácio et al., 2007; Goldsmith et al., 2011; Prach et al., 2001; Putz & Canham, 1992; Richardson et al., 2014; Sarmiento, 1997). These create opportunities for some early-successional highly tolerant species to thrive well while restricting other species from establishment. In these instances, controlling plant barriers such as strategic removal of overtopping vegetation, opening the canopy, or increasing the availability of possible seed sources through enrichment planting has been usually recommended (Curt et al., 2009; Luken et al., 1997; Yang et al., 2013).

Competition among successional species that results to arrested forest succession represents a difficult challenge that may require more active interventions and sustainable integration of native species into New Zealand degraded landscapes especially at these times of rapid climate change and habitat conversions (Kelly & Sullivan, 2010; Norton, 2009). Similar to plant communities development in degraded environment elsewhere (cf. Callaway & Walker, 1997), ecosystem succession in New Zealand degraded landscapes can go in different successional trajectories with the current novel assemblages of exotic and native species in many of its successional habitats (Cieraad et al., 2015; Norton, 2009; Wyse et al.,

2018). Any disturbance can provide opportunities for successful invasions by exotic species in many of New Zealand's modified landscapes particularly because of the reported dominance of exotic species in seed banks and in other native ecosystems (Meurk & Hall, 2006; Norton, 2009).

1.1.3. Why restoration of canopy tree species

Getting the mature canopy species or forest to establish successfully in an area is critical as their presence was observed to be positively related to improvement of biodiversity (e.g. Smith et al., 2011; Weibull & Rydin, 2005), productivity (e.g. Naito et al., 2008) and ecosystems microclimate regulations (e.g. Mejía-Domínguez et al., 2011). For example, bird species diversity (an important agent for seed dispersal) tend to be high in a mature spruce forest in the eastern USA with higher tree canopies because of the increasing availability of niches as tree foliage height increases (MacArthur & MacArthur, 1961). Even the structuring of fungal diversity and community in a Neotropical rainforest (Smith et al., 2011) and bryophytes diversity in a deciduous forest (Weibull & Rydin, 2005) were associated with the presence of canopy tree species. Canopy trees are also largely responsible for a range of environmental heterogeneity in the understory of species-rich tropical and subtropical forests because of their influence on the local modifications of light levels, soil properties, soil moisture, among others (Mejía-Domínguez et al., 2011).

In New Zealand, another reason for this interest on canopy tree species establishment is the lack of possible rehabilitation procedures to accelerate their recovery in degraded or disturbed environments (Ledgard & Davis, 2004). Of the restoration methods such as planting, seeding, and encouraging natural regeneration; planting is a highly recommended restoration method for some valid reasons. It is considered most suitable for most climatic and soil environments (Davis et al., 2009). It can be used as a strategy to facilitate forest recovery and create favourable environmental conditions for fauna by planting most preferred species in small patches (Lamb et al., 2005). This, in turn, will eliminate dispersal problems in fragmented landscapes as all species are suitable candidates for planting (Del Moral et al., 2007). However, this method can be very expensive as nursery propagation of native species may take several months before they can be out-planted. It can be even more costly when used in large areas or when restoration management is inappropriate. Large-scale restoration using native species in

New Zealand can range from \$15,000 ha⁻¹ for bare-root stock to \$35,000 ha⁻¹ for container grown stock (Davis et al., 2009) and because of this cost, the main method for restoration over large areas in New Zealand usually involve land sparing or allowing forest fragments to regenerate back to forest naturally by removing degrading factors (e.g. grazing) (Norton et al., 2018), otherwise optimizing the success of restoration plantings is a critical objective. The problem however with natural regeneration as main method of restoration particularly in grassland areas is that it increases the risk of wildfires in drier regions (Lamb et al., 2005) and/or can be easily overcome or suppressed by persistent exotic species and browsing animals (Aronson & Handel, 2011). Moreover, a simulation study by Meurk and Hall (2006) of indigenous forest succession in eastern South Island predicted that it will take at least 200 years for original indigenous canopy species to be established in degraded lands that are now widely dominated by successional grass and shrubs.

At present, there is still a considerable knowledge gap on restoration prescriptions to establish indigenous canopy species or accelerate their successional processes in New Zealand degraded grasslands and shrublands despite of their ecological and environmental significance. Species-specific restoration method in a range of ecosystem types would be needed as different tree species at various stages of growth have different ecological requirements for germination, growth, survival, and spread. There is also a need to address the factors that limit natural succession that will also limit any restoration planting project (Norton et al., 2018).

1.2. OBJECTIVES OF THE STUDY

The objectives of this thesis are three-fold and are designed to provide inputs for developing options to establish native forest vegetation especially later-successional canopy tree species into degraded early-successional communities.

The first objective is to understand the successional dynamics of native woody species in dense patches of early-successional communities that have developed in abandoned degraded environment.

The second objective is to explore the potential of artificial gaps to establish later-successional canopy tree species and other native woody species within early-successional forest stand. I propose that while canopy gaps hold so much potential to accelerate forest

succession, it is important to understand their viability in forest restoration as outcomes may vary with the type of habitat and/or species under considerations.

The third objective is to examine the nurse-protégé interactions between early-successional communities and later-successional canopy tree species. I suggest that while the current literature on plant-plant interactions may provide a framework to restore degraded lands, careful selection of nurse vegetation to facilitate the success of restoration projects under specific field conditions is critical as outcomes could be dependent on the target species and nurse vegetation involved.

1.3. THESIS OUTLINE

Through Chapter 1, I begin with the description of the changes in New Zealand's native forests and how the history of ecosystems disturbances has altered most of the original woody ecosystems, especially those associated with the eastern 'drylands' zone of the South Island where much of the forest were destroyed and transformed rapidly to grasslands and successional shrublands. The chapter provides answers to question about the importance of ecological restoration in New Zealand dryland zone, which is projected to change towards a highly degraded state as indicated by the current rate of indigenous species loss and slow recovery of forest ecosystems in the area. I identify important factors that might limit forest recovery or establishment of mature forest species in degraded landscapes and stress that natural forest succession can go in different successional trajectories in the absence of active management intervention.

I then propose the integration of canopy tree species in degraded landscapes as their presence is positively related to the improvement of biodiversity and successional sites environmental conditions. I highlight the need for experimental set-ups to address the lack of viable restoration procedures to accelerate forest recovery in degraded environments including restoration prescriptions for several indigenous canopy species in New Zealand. Having established this rationale, I introduce the three-fold objectives of this thesis that include to: (1) understand the long-term successional dynamics of native woody species in dense patches of regenerating shrubs in abandoned farmland, (2) explore the potential of canopy manipulations or artificial gaps to facilitate the establishment of later-successional canopy trees and other native woody species within early-successional stands, and (3) examine the nurse-protégé or

plant-to-plant interactions via restoration planting of mature forest species in early-successional communities.

In Chapter 2, I describe the characteristics (e.g. climate, current vegetation, among others) of two study sites for this thesis as a separate chapter to avoid repetition of their descriptions as three chapters of this manuscript were conducted in the same restoration site or successional environment.

In Chapter 3, I then address the first objective by assessing the long-term compositional structure and growth of native woody species in a regenerating kānuka (*Kunzea robusta*, Myrtaceae) forest, which have developed following farm abandonment and removal of grazing. Kānuka is a native species in New Zealand and is regarded as an early-successional species. There is evidence in New Zealand and elsewhere that woody species succession in seral communities in degraded abandoned farmlands are usually arrested or are delayed indefinitely. To ascertain this, I exploit the available permanent vegetation plots that were established in 2007 in patches of regenerating kānuka stands. Using the result from this chapter, I ask the question whether canopy manipulation through artificial gaps can improve or accelerate the recruitment and establishment of canopy trees and other native woody species in dense regenerating communities. In New Zealand, there is still a limited application of artificial canopy gaps in restoration projects, although gap environments are critical for New Zealand native canopy species as their successful regeneration in forest understories have been observed in forest areas with natural canopy gap formations.

Thus, the next chapters of this thesis explore the potential of canopy manipulation in the restoration of less shade-tolerant woody species within early-successional communities. In Chapter 4, I explore the potential of artificial canopy gaps to facilitate the natural regeneration and establishment of native woody species in dense regenerating kānuka forests. I hypothesize that canopy gap creation may reduce the intensity of competition and provide opportunities for less shade-tolerant woody species to persist or coexist with more tolerant or predominant counterparts. I describe the species composition, density, growth, and survival of regenerating native woody species under the canopy gaps and intact kānuka canopy over a 28-month measurement period.

In Chapter 5, I also examine the opportunity that canopy manipulation can provide in the restoration planting of light-demanding canopy species, especially tree species with seed dispersal limitation and do not establish under heavy shades. I explore the potential of different methods of canopy interventions (i.e. artificial gaps, ring-barking and edge planting) to facilitate the establishment of a light-demanding late-successional canopy tree species, tōtara (*Podocarpus totara*, Podocarpaceae), within the regenerating kānuka. I expect that the higher understorey irradiances among these canopy treatments would be more significant to the growth and survival of the light-demanding tōtara seedlings.

In Chapter 6, I examine the nurse-protégé or plant-to-plant interaction between canopy species and early-successional shrubland communities with different canopy interventions in a degraded high-country environment. I test the initial growth and survival of 420 potted seedlings of late-successional mountain beech (*Fuscospora cliffortioides*, Nothofagaceae) for over 30 months in five experimental treatments that include: open grassland, mānuka (*Leptospermum scoparium*, Myrtaceae) shrubland with intact canopy, mixed-species shrubland with intact canopy, artificial gaps in mānuka shrubland; and the grassland edge of the mixed-species shrubland. I propose that controlling the shade of nurse shrubs through minimal canopy interventions would be favourable for the growth and survival of the light-demanding late-successional species like mountain beech than in the open grassland and intact shrub canopy where they could suffer from winter or drought-related desiccation and intense competition, respectively.

Finally, Chapter 7 provides overall conclusion and specific recommendations from the findings of each chapter especially in the restoration of canopy trees and less-tolerant woody species in degraded successional communities in degraded eastern South Island (New Zealand) ecosystems. All references are found in Chapter 8 to avoid repetition among chapters. Appendices are listed in Chapter 9 and include a published chapter of this thesis (Appendix C).

2. CHAPTER TWO

STUDY SITES

2.1. Tiromoana Bush, North Canterbury, New Zealand

The first three studies of this thesis, that is, the Chapters 3-5 were conducted at Tiromoana Bush, a 410 ha restoration project in North Canterbury, New Zealand (43° 06' S 172° 51' E, 0–360 m a.s.l.; Norton 2005). The area has undulating terrain formed from greywacke, argillite and Tertiary sedimentary rocks, Quaternary outwash gravels, and coastal gravels and sands (Norton, 2019). It experiences warm dry summers and cool winters. Annual rainfall is 921 mm, with January and June mean temperatures of 16.9 °C and 6.6 °C. The present vegetation is a mosaic of grassland, seral forests, regenerating shrubland and restoration plantings (Fig. 1).

Domestic livestock grazing was removed in 2003, although some browsing by introduced mammals (mainly brushtail possum and red deer), which were introduced in New Zealand in the 19th Century, still have some impacts on natural regeneration (Norton, 2019). The pre-human vegetation would have been a mixed angiosperm-conifer forest with *Podocarpus totara* (tōtara) as one of dominant canopy species (Norton, 2019; Wyse et al., 2018).



Figure 1. Present vegetation at Tiromoana Bush, North Canterbury, New Zealand (Photo courtesy: David A. Norton).

2.2. Cass Mountain Research Area (CMRA), North Canterbury, New Zealand

The study presented in Chapter 6 of this thesis was conducted at Cass Mountain Research Area (CMRA), a 1775 ha research area owned and managed by the University of Canterbury. CMRA is situated on the eastern side of the Southern Alps ($43^{\circ} 01' \text{ S}$, $171^{\circ} 47' \text{ E}$), North Canterbury, New Zealand with an altitudinal range of 560 to 1359 m (Young et al., 2013). The area is characterized by steep mountain slopes and fans with an annual average rainfall of 1300 mm (Greenland, 1977). Although historically forested, fire and grazing have transformed the area from *Fuscopora cliffortioides* (mountain beech) dominated forests to extensive areas of grassland and shrubland (Young et al., 2013) (Fig. 2).



Figure 2. Early-successional vegetation at the University of Canterbury, Cass Mountain Research Area (CMRA), Cass, Canterbury, eastern South Island high country, New Zealand.

3. CHAPTER THREE

Succession of native woody species within a kānuka-dominated regenerating forest following the removal of livestock grazing

3.1. ABSTRACT

Removing degrading factors such as grazing animals is widely used for forest restoration especially in temperate regions where pastoral farming is extensive. However, the success of this approach for native woody species recovery in remnant woody vegetation is not always guaranteed because of the prevalence of competitive exclusion by dominant species in early-successional communities. In this study, quantitative data on species composition and growth, mortality, and recruitment rates over 11 years in a regenerating kānuka (*Kunzea robusta*, Myrtaceae) stand are presented to understand the regeneration of native woody species in an early-successional vegetation that has established as a result of grazing exclusion. We found that succession of native woody species in the kānuka stand is characterised by lack of diversity in species composition, high mortality rates and low recruitment rates, and the strong dominance of a single species māhoe (*Melicytus ramiflorus*, Violaceae), which may represent a state of arrested or delayed succession. These results could be related to the unfavourable light condition or high competition for light under the dense kānuka canopy. While there was a slight compositional change in canopy tree species abundance, this was mainly due to gains in māhoe abundance in the overstorey suggesting the possible transition in dominance from kānuka to māhoe. This transition is highly likely given the dominance of māhoe in the understorey and the height growth of this species over time was about twice higher than any other regenerating woody species in the area. The dominance of kānuka and māhoe is likely to last for many years unless a major disturbance occurs, or canopy intervention is undertaken to control the density of these species and introduce new species.

Keywords: Grazing exclusion, *Kunzea robusta*, *Melicytus ramiflorus*, New Zealand, Regeneration, Restoration, Secondary forest

3.2. INTRODUCTION

The presence of successional native woody vegetation is often a distinctive feature of abandoned farmland and offers considerable potential for forest restoration (Cramer et al., 2008; Norton et al., 2018). The expectation is that such successional vegetation will, in time, develop into a more mature condition. However, where successional sites have been heavily degraded (e.g. due to grazing), the processes of natural forest recovery even beneath existing native plant canopies can be slow or uncertain (Aide et al., 1995; Norton et al., 2018; Royo & Carson, 2006; Wyse et al., 2018). This can occur for a range of reasons including changes in soil conditions (Cramer et al., 2008), lack of seed dispersal (Norton, 2009) and competitive exclusion by the dominant seral canopy species (Putz & Canham, 1992). Several studies have reported how the dominance of early-successional communities alter or influence the composition and establishment of their immediate successors (e.g. Bartha et al., 2014; Spooner et al., 2002), although the long-term successional consequences of such dominance on local diversity or recruitment can be unpredictable and deserves further consideration when managing regenerating forests for conservation.

In New Zealand, where pastoral agriculture covers at least 50% of the land area (Norton & Pannell, 2018), and an even greater proportion of lower altitude areas, the retirement of forest fragments and seral communities from livestock grazing is considered a significant management approach to facilitate recovery of lowland mature forests (Norton & Miller, 2000). The success of this approach in the recovery of later-successional native woody species is, however, not well understood (Spooner et al., 2002) and additional management interventions are may be necessary as the dominance of one or few species for a prolonged successional period appear to be common in many regenerating communities of degraded areas (Putz & Canham, 1992). In the New Zealand situation, native woody communities associated with abandoned farmland are usually dominated either by the native kānuka (*Kunzea robusta*), mānuka (*Leptospermum scoparium*), or by other species such as bracken fern (*Pteridium esculentum*), māhoe (*Melicytus ramiflorus*), kowhai (*Sophora* species), gorse (*Ulex europaeus*), and broom (*Cytisus scoparius*) (Allen et al., 1992; Smale et al., 1995; Williams, 1983). Kānuka and mānuka are important early-successional species of abandoned pastures comprising about 5% or more than 13,000 km² of the New Zealand total land area (Whitehead et al., 2004). Kānuka stands can dominate for more than 100 years (Meurk & Hall, 2006), and in some situations are likely to be replaced or co-dominated by the shade-tolerant tree māhoe

(Allen et al., 1992; Smale et al., 1995). Similar replacement patterns have been observed in other regenerating stands elsewhere in the world (Clebsch & Busing, 1989; Lorimer, 1984). This occurs because māhoe has high seed production and dispersal, is relatively shade tolerant, and is often the dominant understorey species (Williams, 1983).

Transition of early-successional stands to more complex later-successional forest, however, may take many years (e.g. at least 50-100 years or more) depending on the density of tree species regenerating in the understorey of initial cohorts, but usually proceed as a thinning process (e.g. declining stem density and increasing basal area) dominated by mortality of the initial stand and recruitment of new individuals occurs (Peet & Christensen, 1987). The latter depends on the availability of seed sources and successful establishment of seedlings. However, even in areas with adequate seed sources, successful seedling recruitment is not always guaranteed as conditions within the regenerating stands may not be favourable for the establishment of later-successional species (Guariguata & Ostertag, 2001), with early colonizer species resisting invasions or pre-empting the space to restrict later-successional species, thus slowing the forest restoration process or delaying the succession indefinitely (Connell & Slatyer, 1977). Such a long recovery period may pose threats to conservation gains or targets, especially in areas where invasive alien organisms are a problem (Norton, 2009). Thus, within the context of managing early-successional vegetation for forest restoration, understanding successional change is critical to guide the system towards the desired state as variability in site attributes and management measures make it difficult to generalize successional outcome over time (Barbier et al., 2008).

The aim of this study was to quantify the natural development processes in early-successional vegetation that has established as part of a restoration project. The study used permanent monitoring plots to measure vegetation change in a regenerating kānuka-dominated forest where māhoe is a dominant understory species. The specific objectives of this study were threefold: (1) describe the changes in species composition, density, and growth of native woody regeneration over time, (2) test the hypothesis that even with grazing exclusion, arrested succession can occur because of competitive exclusion by dominant early successional species, and (3) identify possible interventions to facilitate recovery of mature forest species in such seral communities.

3.3. METHODS

3.3.1. Sampling plots design

The study was carried out using permanent vegetation monitoring plots initially established in November 2007 (four years after grazing removal). The monitoring plots were located along ten transects (at least a kilometre away from each other) and extend through the main patches of regenerating kānuka-dominated forests which at the time of their establishment still showed the effects of 100+ years of heavy grazing with little understorey vegetation. Each transect comprised two permanently marked 10 x 10 m sample plots that are about 200 m apart. Two permanently marked 1.5 x 1.5 m seedling plots were located within each 10 x 10 m plot on a diagonal line across the main plot, with origins being at ca. 4.8 and 9.6 m, respectively, from the start of the diagonal line.

3.3.2. Measurements

Within each 10 x 10 m plot, the diameter of all woody species >2 cm diameter at breast height was measured at 1.2 – 1.3 m above ground level. All measured stems were tagged at the first measurement and those without tags at subsequent measurements were considered new recruits. Only stems that were rooted in the plot were measured, and the diameters of branches of multi-stemmed stems were measured separately. The height of all woody seedlings > 20 cm height was measured within the seedling plots. Both diameter and seedling height were first measured in 2007 and have been remeasured twice since then with the final remeasurement in June 2018. Tagged seedlings/trees that were not found in the plots were presumed dead.

3.3.3. Data manipulation and analyses

Data analyses were performed separately for woody species in the overstorey (>2 cm dbh) and those in the understorey layer hereafter referred to as trees and regenerating seedlings, respectively. Different non-parametric estimators were used to estimate the true species richness of the area applying the ChaoSpecies function in SpadeR package (Chao et al., 2016). The analysis was performed using the mean abundance of each species in four measurement periods from 2007 to 2018.

Non-metric multi-dimensional scaling (NMDS, 50 iterations, three dimensions, Bray-Curtis distance) in vegan package (Oksanen et al., 2018) was applied to display the species compositional structure within each of the measurement period. A zero-adjusted Bray–Curtis coefficient method for denuded assemblages was applied for seedling data ordination by adding a ‘dummy species’ that has the same abundance in all samples (Clarke et al., 2006). Permutational Multivariate Analysis of Variance (PERMANOVA) with the adonis function in vegan package was used to examine significant variations in species composition among the three measurement time points and betadisper function was used to assess the significant contribution of within time points variability. The NMDS was further assessed to determine discriminating species between measurement time points using Bray-Curtis dissimilarities applying the similarity percentages (SIMPER) function in vegan package.

To evaluate changes in the kānuka vegetation structure over time, mixed effects models with the number of plots and transects as random variables were used in the analyses to account for issues on temporal pseudo-replication. Because density data contained more zeros than would be expected from the typical error distributions, a zero-inflated GLMM model in glmmTMB package (Brooks et al., 2017) was applied to analyse changes in mean stem density per plot as influenced by time and species factors. The interaction of time and species was excluded in the density data analysis due to overparameterized issues in the glmmTMB model. The Akaike information criterion (AIC) function in bblme package (Bolker & Team, 2017) was used to select the best response distribution in the glmmTMB zero-inflated models via Poisson and negative binomial response distributions (NB1 and NB2 parameterizations). A Wald chi-squared test, applying the Anova function in car package (Fox & Weisberg, 2011), was performed to determine the significance of the parameters in the glmmTMB models and then *post hoc* test was performed using the glht function in multcomp package (Hothorn et al., 2008).

The interaction of time and species were included in the assessment of changes in tree DBH and basal area, seedling mean height and maximum height among the woody species, and their respective mortality and recruitment rates in percent per year. The growth data were log transformed prior to analyses using the lmer function in lme4 package (Bates et al., 2015) or the Bayesian linear mixed-effects regression (blmer) function of the R blme package (Chung et al., 2013) when there were singularity fit issues with lmer. For mortality and recruitment rates, arcsine (square-root) transformation of the data was performed and proceeded with the

analyses using repeated measures analysis of variance (ANOVA) applying the blmer function in the blme package. A Wald chi-squared test, applying the Anova function in car package (Fox & Weisberg, 2011), was used to test the significance of the parameters in the lmer and blmer models. *Post hoc* tests were performed using the emmeans function in emmeans package (Lenth, 2018).

The data on species mortality and recruitment rates per year were calculated following the equations used by Richardson et al. (2014):

$$r = 100 \times \left[\left(1 + \frac{N_r}{N_0} \right) \times \left(\frac{1}{t} \right) - 1 \right]$$

where: N_0 is the population count at the beginning and N_r is the number of recruits in one census, t .

$$m = 100 \times \left[1 - \left(\frac{N_1}{N_0} \right)^{\frac{1}{t}} \right]$$

where: N_0 and N_1 are population counts at the beginning and the end of the measurement interval, t .

3.4. RESULTS

3.4.1. Species richness and composition

Species richness was very low in the sample plots, ranging only from 2.0 ± 0.3 to 3.6 ± 0.5 for trees and from 1.8 ± 0.3 to 2.4 ± 0.2 for regenerating seedlings. Overall, 13 species of trees comprising 744 individuals were recorded in the overstorey and a total of 16 species (430 individuals) were identified as regenerating seedlings. The proportion of observed species richness relative to the non-parametric estimates ranged from 68.8% to 87.2% for trees and 76.6% to 91.4% for seedlings, an indication of almost complete inventory of woody species within the area.

The NMDS ordination showed a very similar compositional structure for tree species between 2007 and 2010 measurement time points and a moderate separation in 2018 (Fig. 3a). Species composition of regenerating seedlings was rather similar among the three measurement time points (Fig. 3b). Although there was some clustering of species among time points, there were no distinct groupings observed for both trees and seedlings. These results were supported by the PERMANOVA, which showed significant variations in species composition among time points for trees ($F_{[2,57]} = 2.22$, $P=0.035$, $R^2=0.07$) and not significant for regenerating seedlings ($F_{[2,117]} = 1.08$, $P=0.324$, $R^2=0.02$). Within time points, variations in species composition from the betadisper analysis were not significant among plots for both trees ($F_{[2,57]} = 0.25$, $P=0.778$) and seedlings ($F_{[2,117]} = 1.08$, $P=0.324$) within the three measurement time points. The most influential or discriminating species from the SIMPER analysis were *Kunzea robusta* and *Melicytus ramiflorus* for trees and *Coprosma rhamnoides* and *Melicytus ramiflorus* for the regenerating seedlings (Table 1). There were notable gain and reduction in abundance for *M. ramiflorus* and *K. robusta* in the overstorey, respectively, over time and a reduction in seedling abundance for both *C. rhamnoides* and *M. ramiflorus* in the understorey.

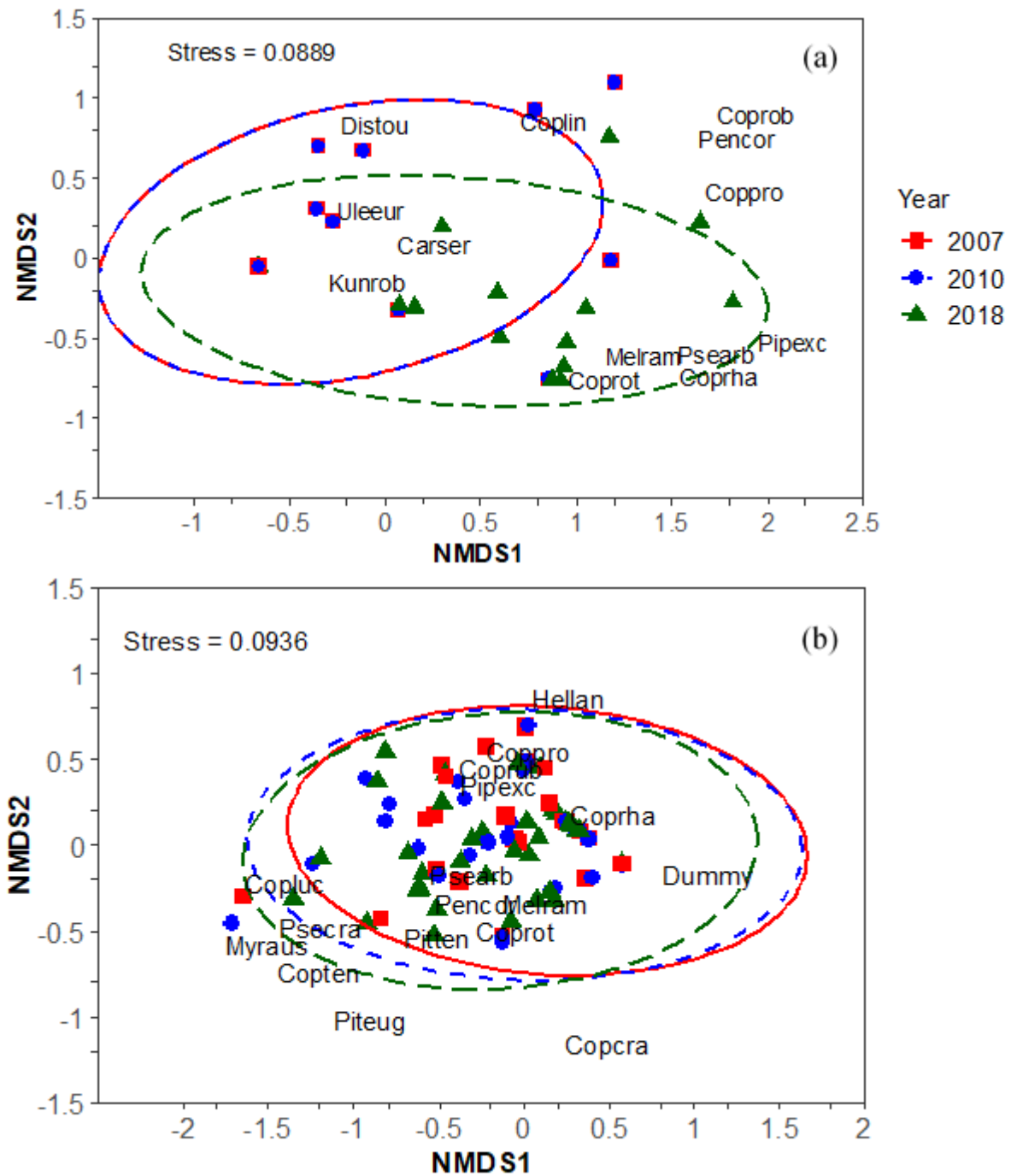


Figure 3. Non-metric multidimensional scaling (NMDS) plot of species composition of (a) trees and (b) regenerating seedlings tallied in the three measurement time points from 2007 to 2018 within the kānuka-dominated forests. The positions of the woody species on the ordination space are also presented. Note the dummy species is denoted with Dummy. Species codes are described in Tables 2 and 3.

Table 1. Discriminating species between years based on SIMPER analysis. Species average percent contribution (Contr.) and cumulative contributions (Cum.) to species dissimilarity between years are presented.

Species	Mean density (m ² /ha)			2007-2010		2010-2018	
	2007	2010	2018	Contr. (%)	Cum. %	Contr. (%)	Cum. (%)
Trees							
<i>Kunzea robusta</i>	3,130	3,130	2,820	37.1	80.7	30.7	56.5
<i>Melicytus ramiflorus</i>	-----	75	1,200	-----	-----	15.1	84.1
Seedlings							
<i>Coprosma rhamnoides</i>	29,444	33,333	19,778	19.5	55.5	16.4	45.5
<i>Melicytus ramiflorus</i>	9,667	15,000	12,333	9.2	82.1	10.1	73.3

3.4.2. Density of trees and regenerating seedlings

In terms of relative density, the stems of *K. robusta* (49.6%), *M. ramiflorus* (12.6%) and *Coprosma rotundifolia* (10.1%) were the most dominant in the overstorey (Table 2); while the regenerating seedlings were dominated by *C. rhamnoides* (56.3%) and *M. ramiflorus* (25.2%) species (Table 3). The mean density between years did not vary significantly for both trees ($W^2_{[2]} = 0.62$, $p = 0.735$) and regenerating seedlings ($W^2_{[2]} = 4.55$, $p = 0.103$), although there was a decline for seedling density in 2018 (Fig. 4a). Significant differences in mean stem density were strongly dependent on species identity for both trees ($W^2_{[12]} = 298.68$, $p < 0.001$) and regenerating seedlings ($W^2_{[15]} = 561.13$, $p < 0.001$). Among the species in the overstorey, *K. robusta* had significantly the highest mean density (2893.3 ± 296.2 stem ha⁻¹), followed *M. ramiflorus* (735.9 ± 190.5 stem ha⁻¹), *C. rotundifolia* (586.7 ± 151.1 stem ha⁻¹), and *P. arboreus* (383.3 ± 249.9 stem ha⁻¹). For regenerating seedlings, *C. rhamnoides* ($27,518.6 \pm 4,866.7$ stem ha⁻¹) and *M. ramiflorus* ($12,333.3 \pm 2,103.6$ stem ha⁻¹) had significantly the highest mean density among the woody species (Fig. 4b) although changes in density of *C. rhamnoides* do not really matter as it is unlikely to form trees.

Table 2. Composition and density of woody species in the overstorey within the kānuka-dominated forests in Tiromoana Bush, Kate Valley, New Zealand.

Code	Species	Mean density (stem/ha)	Std. error	Relative density (%)
Kunrob	<i>Kunzea robusta</i> *	2,893.3	296.2	49.6
Melram	<i>Melicytus ramiflorus</i> *	735.9	190.5	12.6
Coprot	<i>Coprosma rotundifolia</i>	586.7	151.1	10.1
Psearb	<i>Pseudopanax arboreus</i> *	383.3	249.9	6.6
Coppro	<i>Coprosma propinqua</i>	200.0	161.2	3.4
Pencor	<i>Pennantia corymbosa</i> *	200.0	28.9	3.4
Carser	<i>Carpodetus serratus</i> *	233.3	66.7	4.0
Distou	<i>Discaria toumatou</i>	166.7	33.3	2.9
Uleeur	<i>Ulex europaeus</i>	133.3	66.7	2.3
Pipexc	<i>Piper excelsum</i>	116.7	83.3	2.0
Coplin	<i>Coprosma linariifolia</i>	83.3	16.7	1.4
Coprha	<i>Coprosma rhamnoides</i>	66.7	23.6	1.1
Coprob	<i>Coprosma robusta</i>	33.3	33.3	0.6
Total		5832.6		100

Note: Canopy tree species are indicated with asterisk (*).

Table 3. Composition and density of woody seedlings within the kānuka-dominated forests in Tiromoana Bush, Kate Valley, New Zealand.

Code	Species	Mean density (stem/ha)	Std. error	Relative density (%)
Coprha	<i>Coprosma rhamnoides</i>	27,518.6	4,866.7	56.3
Melram	<i>Melicytus ramiflorus</i> *	12,333.3	2,103.6	25.2
Psearb	<i>Pseudopanax arboreus</i> *	2,407.4	687.6	4.9
Coprot	<i>Coprosma rotundifolia</i>	1,925.9	645.8	3.9
Coppro	<i>Coprosma propinqua</i>	1,370.4	525.4	2.8
Pitten	<i>Pittosporum tenuifolium</i> *	777.8	201.4	1.6
Hellam	<i>Helichrysum lanceolatum</i>	703.7	246.7	1.4
Pencor	<i>Pennantia corymbosa</i> *	555.6	214.1	1.1
Copten	<i>Coprosma tenuifolia</i>	296.3	164.1	0.6
Psecra	<i>Pseudopanax crassifolius</i> *	222.2	103.2	0.5
Coprub	<i>Coprosma rubra</i>	222.2	103.2	0.5
Copluc	<i>Coprosma lucida</i>	185.2	96.9	0.4
Myraus	<i>Myrsine australis</i>	148.2	90.1	0.3
Copcra	<i>Coprosma crassifolia</i>	74.1	52.2	0.2
Pipexc	<i>Piper excelsum</i>	74.1	74.1	0.2
Piteug	<i>Pittosporum eugenioides</i> *	37.0	37.0	0.1
Total		48,852.0		100

Note: Canopy tree species are indicated with asterisk (*).

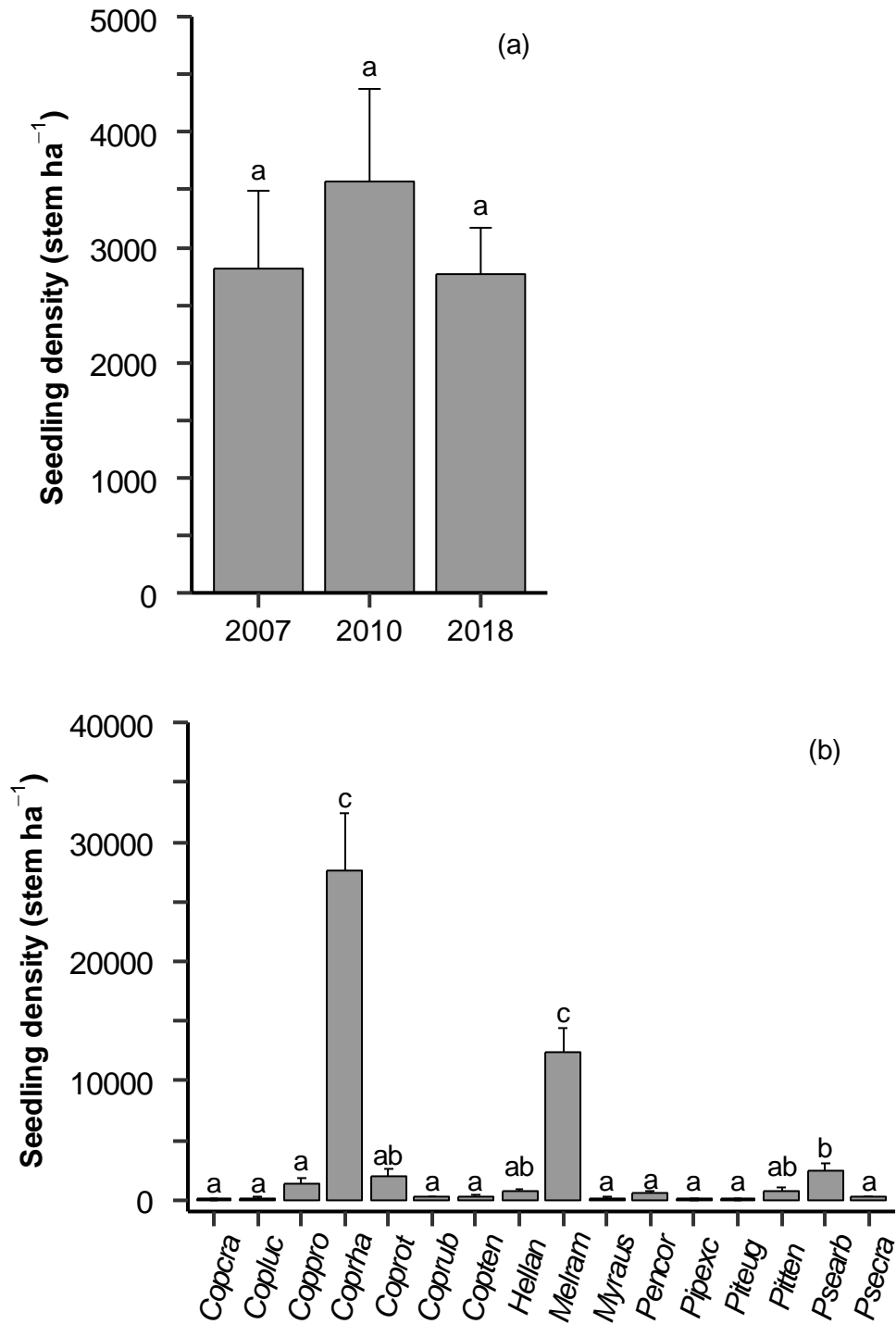


Figure 4. Mean stem density per hectare of regenerating seedlings (a) over time and (B) among species over all three observations within the kānuka-dominated forests. Species codes are described in Table 3. Error bars represent \pm S.E.

3.4.3. Diameter and basal area of overstorey trees

Mean diameter at breast height (dbh) of overstorey trees did not vary over time independent of species ($W^2_{[2]} = 0.16, p > 0.05$). Significant differences in mean dbh were species-dependent ($W^2_{[12]} = 259.23, p < 0.001$) with *K. robusta* having the largest mean dbh (13.8 ± 0.8 cm) among the tree species, followed by *C. serratus* (8.7 ± 0.9 cm), *P. corymbosa*, (7.3 ± 0.4 cm), and *D. toumatou* (7.1 ± 0.5 cm). The effect of the interaction of time and species factor on the mean dbh was also significant ($W^2_{[24]} = 55.47, p < 0.001$) but the increases over time were observed only in the mean dbh of *C. rhamnoides*, *M. ramiflorus*, and *P. arboreus*.

Basal area did not vary with time independent of species ($W^2_{[2]} = 0.59, p = 0.745$). Significant variations in the basal area were influenced by species identity ($W^2_{[12]} = 836.90, p < 0.001$) and was largely dominated by *K. robusta* with mean basal area of 33.8 ± 1.4 m² compared to other species ($0.01 \pm 0.01 - 1.7 \pm 0.5$ m²). The effect of the interaction of time and species factor was not significant ($W^2_{[24]} = 21.19, p = 0.627$) although significant increases in the basal area over time were observed among the seedlings of *M. ramiflorus* (Fig. 5).

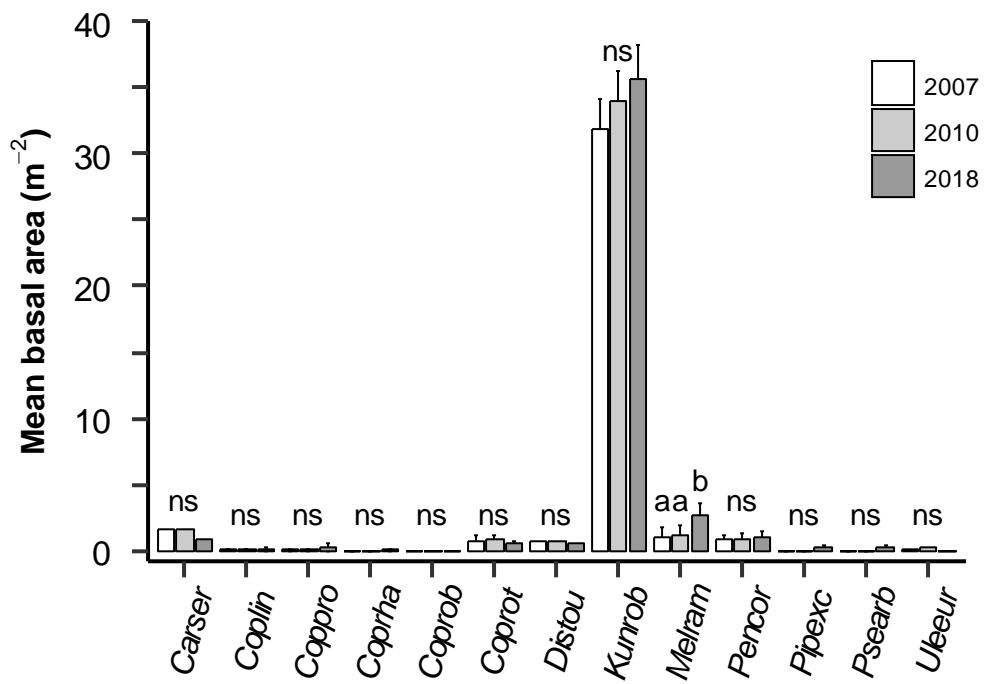


Figure 5. Mean basal area (m²) of tree species over time within the kānuka-dominated forests. Species codes are described in Table 2. Error bars represent ± S.E.

3.4.4. Mean and maximum height of regenerating seedlings

Mean height of regenerating seedlings did not differ significantly over time independent of species ($W^2_{[2]} = 0.18, p = 0.916$). Significant variations were observed among species ($W^2_{[15]} = 156.41, p < 0.001$) and between species and time interaction ($W^2_{[30]} = 88.53, p < 0.001$). Among the species, the highest mean height was observed from the seedlings of *M. ramiflorus* (52.0 ± 7.1 cm) followed by the *C. rhamnoides* (43.2 ± 4.0 cm), and *P. arboreus* (19.6 ± 4.2 cm), but only *M. ramiflorus* and *P. arboreus* indicated significant changes in mean height over time (Fig. 6).

Similar to mean height, seedling maximum height did not differ significantly over time independent of species ($W^2_{[2]} = 0.16, p = 0.924$). Significant variations were species-dependent ($W^2_{[15]} = 169.72, p < 0.001$) and had significant interaction with time ($W^2_{[30]} = 87.68, p < 0.001$). The highest maximum height was observed among seedlings of *M. ramiflorus* (71.6 ± 9.6 cm), followed by the *C. rhamnoides* (62.6 ± 5.8 cm), and *P. arboreus* (23.4 ± 4.9 cm). Significant increases in maximum height over time were observed in *M. ramiflorus* and *P. arboreus* seedlings.

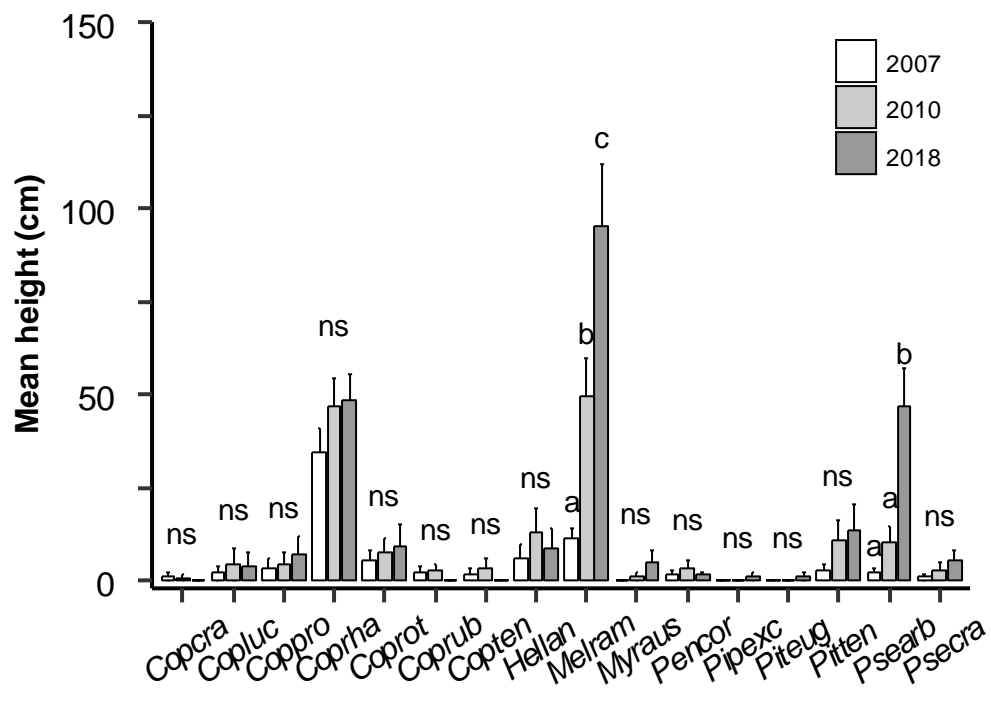


Figure 6. Mean height (cm) of regenerating seedling species over time within the kānuka-dominated forests. Species codes are described in Table 3. Error bars represent \pm S.E.

3.4.5. Mortality and recruitment rates per year

Mean mortality rates per year for trees did not differ significantly over time independent of species ($W^2_{[1]} = 1.38, p = 0.770$) and among species independent of time ($W^2_{[12]} = 0.36, p > 0.05$). Significant variations were observed from the interaction of species and time ($W^2_{[12]} = 64.46, p < 0.001$) with significant increases in mortality rates over time were observed from shrub species, such as *U. europaeus*, *C. linariifolia*, *C. propinqua*, and *C. rotundifolia*, reflecting forest replacing shrubs (Fig. 7a). Recruitment rates for trees also did vary significantly over time independent of species ($W^2_{[1]} = 0.0, p > 0.05$) and among species independent of time ($W^2_{[12]} = 0.07, p > 0.05$). Significant variations were due to the interaction of species and time ($W^2_{[12]} = 69.3, p < 0.001$) with significant increases in recruitment rates were strongly evident among the species of *C. rhamnoides*, *C. robusta*, *M. ramiflorus*, *P. exelsum*, and *P. arboreus* (Fig. 7b). The latter two species are canopy forming species.

For regenerating seedlings, mortality rates increased significantly over time independent of species ($W^2_{[1]} = 15.58, p < 0.001$) from $0.8 \pm 0.3\%$ year⁻¹ in 2010 to $3.8 \pm 0.7\%$ year⁻¹ in 2018. Significant differences in mortality rates were also influenced by species individuality ($W^2_{[15]} = 65.94, p < 0.001$) and were higher especially among the seedlings of *C. rhamnoides* ($9.2 \pm 2.9\%$ year⁻¹), *C. robusta* ($6.5 \pm 2.7\%$ year⁻¹), and *C. rotundifolia* ($5.6 \pm 2.5\%$ year⁻¹). The effect of the interaction of time and species factor on seedling mortality rates was not significant ($W^2_{[15]} = 22.7, p = 0.089$), although there were significant increases in mortality rates over time among the seedlings of *C. rhamnoides* and *P. tenuifolium* (Fig. 8a). Changes in seedling recruitment rates over time (independent of species) were not significant ($W^2_{[1]} = 0.24, p = 0.623$) although it decreased from $1.7 \pm 0.3\%$ year⁻¹ in 2010 to $0.9 \pm 0.1\%$ year⁻¹ in 2018. Significant variations in recruitment rates were influenced by species individuality ($W^2_{[15]} = 211.73, p < 0.001$) with *M. ramiflorus* and *C. rhamnoides* having the higher recruitment rates among the species with 6.1 ± 1.2 and $3.9 \pm 0.9\%$ year⁻¹, respectively. There was no significant effect on recruitment rates associated to the interaction of time and species factor ($W^2_{[15]} = 17.37, p = 0.297$), but there was a significant reduction in recruitment rate between 2010 and 2018 for *M. ramiflorus* seedlings (Fig. 8b).

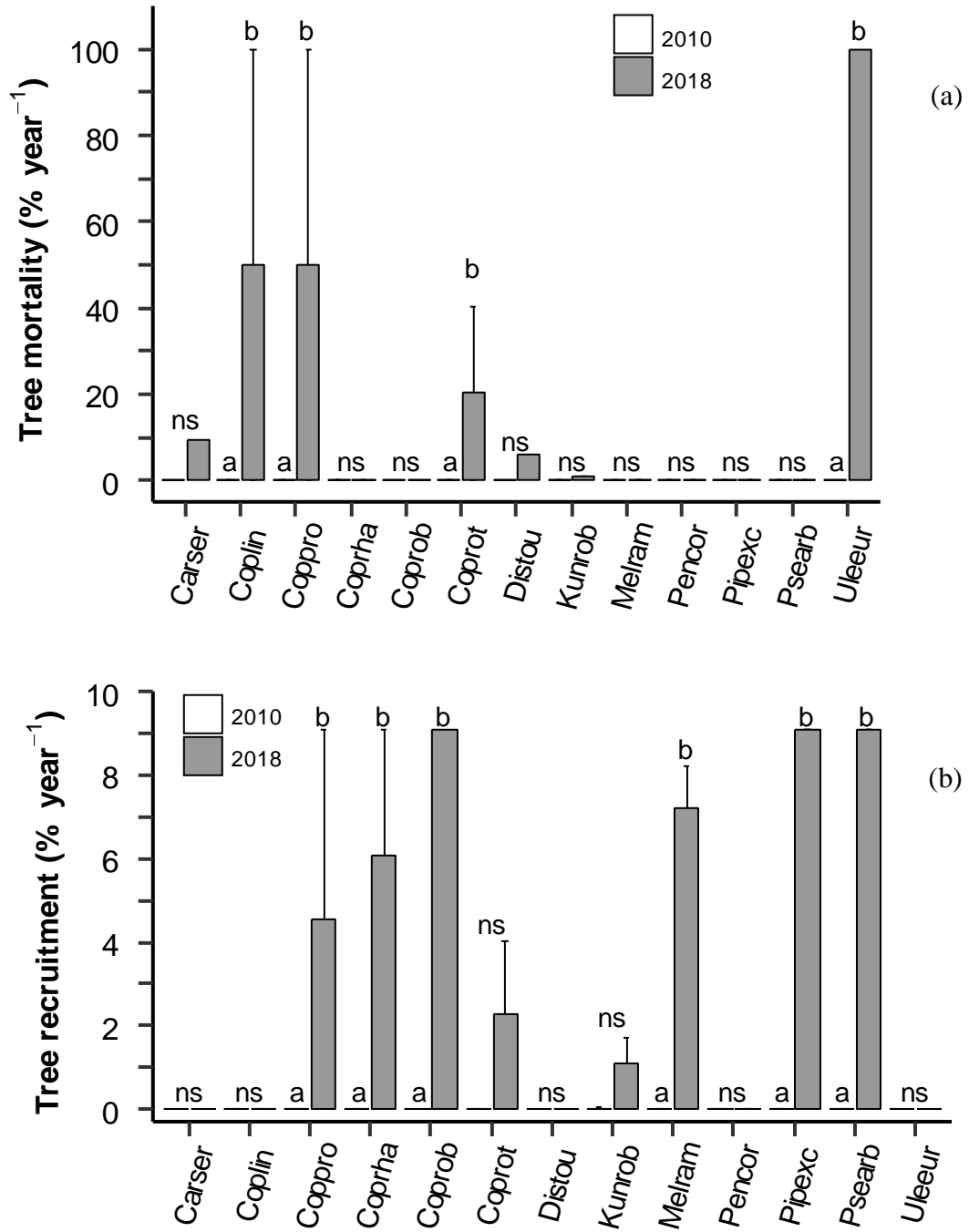


Figure 7. Mean (a) mortality rates (% year⁻¹) and (b) recruitment rates (% year⁻¹) of tree species over time within the kānuka-dominated forests. Species codes are described in Table 2. Error bars represent \pm S.E.

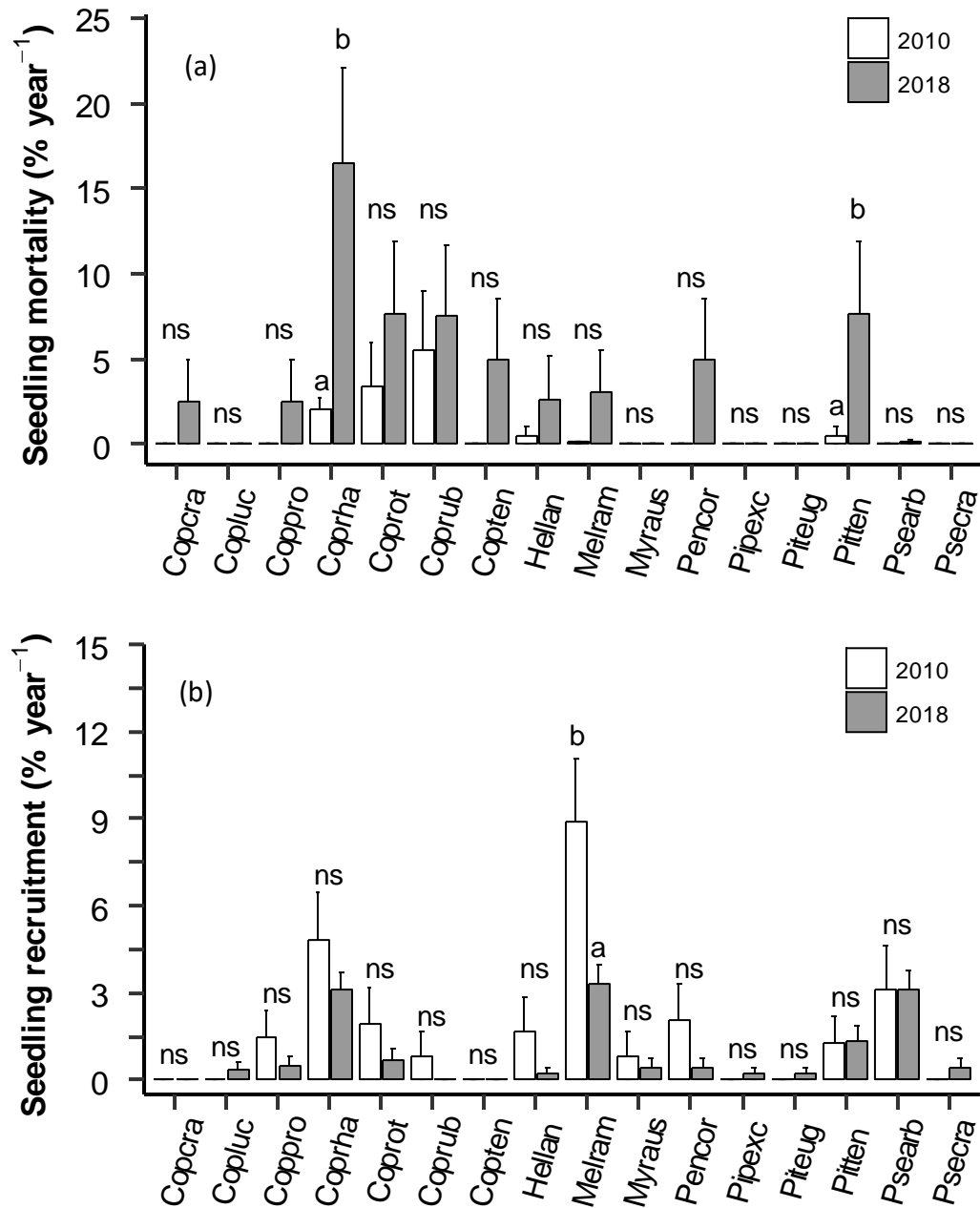


Figure 8. Mean (a) mortality rates (% year⁻¹) and (b) recruitment rates (% year⁻¹) of seedling species over time within the kānuka-dominated forests. Species codes are described in Table 3. Error bars represent \pm S.E.

3.5. DISCUSSION

3.5.1. Compositional structure

Early-successional kānuka stands can live for more than 100 years and our 11 years data showed some indications what might be occurring over time following the removal of domestic livestock grazing. Our study showed no significant compositional change for woody species as the same species were dominating the area over time, that is *K. robusta* in the overstorey and *M. ramiflorus* and *Coprosma* species in the understorey. While there has been regeneration of other potential canopy trees (e.g. *P. eugenoides*, *P. tenuifolium*, and *M. australis*), they were quite rare in comparison and many other species that might be expected in these forests (e.g. *Plagianthus*, *Hoheria*, *Sophora*, *Griselinia*, *Pennantia* and the podocarps) were absent. For instance, the study did not observe the presence of conifer species like *Podocarpus totara* (totāra) and *Prumnopitys taxifolia* (matai), which are dominant components of mixed conifer-angiosperm forests in New Zealand (Leathwick, 1995).

The main compositional change over time in the kānuka overstorey was mainly due to significant gains in māhoe abundance in the canopy and sapling stage suggesting the likely transition in dominance from kānuka to māhoe dominated forest, rather than a more diverse forest. The BA data support this assertion indicating that māhoe are starting to be counted in the overstorey with significant increases in BA of this species over time compared to other canopy tree species. The transition is highly likely given that māhoe is the only dominant canopy tree species in the understorey and the height growth of this species over time was about twice that of any other regenerating species in the area, which reflect the high shade tolerance of this species in dense forest understories (Allen et al., 1992; Smale et al., 1995). In other regenerating forests elsewhere such as the *Liriodendron* stands in North America (Clebsch & Busing, 1989), gap model projections indicated similar successional pathway with the shade-tolerant *Acer saccharum* estimated to dominate the forest after about 200 years, as also observed in actual old-growth stand. The same dominance hypothesis was considered for shade-tolerant red maple (*Acer rubrum*) understorey in Northeastern oak forests (North America), which can grow faster in height compared to oak regeneration even in sites with gap formations (Lorimer, 1984).

Stalled succession of kānuka stands have been observed by Smale et al. (1995) in South Kaipara, New Zealand with māhoe replacing the existing kānuka canopy following the reduction of introduced fallow deer, although the latter's influence in the understorey regeneration remained considerable over time with the influx of highly palatable shrub species. In a post-fire kānuka-dominated forest fragment in Te Urewera, North Island, New Zealand, arrested succession also occurred due to minimal compositional change and the high density of tree ferns in the understorey that after 30 years these tree ferns became a co-dominant species with kānuka in the canopy (Richardson et al., 2014). This is likely a similar successional pattern for the kānuka forest in this study, although at this time kānuka in the area remained the most dominant in the canopy in terms of density and BA and tree ferns are absent. Such dominance is also likely to last for many years unless major disturbance occurs, or canopy intervention is undertaken to control the kānuka canopy density including the dominance of māhoe and shrub species in the understorey. With the mean tree diameter of 13.8 ± 0.8 cm and age of 40-50 years old (D. Norton, personal communication, November 30, 2018), the kānuka stands at this site are growing very slowly, and would likely persist for 80-100 years according to the simulation model of Meurk and Hall (2006). Such long recovery time is similar to many seral communities in abandoned pastures (e.g. Smale et al., 2005), although, in such a degraded condition forest recovery is always not guaranteed (Aide et al., 1995) or often considerably slower with long-lasting effects on species composition (Chazdon, 2003).

3.5.2. Factors to consider when managing successional communities for restoration

Important barriers to the improvement of compositional structure in the study about 15 years after grazing exclusion (D. Norton, personal communication, November 30, 2018), could be due to the low-light environment or competitive exclusion by few dominant species (cf. Putz & Canham, 1992; Spooner et al., 2002). For instance, the continued dominance of kānuka in the overstorey or māhoe and the shrub *C. rhamnoides* species in the understorey could be responsible to the slow recruitment processes as indicated by the lower stem density, BA, and the high mortality rates of other emerging tree species in the area. It is widely known that the effects of intact canopies differ between shade-tolerant and light-demanding species, with the latter to likely have low survivorship and slow growth in dense canopies (Pacala et al., 1996). Most late-successional canopy tree species are light-demanding and do not establish in dense

canopies even when seed sources are available (e.g. Norton, 1991). The results could represent a state of arrested or delayed succession similar to other early-successional communities in abandoned pastures elsewhere (e.g. Northern America, Putz & Canham, 1992) and to those with long history of disturbance such as grazing (Chazdon, 2003). However, the result could also indicate a shift along a different successional trajectory to a different state, which is common to many old-fields in New Zealand that are poorly connected to remnant native vegetation (Standish et al., 2008), although post-disturbance forest dynamics in New Zealand are generally complex and can involve multiple potential pathways depending on the interplay of species with differing life-history and regeneration strategies (Wyse et al., 2018).

Thus, our findings indicate that simply removing grazing animals is not in itself likely to be sufficient to insure that this forest will develop into a more mature condition (quickly) without management interventions. This situation suggests the need for assisted succession or for a manipulative approach to restoration especially where dense successional habitats are involved. Low light levels are common to early-successional communities, and often restrict the establishment of later-successional or shade-intolerant species (e.g. Li & Ma, 2003), thus, the increasing number of gap-based restoration management interventions around the world primarily to initiate successional processes and facilitate forest recovery in dense regenerating stands (e.g. Fahey & Lorimer, 2013). In New Zealand, there is still a limited information on the potential of gap-based restoration methods to facilitate forest succession, although information of the positive role of artificial gaps on forest recovery and development are widely available in the literature (e.g. Collet et al., 2001; d'Oliveira & Ribas, 2011; Van Der Meer & Dignan, 2007). Recent applications of artificial gaps in New Zealand have been in the restoration planting of light-demanding canopy species such as *P. totara* and *Beilschmiedia tawa*, which were found to have rapid establishment and better survival rates under exotic *Pinus radiata* plantation with artificial gaps than within the intact radiata canopies (Forbes et al., 2016a). Further testing of this intervention is necessary as its effect could be species-specific or may differ depending on the disturbance regimes involved (Caplat & Anand, 2009).

However, in the kānuka dominated system studied here, there is considerable potential for gap creation in the kānuka canopy to benefit and enhance the dominance of māhoe species (cf. Lorimer, 1984) as it is currently the second most dominant tree species in the canopy in terms of density and BA. Future forest composition is usually dependent on the density and BA of trees in the understorey as they are the most available in the event of mortality and tree

replacement processes in the canopy (Peet & Christensen, 1987). The possibility of māhoe replacing or co-dominating with kānuka in the canopy could result in the maintenance of a relatively closed-canopy stand as has been observed in other cases of tree replacement where dominant shade-tolerant species have eventually formed the canopy layer of regenerating stand (e.g. Kneeshaw & Burton, 1997). However, all these assumptions could only be ascertained by actual testing of these canopy manipulative interventions within the kānuka stand and the subsequent monitoring of light environments and their long-term effects on successional change.

Moreover, while successful recruitment in New Zealand forests could be dependent on seed sources or seed rain (cf. Moles & Drake, 1999), the low number of recruits in the study was likely due to the lack of seed input from several adult canopy trees around the study area (ca. <500 m) or many of the dispersed seeds were unable to regenerate spontaneously under low-light condition. Species of several bird-dispersed native trees that are present in small patches within and around the Tiromoana Bush site such as the *Fuscospora solandri* var. *solandri*, *Myoporum laetum*, *Cordyline australis*, *Podocarpus totara*, and *Sophora microphylla* (Norton, 2019) were absent in the study sites. It is likely that, besides the intact kānuka canopy, the formation of dense māhoe and shrub cover in the understorey, especially *C. rhamnoides*, may have limited seed dispersal processes or successful establishment of regeneration within the area. Such dense understorey layer by shrub species is known to diminish tree recruitment opportunities (e.g. via competition) with their ability to colonize sites more rapidly than trees, which can alter the rate and direction of forest succession (Royo & Carson, 2006). Without intervention, it is likely that māhoe and *C. rhamnoides* species are the future dominants of the canopy and understorey structure in the area, especially, once the kānuka density starts to decline through natural mortality or senescence. In this situation, active restoration plantings are may be required to facilitate mature forest recovery and/or achieve positive outcomes for biodiversity conservation (Norton et al., 2018). There is evidence to suggest that this approach will modify ecosystem thresholds that limit natural succession and eventually catalyse the establishment of more mature and diverse forest including quality ecosystem functionality (Cortina et al., 2011).

3.5.3. Conclusion

Even after 15 years of grazing exclusion, succession within the kānuka-dominated forest in Tiromoana Bush still showing a state of arrested or delayed succession characterized by the absence of significant improvement in species compositional structure, high mortality rates, low recruitment rates, and the prolonged dominance of kānuka and māhoe in the area in terms of density and BA. This successional pattern is similar to other regenerating forests in New Zealand and elsewhere where succession have been arrested or delayed for an extended period even after several years of protection or grazing removal. The high competition for light or the low light condition within the intact kānuka forests could be limiting the successful establishment of woody regeneration – a particular case of competitive exclusion by dominant early successional species. The low light condition is likely due to the high density and BA of kānuka and māhoe in the overstorey, and the high density of māhoe and shrub cover in the understorey, especially *C. rhamnoides*.

Without immediate active intervention (e.g. artificial canopy gaps, enrichment plantings) to manage succession and control the intact kānuka canopy including the density of māhoe and shrubs in the understorey, it is highly likely that succession will remain arrested for at least 80 or 100 years, similar to other early-successional communities in degraded pastures. By then, the possibility of māhoe replacing or co-dominating with kānuka in the canopy is very high given the high density and BA of māhoe in the understorey compared to other tree species. Such eventuality could result in the maintenance of the relatively closed-canopy of the stand and may slow further or alter the rate and direction of forest succession in the area. Therefore, the results indicate the need for canopy manipulations to control the density of few dominant species and to create favourable light conditions for seed dispersal processes and subsequent establishment of light-demanding tree species. Although the potential of gap-based forest restoration is still poorly understood, the promising results of restoration plantings under artificial canopy gaps using some important canopy species such as totara (Forbes et al., 2016a) are good examples that need further considerations.

4. CHAPTER FOUR

Response of understorey native woody regeneration to artificial canopy gaps in an early-successional angiosperm canopy

4.1. ABSTRACT

Gap creation may reduce the intensity of competition and provide opportunities for less tolerant species to persist or coexist with more tolerant or predominant counterparts. This study examined the potential of artificial gaps to facilitate the natural regeneration and establishment of woody species in dense regenerating stands of kānuka (*Kunzea robusta*, Myrtaceae) that have developed following the removal of degrading factors especially grazing. Artificial gaps were created through selective felling of kānuka canopy trees and the species composition, density, growth, and survival of regenerating native woody species under the canopy gaps and intact kānuka canopy were monitored for 28 months. Gap creation resulted in a significant increase in the number of species and density of woody regeneration including both shade-tolerant and intolerant native woody species. There was no significant effect detected with respect to the interaction of time and gap creation on species recruitment. Survival and growth of woody regeneration were significantly greater in canopy gaps than beneath the intact canopy despite the higher proportions of ground vegetation and browsing incidence by ungulates in gap treatments. The tendency of woody seedlings to grow better in canopy gaps may have provided them the competitive ability and browsing tolerance to offset the effects of browse. The duration of the study was too short to capture fully the potential of canopy intervention, but woody regeneration within the artificial gaps are likely to accelerate as the regeneration proceeds and the results presented here provide useful insight into the early stages of this process.

Key words: artificial gaps, canopy species, early-succession, forest restoration, *Kunzea robusta*, woody regeneration

4.2. INTRODUCTION

Delayed or arrested succession under few dominant species is a typical situation in many regenerating forest communities (Acácio et al., 2007; Denslow, 1980; Prach et al., 2001). Arrested succession appears to be particularly common in dense regenerating vegetation associated with abandoned pastures where competition for light and soil resources can be intense (Putz & Canham, 1992; Sarmiento, 1997). Reinitiating forest successions in such communities may require deliberate disturbance of canopies to reduce the density of overtopping plants and provide more favourable understorey light conditions for less tolerant species (d'Oliveira & Ribas, 2011; Van Der Meer & Dignan, 2007). Existing theories (e.g. intermediate-disturbance hypothesis; cf. Grime 2006) suggest that disturbance regime and resource availability (especially light) are key factors for structuring forest ecosystems and controlling the competitive dominance of one or a few species (Denslow, 1980; Roberts & Gilliam, 1995; Tilman, 1994). In the forest growth cycle, for instance, the formation of gaps is considered the most important phase that facilitates species recruitment and establishment of canopy species that have been suppressed under forest canopies (Whitmore, 1989). The meta-analysis of Suding (2001) on the effects of gap creation on competitive interactions suggests that gap creation not only reduces the intensity of competition but also provides opportunities for less tolerant canopy species to persist or coexist with more tolerant counterparts.

While canopy gaps hold much potential to facilitate forest successions, some studies suggest that canopy species are inferior competitors and that successional pioneers or predominant species have the competitive advantage to maintain their population or dominate in gap environments (Oliver, 1980; Royo & Carson, 2006). In some situations, canopy interventions may fail to promote regeneration (including shade-tolerant and shade-intolerant species) in disturbed communities due to interference from more aggressive species as well as competition in gaps (Beckage et al., 2000; Putz & Canham, 1992; Royo & Carson, 2006). Instances of enhanced herbivory by ungulates have also been documented in regenerating communities following gap formations, either in naturally (e.g. Howe, 1990) or artificially (Forbes et al., 2016a), which can reduce the competitive ability of gap-dependent species to colonize these high light environments. The confounding effect of herbivory to plant competition (e.g. Reader, 1992) has also been suggested as a driver of species compositional structure change towards a browse-tolerant dominated community (Hidding et al., 2013).

These differing views on the success of gaps in promoting succession reflect the inherent unpredictability of regeneration dynamics in degraded environments (Aide et al., 1995; Hobbs & Norton, 2004). Notwithstanding this, field testing can help understand site- and species-specific variability, which remains rarely tested empirically, especially the assumption that gap species are always inferior competitors compared to shade-tolerant or pre-dominant understorey species (Suding, 2001). Understanding the feedbacks and limitations associated with canopy intervention is critical to assess the viability of artificial gaps in degraded habitat recovery and to identify options to optimize the benefits of this intervention in restoration projects.

I proposed that artificial gaps are likely to be important for facilitating natural regeneration in seral communities especially those dominated by one or few species such as the *Kunzea robusta* (kānuka) regenerating forests in New Zealand (cf. Smale et al., 1995). An increasing area of seral woody vegetation is being managed in New Zealand for succession to mature forest (Norton et al., 2018; Walker et al., 2009a), usually by removal of livestock grazing (Norton et al., 2018). However, results from studies in regenerating forests, where grazing has been excluded, indicate that successions can be delayed or arrested for several years (e.g. Smale et al., 2005). Aside from their degraded abiotic conditions, the high-density canopies and understorey layers of seral communities often act as barriers to succession and seedling survival, thus, resulting in one or a few species dominating the community for several decades or centuries (Allen et al., 1992; Reay & Norton, 1999a). In a 70-year old kānuka stand in Otago New Zealand, for instance, only a few scattered podocarp seedlings had been able to establish in the canopy and it was suggested that only through a substantial reduction of kānuka stem density that other species would be able to establish and colonize (Allen et al., 1992). This study was conducted to ascertain the importance of artificial gaps on the natural regeneration and establishment of woody species in dense regenerating communities such as kānuka where the understorey is also typically dominated by one or few species including the high shade tolerant *Melicytus ramiflorus* (māhoe, Violaceae) (Reay & Norton, 1999a; Smale et al., 1995). Artificial gaps were created through selective felling of kānuka canopy trees and the natural regeneration and growth response of native woody species beneath intact kānuka canopy and artificial gaps were compared. Specifically, the study seeks to ascertain whether artificial gaps can provide better conditions than the intact kānuka canopy for the successful recruitment and establishment of native woody regeneration, especially potential future canopy

species. This was accomplished by assessing differences between canopy treatments in terms of woody seedling species composition, density, growth, and survival.

4.3. METHODS

4.3.1. Experiment design and measurements

The study was carried out in 16 replicates of artificial gaps and intact canopy (control) treatments (or a total of 32 sample plots) within the dense 10-15 m tall kānuka-dominated forests. Kānuka were the first cohort of trees to establish on these previously farmed sites. Canopy gaps were created in December 2015 by removing six (6) kānuka canopy trees in each gap replicate, creating around 16 m² canopy opening. A permanent 2m x 2 m plot was then established at the gap centre, and another one (five meters away from the edge of the gap treatment) was located under the intact kānuka canopy; thus, keeping the physical variables (aspect and slope) similar for the paired plots: terrain slope ($\chi^2_{[1]} = 0.002$, $P=0.966$), slope aspect ($\chi^2_{[1]} = 0.313$, $P=0.576$). The 16 paired sample plots (approximately 200 m away from each other) were established in two separate dense stands of kānuka-dominated forests (Fig. 9). Ten (10) paired plots were established at the first site and another six (6) paired plots were located at the second site. The second site was about three (3) kilometres away from the first site. After plot establishment, all plants within and around the 2 x 2 m plots were removed or uprooted, both in the treatment and control.

The regeneration of native woody tree and shrub species within each plot was monitored for 28-months with the first seedling height measurement carried out in December 2016 or a year after plot establishment. Succeeding height measurements were conducted in 2017 (February, April, and September) with the final measurement in April 2018. During each measurement, all new woody species inside each plot were tagged, identified to species level, and their heights measured. The monitoring of the incidence of browsing for tagged seedlings started in the second measurement period (in February 2017) and continued in succeeding measurements. The browsing incidence was recorded per stem to estimate the proportion of browsed seedlings for each plot. For survivorship, seedlings were considered dead if they cannot be found inside the plot at each measurement. The proportion covered by non-woody plants (e.g. herbs, grass, fern, climber) relative to the size of the plot was also estimated during each measurement starting in December 2016.

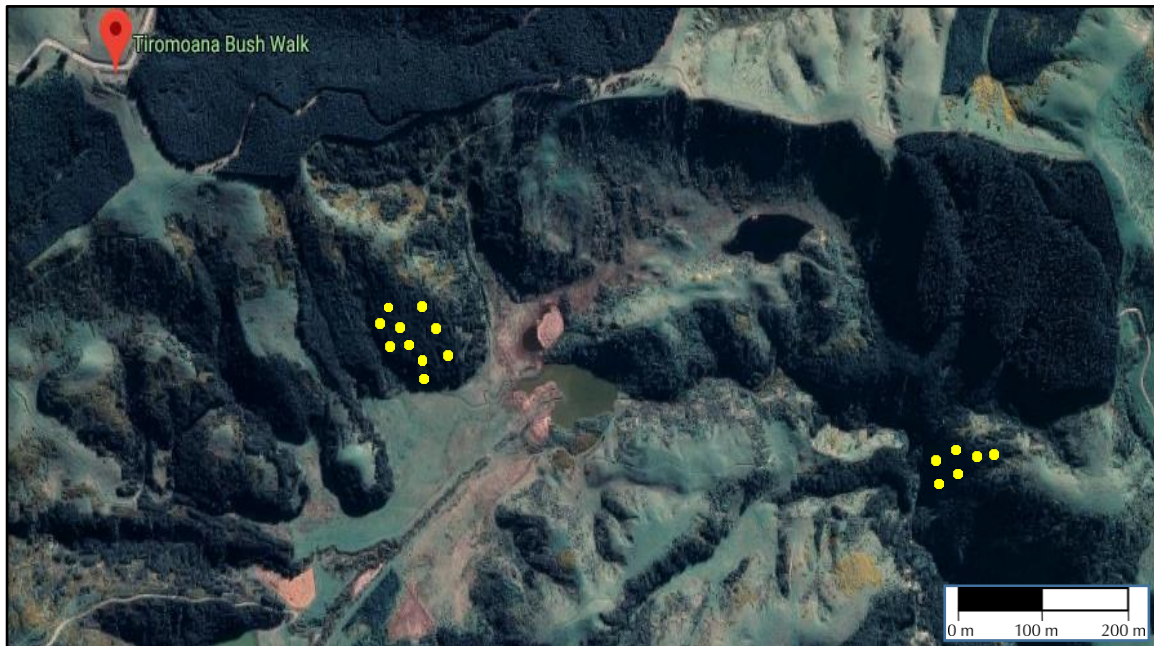


Figure 9. Location of the 16 paired plots within the two dense stands of kōnuka-dominated forests at Tiromoana Bush, North Canterbury.

4.3.2. Topography and hemispherical photography

The slope angle (degrees) and aspect (degrees) of plots were determined using a Suunto clinometer and compass. Understorey light environment and canopy openness in each plot were assessed in 2016 using hemispherical photography. The hemispherical photographs were taken at 1.3 m above the ground during overcast skies or cloudy days using a digital camera (Nikon D3100) fitted with a Sigma 4.5 mm circular fisheye lens. The camera was set up at the centre of each plot, levelled with a bubble level and oriented towards the magnetic north. The canopy openness (%) and understorey light transmittance, percent total light transmitted and total photosynthetically active radiation (PAR, $\text{mol m}^{-2} \text{ day}^{-1}$), were estimated from the hemispherical photos using the Gap Light Analyzer computer software (GLA version 2; Frazer et al., 1999). The GLA software estimates the percent canopy openness as the proportion of open sky captured in the photo from beneath the forest canopy, while the total PAR as the sum of the diffuse and direct solar radiation transmitted by the canopy (Frazer et al., 1999). In the GLA modelling, the growing season was specified from 1 September to 31 March to match the estimated local plant growth patterns.

4.3.3. Data computations and analyses

All statistical analyses were performed in R software (R Core Team, 2018). The differences in topography, terrain slope and slope aspect data, among plots between treatments were assessed respectively using Kruskal-Wallis rank-sum test and Wallraff test of angular distances (circular package; Agostinelli & Lund, 2017). Differences in the percentages of light transmittance and canopy openness among plots between the intact kānuka canopy and canopy gaps were assessed separately using generalized linear model (GLM) with a binomial family (*Chisq* test) or quasibinomial with *F*-test when a model was over-dispersed. Differences in the total amount of photosynthetically active radiation (PAR, $\text{mol m}^{-2} \text{ d}^{-1}$) transmitted among plots between treatments were analysed using one-way analysis of variance (ANOVA) with log transformation to improve the distribution probabilities of the data. Repeated measures analysis of variance (ANOVA) with the lmer function (lme4 package; Bates et al., 2015) was used to assess the effects of canopy treatments, time (in months), and treatments-by-time interaction on the arcsine (square-root) transformed percent ground vegetation cover and browsing incidence data with the number of plots as random effects. The significance of the explanatory

variables in the lmer models was obtained using a Wald chi-squared test, applying the Anova function in car package (Fox & Weisberg, 2011). *Post hoc* pairwise comparisons of significance were conducted using the emmeans function (emmeans package; Lenth, 2018).

Non-metric multidimensional scaling (NMDS) was used to make inferences on the species compositional structure between the two canopy treatments in two dimensions applying the metaMDS function (20 iterations, Bray-Curtis distance) of vegan package (Oksanen et al., 2018). Permutational multivariate analysis of variance (PERMANOVA, 999 permutations, Bray-Curtis method, adonis function in vegan package) was run to assess the effects of canopy treatments, time, ground cover, browsing incidence and the interaction between them on the species compositional structure. Zero-adjusted Bray-Curtis coefficient method for denuded assemblages (Clarke et al., 2006) was applied prior to ordination and PERMANOVA analysis since several sample plots in our study had zero observations. The influence of within-treatment variability was assessed using the betadisper function in vegan package. Similarity percentage analysis (SIMPER) was used to determine the discriminating species between the two canopy treatments.

Generalized linear mixed-effects models were used to assess the mean seedling density per plot, analysing the variations due to treatments, time (in months), species, percent ground cover, percent browsing incidence, and the interactions between them. To account for excess zeros in the density data, the zero-inflated model with negative binomial distribution in glmmTMB package (Brooks et al., 2017) was used in the analysis. Model selection proceeded by comparing the Akaike's Information Criterion (AIC) of models with different combinations of parameters. The parameters were sequentially removed from the full model that contained independent and two-way interactions, which were then compared using the AICtab function in bblme package (Bolker & Team, 2017). The significance of parameters in the final density model was assessed using a Wald chi-squared test in car package and the *post hoc* pairwise comparisons of significance were conducted using the glht function in the multcomp package (Hothorn et al., 2008).

For the analyses of seedling mean survivorship and absolute height (cm) of each species per plot, I used the dominant species in the data to facilitate the comparison of treatment and time effects on seedling performance as several species had zero or too few observations. Survivorship was the proportion of seedlings counted in the first measurement period that were

still alive in succeeding measurements and the analysis was conducted using the nonparametric method (Kaplan Meier Analysis) of the survival package (Therneau, 2017). The nonparametric survival method was carried out using the `survfit` function to estimate the probability of seedling survival over time with respect to treatments and species factors. Significance of the parameters in the survival model was determined using the *log-rank* test in the survival package. The survival data were interval-and right-censored as some seedlings died between measurements, while others survived after the study. For seedling height, the analysis was performed using the linear mixed effects model of `lme4` package (Bates et al., 2015) with the number of sample plots as random effects and the best model or most parsimonious based on AIC was selected. The significance of the parameters in the height models was determined using the R base `anova` function and the *post hoc* pairwise comparisons of significant parameters were then conducted in `emmeans` library.

4.4. RESULTS

4.4.1. Canopy openness and light transmittance

Canopy openness ($\chi^2_{[1,30]} = 9.11$, $P < 0.001$) and light transmittance ($\chi^2_{[1,30]} = 28.23$, $P < 0.001$) differed significantly between gap and intact canopy. Mean canopy openness was $10.7 \pm 0.2\%$ beneath the intact kānuka canopy and $15.0 \pm 0.7\%$ in canopy gaps, which translated to mean total light transmittance of 11.7 ± 0.4 (under intact kānuka canopy) and $20.1 \pm 1.3\%$ (in canopy gaps). This difference was equivalent to total transmitted PAR of $4.93 \pm 0.17 \text{ mol m}^{-2} \text{ d}^{-1}$ under the intact kānuka canopy and $7.35 \pm 0.46 \text{ mol m}^{-2} \text{ d}^{-1}$ in canopy gaps ($F_{[1,30]} = 34.19$, $P < 0.001$).

4.4.2. Ground cover and browsing incidence

Changes in ground vegetation cover over time were significantly related to canopy treatment (treatment x time interaction) ($W^2_{[4]} = 13.39$, $P = 0.009$) with the canopy gaps having a consistent significantly higher vegetation cover over time than the intact kānuka canopy (Fig. 10a). The effect of time independent of treatment on ground vegetation cover was highly significant ($W^2_{[4]} = 47.67$, $P < 0.001$). Independent of time, canopy gaps had significantly more

than twice the ground vegetation cover ($34.1 \pm 2.5\%$) than the intact kānuka canopy ($13.9 \pm 1.5\%$) ($W^2_{[1]} = 96.12, P < 0.001$).

There was no statistically significant effect that could be ascribed to gap treatment and time interaction on the increasing proportion of browsing incidence ($W^2_{[4]} = 7.78, P = 0.099$), except for the independent significant effect of treatment ($W^2_{[1]} = 12.15, P < 0.001$) and time ($W^2_{[4]} = 175.05, P < 0.001$) (Fig. 10b). The incidence of browsing was more evident only towards the latter time of the study with canopy gaps having significantly higher incidence of browsing compared to intact kānuka canopy.

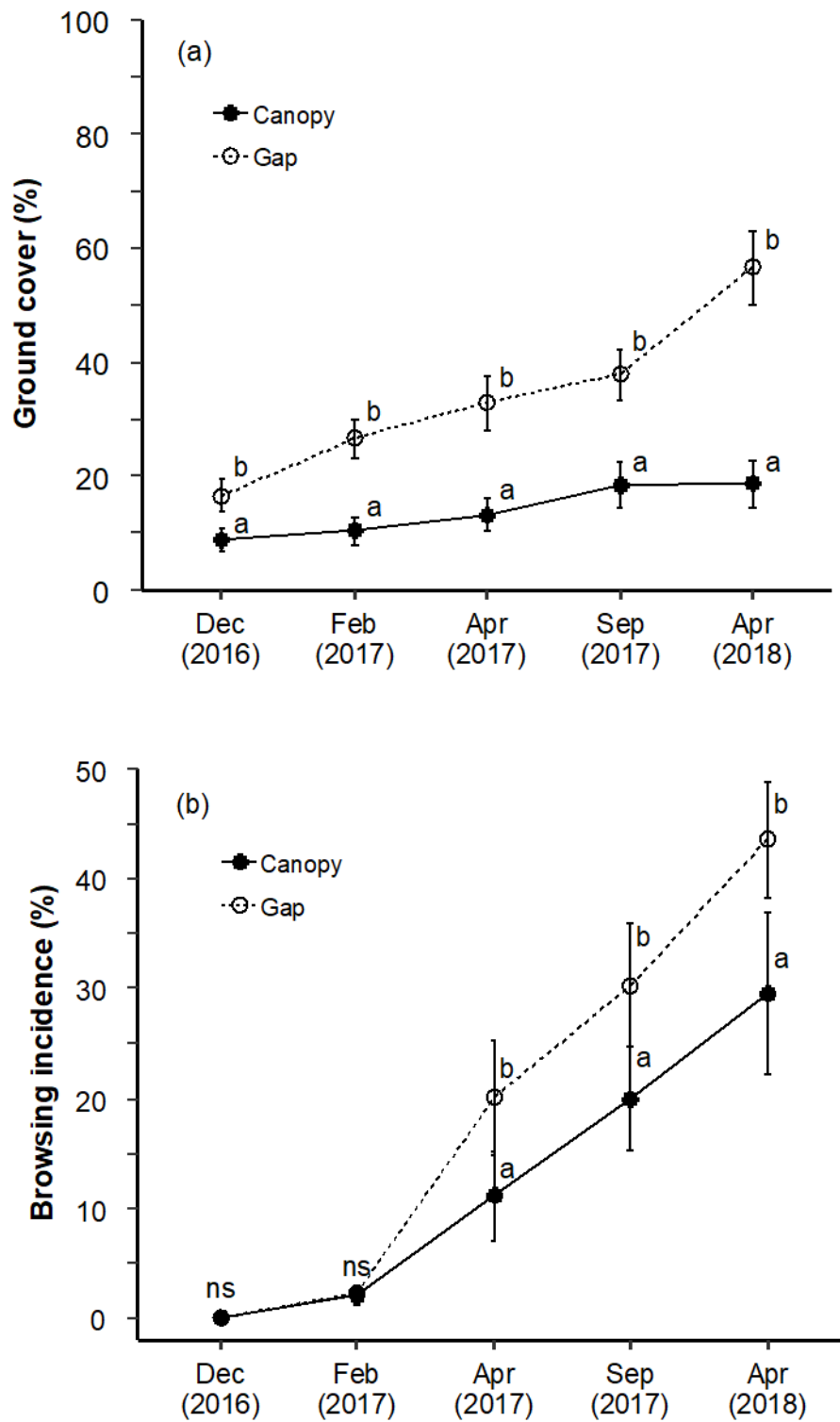


Figure 10. Proportions of (a) ground cover (non-woody plants) and (b) browsing incidence between canopy treatments over time. Different letters on error bars between time points indicate significant difference at $P < 0.05$. Error bars represent \pm SE.

4.4.3. Species composition and density

Over 28 months, a total of 14 native woody species comprising five shrubs and nine canopy forming species were recorded from 32 (2 x 2 m) sample plots across the canopy treatment and intact kānuka canopy (Table 4). Of the nine canopy forming species, six occur under the intact kānuka canopy but all the nine species occur in canopy gaps, and all occur at higher densities in gaps (Appendix A). A mixture of shade-tolerant and intolerant species established in both canopies with *Melicytus ramiflorus* and *Pseudopanax arboreus* species as most abundant in the canopy gaps in terms of density comprising about 44 and 14%, respectively, of the total density; while the seedlings of *Coprosma propinqua* were most abundant (ca. 48%) beneath the intact kānuka canopy. The latter was also the widely distributed species within the kānuka intact canopy with frequency value of 68.75% (cf. 0-50% for other species) at the end of the study. In the canopy gap treatment, *M. ramiflorus*, *P. arboreus*, and *C. propinqua* were the most frequent at 87.50%. *M. ramiflorus* and *P. arboreus* are potential canopy forming species, while *C. propinqua* is a shrub.

Table 4. Species composition and growth form of native woody regeneration beneath the intact kānuka canopy and canopy gaps at the end of the study.

Code	Species Name	Growth Form	Canopy	Gap
Aser	<i>Aristotelia serrata</i>	Canopy forming species		✓
Cluc	<i>Coprosma lucida</i>	Shrub	✓	✓
Cpro	<i>Coprosma propinqua</i>	Shrub	✓	✓
Crha	<i>Coprosma rhamnoides</i>	Shrub	✓	✓
Crot	<i>Coprosma rotundifolia</i>	Shrub	✓	✓
Cser	<i>Carpodetus serratus</i>	Canopy forming species		✓
Fexc	<i>Fuchsia excorticata</i>	Canopy forming species		✓
Hlan	<i>Helichrysum lanceolatum</i>	Shrub		✓
Mlae	<i>Myoporum laetum</i>	Canopy forming species	✓	✓
Mram	<i>Melicytus ramiflorus</i>	Canopy forming species	✓	✓
Parb	<i>Pseudopanax arboreus</i>	Canopy forming species	✓	✓
Pcor	<i>Pennantia corymbosa</i>	Canopy forming species	✓	✓
Pcra	<i>Pseudopanax crassifolius</i>	Canopy forming species	✓	✓
Pten	<i>Pittosporum tenuifolium</i>	Canopy forming species	✓	✓

Results of ordination revealed a moderate separation in composition between the intact kānuka canopy and canopy gaps (nMDS ordination stress = 0.1497; Fig. 11). This was supported by the results of PERMANOVA, which showed a significant difference between the two canopy treatments, although some of the variations could not be explained by the model as indicated by its weak r-squared value ($F_{[1,138]} = 32.9$, $P < 0.001$, $R^2 = 0.17$). The species composition did not vary with time ($F_{[4,138]} = 0.3$, $P = 0.98$, $R^2 = 0.005$), but there was significant effect from the proportion of ground cover ($F_{[4,138]} = 3.3$, $P < 0.001$, $R^2 = 0.02$), the interaction between canopy treatment and ground cover ($F_{[1,138]} = 5.7$, $P = 0.009$, $R^2 = 0.03$), and the interaction between canopy treatment and browsing incidence ($F_{[1,138]} = 4.6$, $P = 0.003$, $R^2 = 0.02$). Dispersion of species composition within the canopy treatment and intact canopy was also significant ($F_{[1,158]} = 20.9$, $P < 0.001$). Results from SIMPER analysis showed a notable increase in density of species in the canopy gaps with respect to the intact kānuka canopy with some species were only observed in the canopy gaps including *Aristotelia serrata*, *Carpodetus serratus*, *Fuchsia excorticata*, and *Helichrysum lanceolatum* which are all potential canopy forming species. The discriminating species that are driving the overall percent dissimilarity between gap and intact canopy based on SIMPER analysis included *M. ramiflorus*, *C. propinqua*, *P. arboreus*, *C. rhamnoides*, and *C. rotundifolia* (Appendix B). Among these species, only *C. propinqua* was substantially lower in the canopy gaps.

Seedling density differed significantly between canopy treatments ($\chi^2_{[1]} = 18.12$, $P < 0.001$; Fig. 12) with the canopy gaps having a higher mean density of regenerating woody species ($6,029 \pm 444$ stem ha^{-1}) than the intact kānuka canopy ($1,962 \pm 185$ stem ha^{-1}). Significant variations in seedling density were species-dependent ($\chi^2_{[13]} = 302.47$, $P < 0.001$) with *M. ramiflorus* ($17,391 \pm 2,553$ stem ha^{-1}) and *C. propinqua* ($12,141 \pm 1,099$ stem ha^{-1}) tallying the highest mean density, followed by *C. rhamnoides* ($6,063 \pm 584$ stem ha^{-1}), *P. arboreus* ($5,766 \pm 616$ stem ha^{-1}), *C. rotundifolia* ($5,156 \pm 720$ stem ha^{-1}), *M. laetum* ($3,266 \pm 534$ stem ha^{-1}), and *C. serratus* ($2,969 \pm 500$ stem ha^{-1}), while the remaining species had < 600 stems per hectare. Although the parameter time was included in the final model, the effect was not statistically significant ($P > 0.05$).

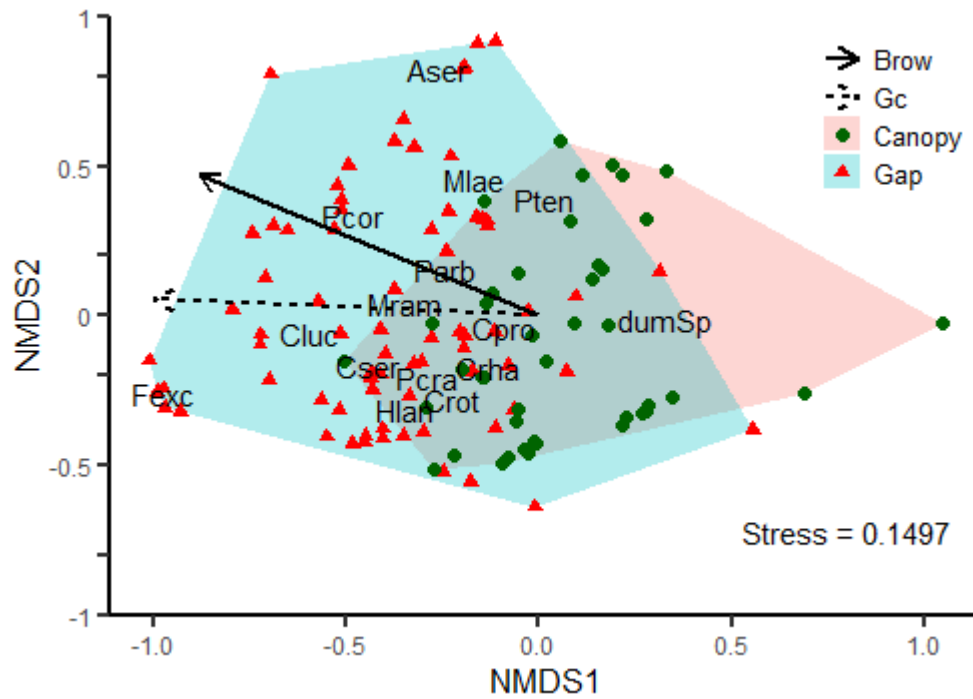


Figure 11. NMDS ordination of regenerating woody species beneath the intact kānuka canopy and canopy gaps at the end of the study. Note the dummy species is denoted with dumSp. The symbols represent 16 canopy gaps and 16 intact canopy sites that were sampled five times (32 sites x 5 times = 160). Significant effect of the proportion of ground cover (Gc) and browsing incidence (Brow) is indicated. The positions of the woody species on the ordination space are also presented. Species codes are described in Table 4.

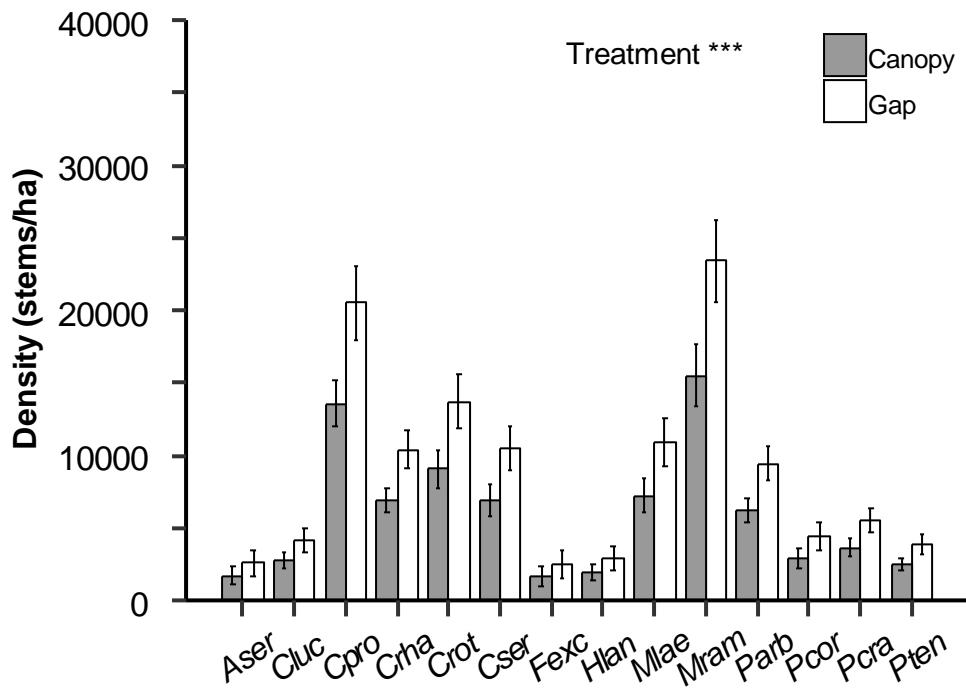


Figure 12. Fitted mean seedling density (stem per ha) per plot of woody regeneration between canopy treatments. Asterisks (***) indicate highly significance or $P < 0.001$. Species codes are described in Table 4. Error bars represent \pm SE.

4.4.4. Survival probability

Survival probability from the nonparametric analysis showed no significant difference between treatments ($P=0.97$) 16 months after the initial measurement but all indicated a decline with time as expected. The variation in survival rate was species-dependent ($\chi^2_{[5]} = 12.4$, $P=0.03$) even among treatments ($\chi^2_{[11]} = 26.1$, $P=0.006$). Among the dominant species, *M. laetum* ($73.0 \pm 6.1\%$) registered the highest survival over the 16-month period, followed by *M. ramiflorus* ($72.7 \pm 3.52\%$), *C. propingua* ($70.8 \pm 3.54\%$), *P. arboreus* ($68.6 \pm 4.84\%$), *C. rhamnoides* ($62.2 \pm 5.26\%$), and *C. rotundifolia* ($58.9 \pm 6.35\%$). In the canopy gaps, all species survived over the 16-month measurement period and the survival rate followed the order: *M. ramiflorus* ($72.7 \pm 3.52\%$), *M. laetum* ($69.3 \pm 7.29\%$), *P. arboreus* ($67.4 \pm 5.23\%$), *C. rhamnoides* ($65.9 \pm 6.7\%$), *C. propingua* ($62.0 \pm 5.46\%$), and *C. rotundifolia* ($48.9 \pm 8.25\%$). Under the intact k nuka canopy, only three species survived beyond 16 months with *C. propingua* ($80.2 \pm 4.09\%$) having the highest survival, followed by *M. ramiflorus* ($74.6 \pm 10.78\%$) and *C. rhamnoides* ($55.6 \pm 8.31\%$).

4.4.5. Height growth

The mean absolute height growth (cm) of dominant woody regeneration was significantly ($P<0.05$) influenced by treatments, species, time, ground cover and browsing incidence; including the interactions between treatments and time, treatments and species, treatments and ground vegetation cover, and between treatments and browsing incidence. The seedlings grew significantly taller in the canopy gaps ($F_{[1,934]} = 53.16$, $P<0.001$) and over time ($F_{[4,928]} = 21.87$, $P<0.001$) than under the intact k nuka canopy (Fig. 13). While there was strong species individuality ($F_{[5,921]} = 29.32$, $P<0.001$), all species were significantly taller ($F_{[5,921]} = 3.02$, $P=0.010$) in the canopy gaps than under the k nuka canopy except for *M. laetum*. On the other hand, the increase in percent ground cover independent of treatments and time generally reduced the height of seedlings ($F_{[1,892]} = 12.48$, $P<0.001$); but between treatments (treatment x ground cover), the effect was more apparent ($F_{[1,832]} = 12.43$, $P<0.001$) in gap treatments than under the intact k nuka canopy. Similarly, browsing incidence also negatively affected the height growth of seedlings independent of canopy treatment and time ($F_{[1,925]} = 27.43$, $P<0.001$) but was more evident to seedlings in the canopy gaps than in the intact k nuka canopy ($F_{[1,936]} = 13.35$, $P<0.001$).

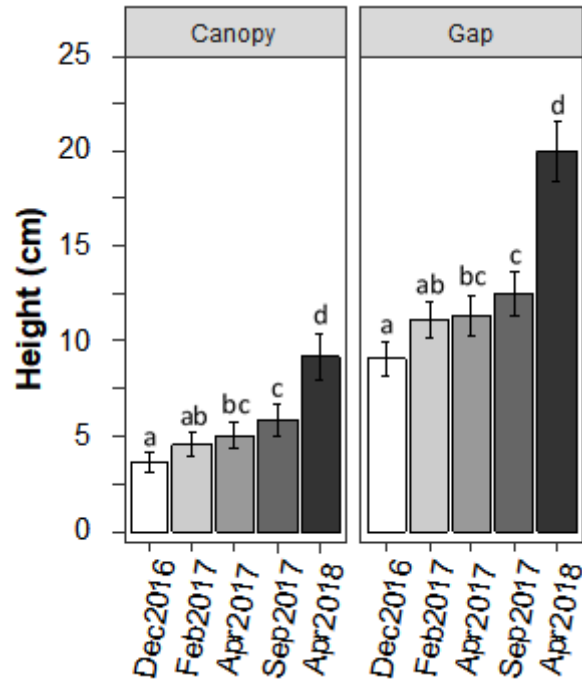


Figure 13. Absolute mean height (cm) per plot of dominant woody regeneration between canopy treatment and intact canopy over the five measurement time points. Different letters on the error bars in each treatment indicate significant difference at $P<0.05$. Error bars represent \pm SE.

4.5. DISCUSSION

4.5.1. Compositional structure and recruitment of woody species in canopy gaps

Gap creation in low-light successional communities is assumed to reduce the intensity of competition and provide opportunities for the coexistence of species with different shade-tolerance or competitive ability (Suding, 2001). In this study, some evidence of coexistence among woody species with different shade tolerance was observed, which may indicate a decline in the intensity of competition following the canopy treatments. For instance, the increase in light transmittance in canopy gaps was significantly related to the increase in number and abundance of recruits that included a mixture of shade-tolerant (e.g. *M. ramiflorus*, *C. propingua*) and intolerant canopy species (e.g. *P. arboreus*, *M. laetum*) suggesting the importance of canopy intervention to structure the regeneration niche of woody species in the area. Out of nine canopy forming species tallied, five canopy forming species occur under canopy but nine occur in gaps, and all occur at higher densities in gaps. The higher density of woody seedlings and species in canopy gaps compared to intact kānuka canopy are notable results that are consistent to the importance of elevated light environments to New Zealand native woody species as previously observed in forest areas with occurrences of canopy disturbances (e.g. Allen & Wardle, 1985; Baxter & Norton, 1989; Ogden et al., 1991).

However, this study demonstrates that initiating succession through artificial canopy gaps can be slow in degraded environments. For instance, I found no significant effect detected with respect to the interaction of time and treatments on species recruitment over the course of this study. It is likely that the 2-3-year duration of the study was too short to account fully the benefits associated with canopy gaps especially in such a degraded condition. Several studies in degraded communities elsewhere have observed consistent successional change only after several years from canopy gaps creation, e.g. 5-12 years (d'Oliveira & Ribas, 2011) or 8 years (Van Der Meer & Dignan, 2007) but were projected to accelerate as the succession proceeds.

The slow species turnover could be related to the inherent difficulty of successions in degraded environments in New Zealand (Norton, 2009; Standish et al., 2008) similar to that in other degraded communities elsewhere (Aide et al., 1995; Putz & Canham, 1992; Sarmiento, 1997) where lack of propagules, poor soil/abiotic condition, among other limitations can be widespread. In other regenerating forests in New Zealand abandoned pastures, successful

colonization by more diverse native trees was observed only after about 30 or 50 years even management intervention such as grazing removal (e.g. Smale et al., 2005). In other studies, possible minimal effects of canopy gaps in regenerating communities as compared to mature forests were reported (e.g. Beckage et al., 2000; Clebsch & Busing, 1989). Clebsch and Busing (1989) suggest that unlike old-growth forest with large and spreading crowns, second-growth stands are characterized by narrow and nonoverlapping canopy structure, which can minimize the effects of canopy gaps in the understorey environment. Thus, even with canopy gaps, single species dominance tends to be more pronounced in second-growth stands than in old-growth forest (Clebsch & Busing, 1989). Oliver (1980) reported many cases of canopy gap creation in second-growth stands with slow species turnover due to stem exclusion by pre-existing dominant understorey species, similar to that observed in other regenerating communities elsewhere (e.g. Putz & Canham, 1992). In this study, the dominance of the shade tolerant *M. ramiflorus* could also be neutralizing recruitment opportunities even in canopy gaps. Earlier studies indicated the tendency of *M. ramiflorus* to overtop regenerating species as succession proceeds especially in post-disturbance communities where this species is the dominant understorey species (Allen et al., 1992; Smale et al., 1995). Initial succession is usually driven by stem exclusion and can be intense in canopy gaps within the first 1-2 years of succession, but once the species survive they can be expected to persist throughout the successional processes (Oliver, 1980; Tilman, 1994).

In addition, the rather sparse regeneration of several species in the study, even in canopy gaps, could be largely driven by poor seed bank condition and/or inadequate seed rain, which are common in degraded environments in New Zealand (Standish et al., 2008). The time elapsed (30 to 40 years) for historical disturbances in New Zealand may have eliminated the potential contribution of seed bank to natural regeneration (Moles & Drake, 1999). Studies cited by Standish et al. (2008) indicated that long-term seed banks (i.e. >2 years) are rare among New Zealand native plants, except for *Fuchsia excorticata* that can persist in soil for more than 20 years. Interestingly, this species was recorded in this study although only in canopy gaps, which may indicate that species persisting in seed banks can regenerate under a favourable light condition. The occurrence of this species, although sporadically, is perhaps the most important effect of artificial gaps in this study as this highlight the potential of canopy intervention to facilitate natural regeneration especially for species that have been suppressed for years in the soil seed bank.

While the seed dispersal pattern was not examined in this study, it is likely that adult trees within or around the study area that are mostly within < 500 m including *Fuscospora solandri* var. *solandri*, *Myoporum laetum*, *Cordyline australis*, *Podocarpus totara*, and *Sophora microphylla* (Norton, 2019) are not producing enough seeds to sustain the species turnover and optimize the favourable environment in canopy gaps. Certainly, there could be a wide array of microenvironment (e.g. soil moisture, nutrients) that have limited the regeneration of several species in the study (cf. Hobbs & Norton, 2004; Moles & Drake, 1999; Norton, 2009; Standish et al., 2008), but the slow species recruitment, especially in canopy gaps, is more likely an indication of propagule limitation rather than niche limitation (Moore & Elmendorf, 2006). The importance of these dispersal filters in degraded environments and fragmented landscapes is well recognized and are expected to limit local seed rain of many canopy species including mutualistic relationships as significant numbers (ca. >50%) of native species in New Zealand are bird dispersed (Canham et al., 2014; Kelly et al., 2010; Moles & Drake, 1999; Norton, 2009). In such situation, active restoration plantings under artificial gaps using native canopy species (cf. Forbes et al., 2016a), would be a viable option to overcome seed dispersal limitations and maximize the restoration benefits associated with canopy intervention.

4.5.2. Seedling survivorship and establishment: effects of competition and browsing incidence in canopy gaps

The increases in the proportions of non-woody vegetation or ground layer plants (e.g. herbs, grasses, climbers) and the incidence of browsing by ungulates including their impacts on species turnover and establishment were significantly associated with artificial gaps as has been observed in other studies (e.g. Royo & Carson, 2006) suggesting the importance of aboveground competition and prevalence of herbivory in the area. However, the study, found no evidence that could be ascribed to the effects of interactions of ground vegetation cover and browsing incidence in gap environments, which may indicate that they influence the woody regeneration in the study independently.

Despite the increase in the proportions of ground layer plants and browsing incidence, survival of woody species was higher in canopy gaps than beneath the intact canopy with all the species in the canopy gaps surviving through the duration of the study as compared to only about 50% of the species that survived in the intact canopy. The latter was dominated mainly

by *M. ramiflorus* and *C. propingua* species, which is expected because of their high tolerance to shade and predominance in the area. Within the canopy gaps, seedlings survivorship was comparable among species with no clear best performer even with the increasing proportions of ground vegetation. The ability of woody seedlings to grow taller in canopy gaps may have allowed them to compensate for any survival disadvantages as a result of competition from ground vegetation, which was observed to affect the growth of seedlings in gap treatments. The result may indicate the importance of growth and mortality trade-offs in the canopy gaps that can create opportunities for coexistence among woody species following canopy intervention.

There was also evidence for more browse in gap sites, but not withstanding this, this does appear to be a good mechanism. Because the woody regeneration grew significantly taller in canopy gaps, the negative impact of browsing by ungulates in the study has been on the seedling growth, particularly, on seedlings with at least 10 cm height which was also observed by Wilson et al. (2006). However, the tendency of seedlings in the canopy gaps to recover quickly as demonstrated by the better seedling growth in the canopy gaps than the intact canopy may have allowed them to offset the negative impact of browsing. This result provides some support to earlier findings that seedling tolerance to herbivory in canopy gaps is due to higher resource availability (Wise & Abrahamson, 2007), in conjunction for a resistance-resilience trade-off with respect to potential growth rates (Bee et al., 2007).

4.5.3. Implications of artificial canopy gaps to forest restoration in seral communities

While initial woody species succession can be slow even under artificial canopy gaps, the results provided evidence of the importance of canopy intervention to facilitate the regeneration of woody species and the coexistence of species with different shade tolerance. I observed that the tendency of woody regeneration to grow better in canopy gaps could be critical to compensate for any growth and survival disadvantages during initial succession where competition from ground vegetation and browsing incidence can be high. While the duration of the study was likely too short to capture fully the potential of canopy intervention, the better density, growth, and survival of woody species in the canopy gaps provide useful insights of the opportunity that canopy manipulation provides and are positive indications that succession can accelerate as the regeneration proceeds. This study provided, therefore, a unique opportunity to understand the viability of artificial gaps in the early stage of succession where

regeneration could be limited not only by inadequate seed supply but also from intense competition with ground vegetation and the occurrence of herbivory, which are rarely empirically observed.

5. CHAPTER FIVE

Canopy manipulation as a tool for restoring mature forest conifers under an early-successional angiosperm canopy

5.1. ABSTRACT

Low-light environments in early-successional forests that have established after the abandonment of farming often restrict the establishment of later-successional species resulting in an arrested succession. This 6-year study tested the potential of different canopy manipulations to facilitate the establishment of a light-demanding canopy tree species, tōtara (*Podocarpus totara*), within a regenerating kānuka (*Kunzea robusta*) stand. Results highlighted the effectiveness of artificial gaps over other methods (ring-barking and edge planting) in accelerating the growth of planted tōtara. Seedlings under gaps grew consistently taller and faster over time indicative of an improved understorey light environment. Ring-barking did not have a significant effect on tōtara growth because only a portion of the treated trees died, and after six years dead trees remained standing with intact branches resulting in insignificant increases in light transmission. At the forest edge sites, tōtara growth was highly variable. Although some seedlings grew as tall as in the gaps, others did not. Survival was also lower in the edge sites than in other treatments, which was likely due to enhanced herbivory from ungulates which impacted some plants at these sites. Gap creation is likely to be an important tool for restoring late-successional canopy species in regenerating stands both through providing ideal sites for the growth of light-demanding species such as tōtara and through natural establishment of other future canopy trees into the gaps.

Keywords: artificial gaps, forest edge planting, *Kunzea robusta*, low-light environment, *Podocarpus totara*, ring-barking

5.2. INTRODUCTION

Restoration of degraded lands including abandoned farmland to forest is often undertaken either by facilitating natural regeneration or through actively planting species into degraded sites (Norton et al., 2018). Restoration by facilitating natural regeneration is a widely used restoration tool and at its simplest involves removing degrading factors (e.g. grazing animals) and leaving a site to naturally regenerate back to forest (Norton et al., 2018). While early-successional species often establish readily, late-successional species can fail to establish, resulting in arrested succession (Reynolds & Pacala, 1993). Arrested successions can occur because of competitive exclusion (Putz & Canham, 1992) or because seed sources are not present (Acácio et al., 2007). In these instances, restoration managers may need to actively intervene to help direct the succession towards the desired goal.

One example of competitive exclusion is where low-light environments in early-successional stands prevent the establishment of late-successional species (Li & Ma, 2003). In some regenerating forests, these low-light environments can persist for many decades before changes in canopy structure allow light environments to increase and recruitment to occur. Hence, gap-based interventions to create a more open stand structure are important in the restoration of many shade-intolerant late-successional species, including oak (e.g. Li & Ma, 2003) and pine species (e.g. Fahey & Lorimer, 2013). However, there is concern about the intermittent effect of gaps on the restoration of shade-intolerant species as the process of gap closure could reduce plant growth over time and restrict seedling development into the canopy (Romell et al., 2008). Some late-successional species can also be less responsive to canopy disturbances, e.g. thinning (Dodson et al., 2012), which pose uncertainties on the likely success of gap-based planting programs. The limited studies on different canopy manipulations on early-successional temperate forest restoration underscore the importance of understanding their effects on the light environment of such ecosystems and their viability on shade-intolerant late-successional species restoration as outcomes may vary with species and disturbance regimes involved (Caplat & Anand, 2009).

This study tested the significance of different canopy treatments on the survival and early growth of planted tōtara (*Podocarpus totara*, Podocarpaceae) seedlings over six years within an early-successional kānuka (*Kunzea robusta*, Myrtaceae) forest. Kānuka is a common early-successional tree in many parts of New Zealand that establishes into abandoned farmland

forming dense patches of 5-10 m tall canopies that can live for up to 100 years (Norton et al., 2018). As kānuka stands open up, they are replaced by mixed conifer-angiosperm species when seed sources are present, with conifers (Podocarpaceae) usually the dominant trees (Smale et al., 1995). However, in situations where seed sources for future canopy dominants are absent, successional development can be arrested, or simply result in kānuka being replaced by other successional shade-tolerant tree species (e.g. *Melicytus ramiflorus*, Violaceae). Similar situations have been described in other early-successional forests (e.g. *Quercus* and *Liriodendron* stands in North America; Lorimer 1984; Clebsch & Busing 1989), where shade-tolerant understorey species preclude the establishment of late-successional shade-intolerant species. In these situations, management interventions such as gap creation and planting of species that are naturally excluded due to dispersal limitation can facilitate a more rapid transition towards more mature forest types. Gap creation is particularly important in many conifer-angiosperm forests in New Zealand as several canopy-forming conifers are light-demanding and will not regenerate under a dense canopy, even when seed sources are present (e.g. Norton, 1991). Tōtara, a widespread canopy dominant, is such a light-demanding species (Ebbett & Ogden, 1998) and manipulation of the canopy structure to increase understorey irradiance is likely to be critical for tōtara's successful establishment and growth.

Specifically, the study hypothesized that canopy treatments (i.e. gap creation, ring-barking, and edge planting) elevate light levels in dense kānuka stands, resulting in better survival and increased height growth of the light-demanding tōtara seedlings compared to those planted under intact kānuka canopies. The study expected that the higher understorey irradiances among the canopy treatments would be more significant to the growth and survival of tōtara seedlings. However, the study assumed that ring-barking would be more favourable over time as the gradual death of the ring-barked trees can create larger canopy openings through unintended damage of residual trees compared to gap creation (cf. Romell et al., 2009) and edge planting. The latter treatment has not been tested experimentally on planted tōtara, although natural tōtara regeneration often favours forest margins where forest floor irradiance is higher than in forest interior (Young & Mitchell, 1994).

5.3. METHODS

5.3.1. Experimental plots and measurements

The trial was established in October 2009 in regenerating kānuka forest with four canopy treatments and five replicates per treatment. Each replicate comprised 20 locally sourced, nursery raised tōtara seedlings planted approximately one meter apart, in four rows of five seedlings. All replicates were located within an altitudinal band of 100-200 m a.s.l. but where possible keeping slope and aspect similar. The treatments were: gap (four canopy kānuka trees felled to create an immediate canopy opening of about 3 m radius), ring-barked (four canopy kānuka trees ring-barked using a chainsaw to cause gradual canopy dieback), forest edge (on the edge between kānuka and grassland) and dense kānuka canopy (control). The canopy in the control and forest edge plots was not disturbed. The kānuka stand has a similar basal area and height across all stands with an average canopy height and diameter at breast height of ca. 10 m and 12 cm, respectively. Tōtara seedlings were ca. 0.55-0.65 m tall at planting. Seedlings were measured at planting (October 2009), tagged and re-measured in May 2013 and April 2015 (approx. four and six growing seasons later). The seedling heights were measured from the substrate level at the base of the stem to the topmost bud. Physical attributes of the plots including slope angle (in degrees) and exposure (aspect, in degrees) were determined using a Suunto clinometer (PM-5/360 PC) and compass (KB-14/360R G), respectively. Soils were sampled (on the same day in April 2015) at each replicate from A Horizon to about 30-cm depth using a soil auger and monitored their dry weights to determine differences in soil moisture among treatments.

Hemispherical photographs were used to quantify differences in understorey light transmittance among treatments (Fig. 14). The photographs were taken in 2015 at the centre of each plot during overcast skies using a digital camera (Nikon Coolpix 5400, Japan) with a fish-eye lens (FC-E9 Nikon, Japan). The camera was set up at 1.37 m above ground, with the lens positioned vertically, and the top of the resulting image orientated to the north. Estimation of percent light transmission from the hemispherical photos was accomplished using Gap Light Analyzer (GLA version 2; Frazer et al., 1999). In the GLA modelling, the growing season was specified from 1 September to 31 March to match estimated local plant growth patterns.

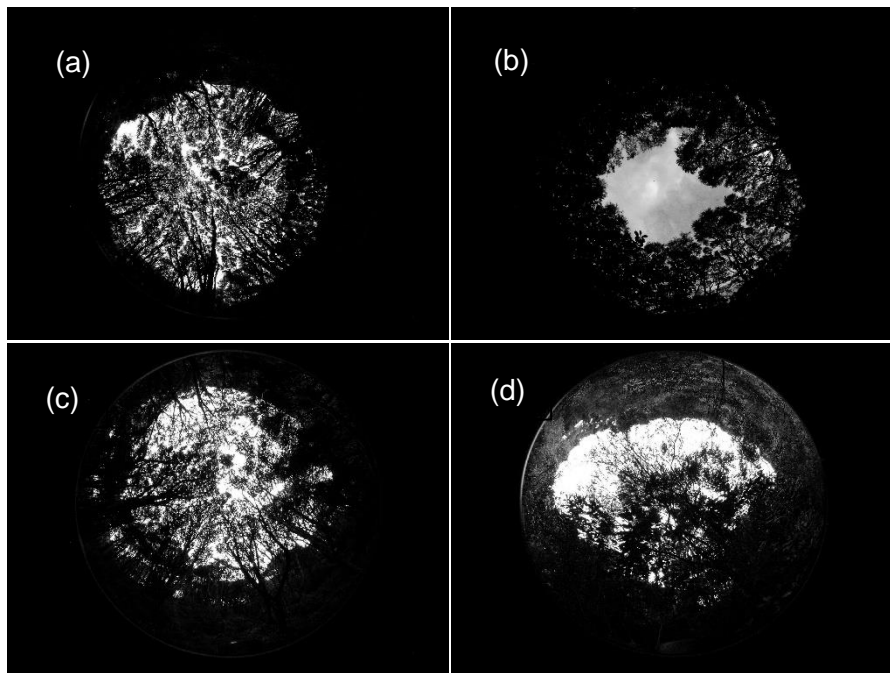


Figure 14. Representative hemispherical photos of the four canopy treatments within a regenerating kānuka forest at Tiromoana Bush in North Canterbury, New Zealand: (a) control, (b) gap, (c) ringbark, and (d) edge.

5.3.2. Data manipulation and analyses

All statistical analyses were performed using R software (R Core Team, 2018). Differences in the terrain slope were assessed using Welch's ANOVA to account for the large variation in standard deviations among treatments. Games-Howell *post hoc* test was then used for multiple pairwise comparisons. Differences in slope aspect among treatments were assessed using Wallraff test of angular distances of the R circular package (Agostinelli & Lund, 2017).

Generalized linear models (GLMs) were used to test the differences in percent light transmittance and soil moisture among treatments, applying the binomial family or quasibinomial when a model was over-dispersed. Differences in initial seedling height among treatments were tested using one-way analysis of variance (ANOVA). Mean relative height growth (RHG) and survivorship per plot were analysed using mixed models to account for issues on temporal pseudo-replication. The RHG was computed as the height gain from 2009 (HT1) until 2013 and 2015 (HT2), respectively, expressed as a proportion of HT1: $RHG = (HT2-HT1)/HT1$. Survivorship is the proportion of seedlings planted in October 2009 that are still alive in 2013 and 2015 measurements. The analyses on seedling RHG were carried out for each time-period and between the two measurements. To define the relationships between the mean tōtara RHG and treatments, the study used the linear mixed-effects (LME) model of the lme4 package (Bates et al., 2015) or the Bayesian linear mixed-effects analysis of the R blme package (Chung et al., 2013) when there were singularity fit issues with lmer i.e. zero estimate of variance of the random variable. In the blmer model, the treatments were entered as fixed effects and the five plot replicates as random effects, followed by a covariance prior with gamma distribution. For the survivorship, a Bayesian generalized linear mixed-effects model (GLMM) with a binomial distribution and default logit link function was used. In the model, canopy treatments were fitted as fixed effects and plot replicates as random effects. Because there was over-dispersion, the survival model was refitted and the analysis followed the approach on variance partitioning in logistic models (Browne et al., 2005). The significance of the treatment effect in the GLM, LME and GLMM models was determined using a likelihood ratio test. *Post hoc* pairwise comparisons of significance were conducted using the glht function of the R multcomp package (Hothorn et al., 2008).

The relationship between tōtara height growth and percent light transmission was assessed using robust regressions of the robustbase package (Rousseeuw et al., 2015). Robust

regression is useful for fitting linear relationship when data are not normal and contain influential observations. In the robust regression model, the response variable (i.e. height growth for a 6-year period) was per-annum scaled and the explanatory variable (i.e. percentage total light transmission) was log transformed. The models provided an R -squared test value like the classical linear regression. The significance of the robust regression model was obtained using a LR test.

5.4. RESULTS

5.4.1. Site attributes, soil moisture, and light condition

Terrain slope differed significantly among treatments ($F_{[3,16]} = 17.387, P < 0.01$) mainly due to edge sites (11.2 ± 1.5^0) being located on flatter slopes ($22.8\text{--}24.4^0$ at the other sites). Slope aspects were generally to the south and did not vary significantly among treatments ($H_{(3)} = 1.8, P = 0.615$). The treatments also had no significant effects on soil available moisture ($\chi^2_{[3,16]} = 0.559, P = 0.906$) which had mean values respectively: $11.62 \pm 1.15\%$ (control), $12.05 \pm 1.48\%$ (edge), $12.24 \pm 1.67\%$ (gap), and $13.13 \pm 1.20\%$ (ringbarked).

Total light transmission ($\chi^2_{[3,16]} = 27.914, P = 0.012$) among treatments was significantly different, but mainly due to gap sites ($33.52 \pm 3.76\%$, $P = 0.006$) which had higher light levels than the ring-bark ($24.38 \pm 2.56\%$, $P = 0.233$), edge ($23.94 \pm 3.58\%$, $P = 0.272$), and control ($19.22 \pm 2.27\%$) (Fig. 15). Light transmissions in the latter three treatments did not differ significantly ($P > 0.05$).

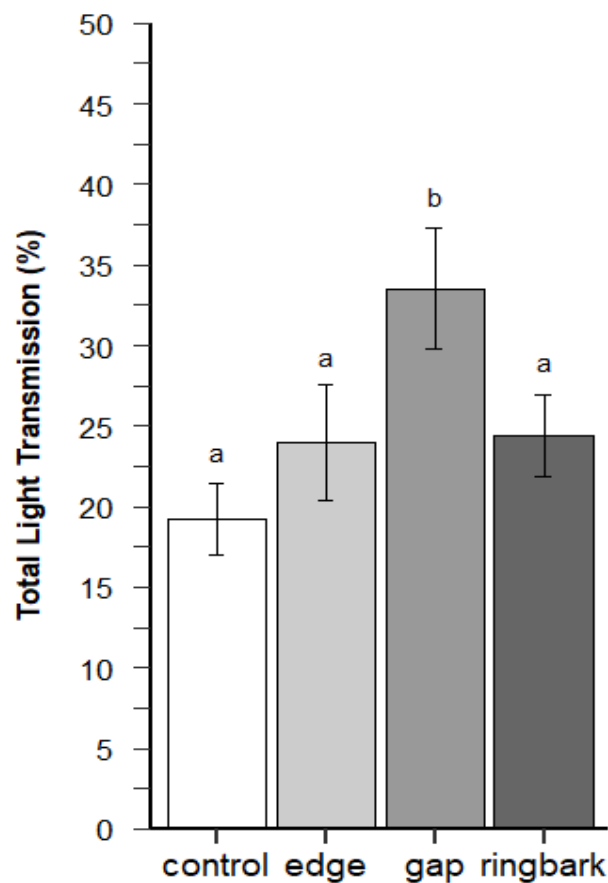


Figure 15. Mean percent total light transmission taken (at 1.37 m above ground level) at the centre of each plot of the four canopy treatments within a regenerating kānuka forest at Tiromoana Bush in North Canterbury, New Zealand. Bars with the same letter indicate no significant difference, while bars with different letters indicate significant differences at 5% level of significance. Error bars represent \pm SE.

5.4.2. Tōtara height growth and survival

Initial seedling heights were not statistically different among treatments ($F_{[3,16]} = 1.325$, $P=0.301$). Four and six growing seasons later, mean (2013, $\chi^2_{(3)} = 12.286$, $P=0.006$; 2015, $\chi^2_{(3)} = 14.99$, $P=0.002$) and maximum seedling growth (2013, $\chi^2_{(3)} = 15.689$, $P=0.001$; 2015, $\chi^2_{(3)} = 14.623$, $P=0.002$) among treatments varied significantly (Fig. 16). The growth also remained significant ($\chi^2_{(3)} = 10.282$, $P=0.016$) between the two measurement periods, but only between gaps and control ($P<0.001$). Over six years, seedlings under gaps grew significantly faster (1.41 ± 0.14 RHG_(Mean) and 2.94 ± 0.35 RHG_(Maximum)), at nearly twice the growth rate of seedlings in the edge (0.81 ± 0.26 RHG_(Mean), $P=0.001$; 1.93 ± 0.49 RHG_(Maximum), $P=0.026$), ring-bark (0.78 ± 0.09 RHG_(Mean), $P=0.011$; 1.56 ± 0.23 RHG_(Maximum), $P<0.001$), and control (0.45 ± 0.11 RHG_(Mean), $P<0.001$; $1.22 \pm$ RHG_(Maximum), $P<0.001$). The improvement in tōtara growth (Height_(Mean), $P=0.027$, $R^2=0.104$; Height_[Maximum], $P=0.0103$, $R^2=0.1597$) over six years was positively correlated to percent total light transmission among treatments (Fig. 17).

Tōtara survival rates among treatments varied significantly after six years ($\chi^2_{(3)} = 9.254$, $P=0.026$), mainly due to lower survivorship recorded at the forest edge sites (89%) compared to other treatments (95-98%). This variation, however, did not cause significant differences ($P>0.05$) among treatments based on multiple comparisons of means. The treatment effect was not apparent on tōtara survival rates four years following planting ($\chi^2_{(3)} = 7.658$, $P=0.5363$).

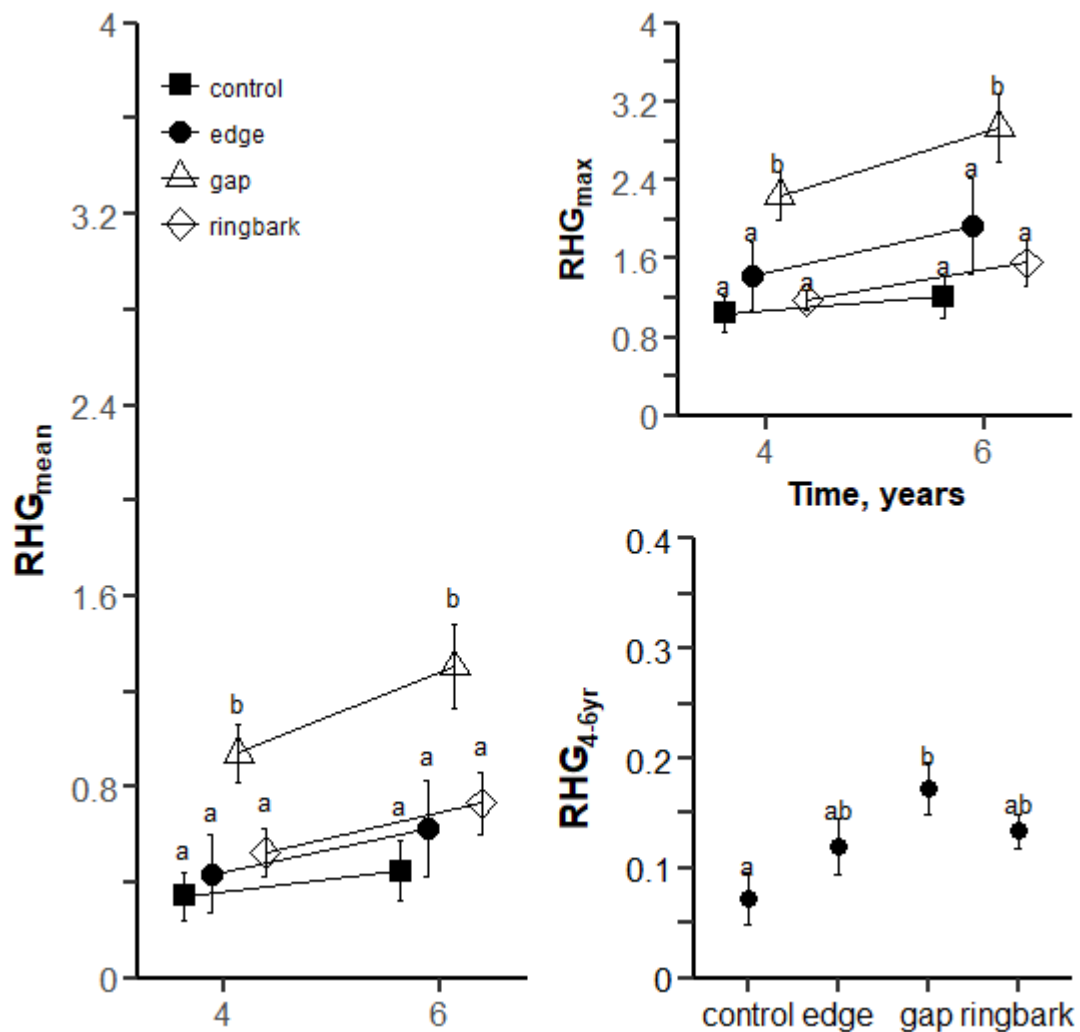


Figure 16. Relative height growth (RHG) of tōtara seedlings among canopy treatments within a regenerating kānuka forest at Tiromoana Bush in North Canterbury, New Zealand. RHG_{mean} is the mean growth rate of all tōtara seedlings, RHG_{max} is the seedlings' maximum growth rate; and RHG_{4-6yr} is the mean growth rate of all seedlings between the 4th (2013) and 6th year (2015) growing seasons. Position dodge (width = 0.5) was applied to the graph to avoid overlapping of points. Points in the same year or between canopy treatments with different letter indicate significant differences at 5% level of significance. Error bars represent ± SE.

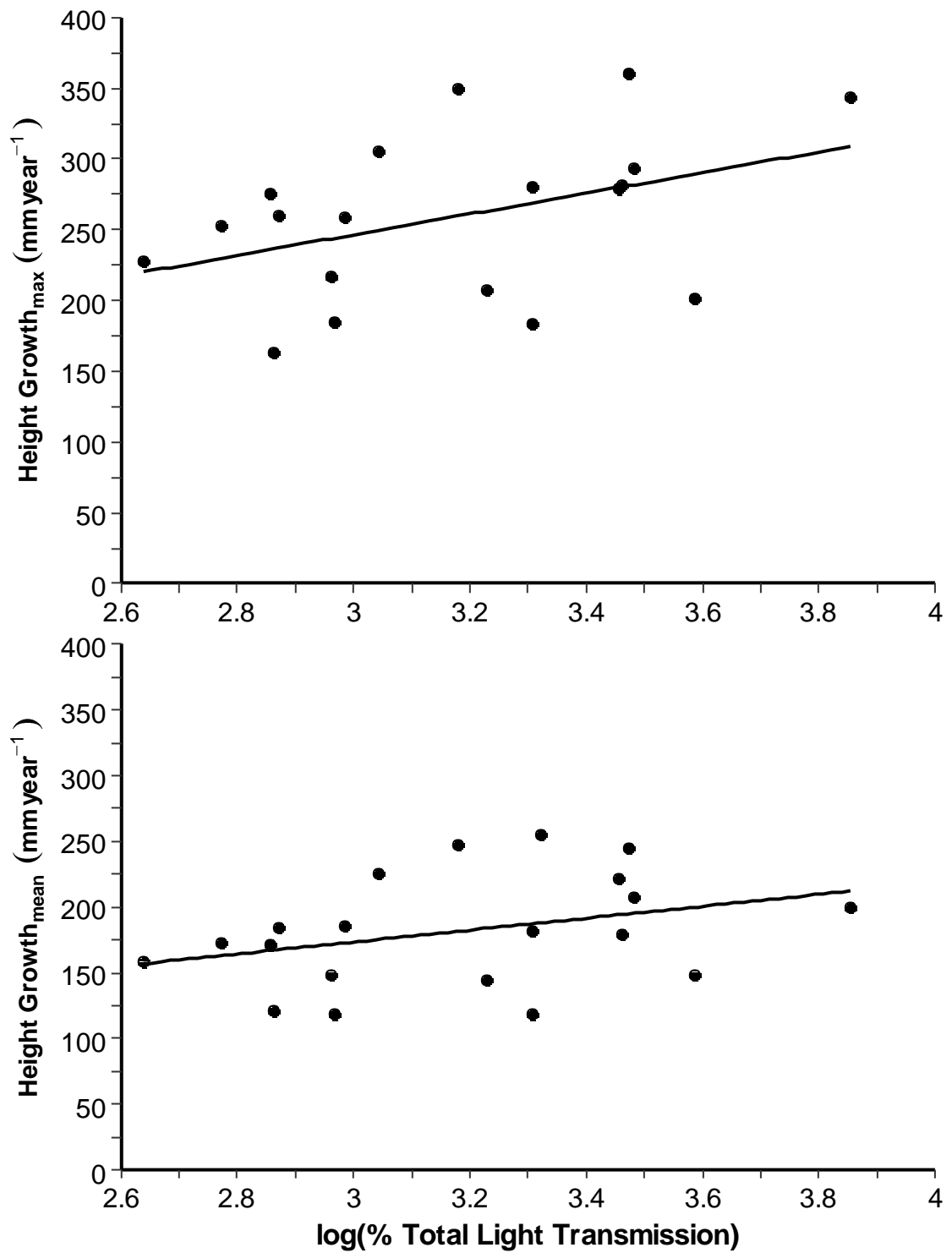


Figure 17. Mean and maximum height growth (mm year⁻¹) of tōtara seedlings per plot ($n = 20$) as a function of log transformed percent total light transmission taken at the centre of each plot (at 1.37 m above ground level) of the four canopy treatments. The experiment was conducted within a regenerating kānuka forest at Tiromoana Bush in North Canterbury, New Zealand.

5.5. DISCUSSION

Gap creation is likely to be an important tool for restoring later-successional canopy species in regenerating forests both through providing ideal sites for the growth of light-demanding species like tōtara and through natural establishment of other future canopy trees into the gaps. Artificial gaps from selective felling of kānuka provided highest light transmission, almost twice the light transmitted in other treatments, thus creating enhanced growing condition for tōtara. The study observed higher growth rates of tōtara seedlings under canopy gaps compared with the control, ringbarked, or forest edge treatments. This influence of gaps on tōtara growth remained significant after four and six years, suggesting that gaps should be maintained to accelerate restoration within the dense kānuka stands.

In this study, total light transmission under gaps was 33% of open sky conditions, similar to the 30% total light transmission under large, naturally formed, canopy gaps in dense mixed forest in central North Island, New Zealand, that was found to result in the best growth of tōtara seedlings in a natural setting (Ebbett & Ogden, 1998). In a study looking at two gap sizes in an exotic *P. radiata* plantation, in central New Zealand, Forbes et al. (2016a) found significantly higher tōtara growth in gaps with at least 50% light transmission, although larger canopy gaps with 84% light transmission were more favourable for planted tōtara seedlings. Similar growth response with increasing light transmittance has been reported in other gap studies (e.g. Coates & Burton, 1999; Fahey & Lorimer, 2013; Ramos & del Amo, 1992). In mature cedar-hemlock forests, for instance, a 30% increase in light transmission was enough to favour seedling growth of five conifer species, although growth continued to increase in gaps with light transmission above 70%, especially for the most light-demanding species (Coates & Burton, 1999). In an 8-year Mexican study involving shade-intolerant and shade-tolerant tropical trees, Ramos and del Amo (1992) reported a consistent growth improvement and highest survival of all planted seedlings in a canopy treatment with 37% light transmission but highly variable seedling growth response in canopies with 68% and 17% irradiance.

Thus, restoration practitioners need to match the light environment to the species' shade tolerance to maximize growth, although other factors such as competition with shrubs and ground layer plants also need to be taken into account (cf. Putz & Canham, 1992). The study did not address such competition following canopy opening, as this aspect was not part of the experiment (and above-ground competition was eliminated through weeding around tōtara

plants). However, the study found no significant difference in soil available moisture among treatments suggesting that any possible competition with other plants was not an issue at the study site. This also appears to be the case for other shade-intolerant species such as late-successional conifers (Fahey & Lorimer, 2013; Lorimer, 1984).

Herbivory, especially by ungulates, can reduce the benefits of elevated light environments. At the forest edge sites, tōtara growth was highly variable. Although some seedlings grew as tall or taller than in the gap treatment, others did not. Survival was also lower in the edge sites, which was likely due to enhanced herbivory (most likely by feral red deer; Norton pers. obs.) which impacted some plants at these sites similar to the effect of herbivory on tōtara seedlings planted into *Pinus* canopy gaps (Forbes et al., 2016a). While the current study did not account for this browsing damage, herbivory by introduced mammals is a common problem in New Zealand forests and has been observed to restrict establishment of many indigenous tree species across a range of light levels (Husheer et al., 2006b). Increased browsing by ungulates has been observed in large canopy gaps compared to small gaps (Forbes et al., 2016a). Thus, in sites where herbivory may impact seedling growth, small-size gaps may be sufficient to improve understorey light conditions and achieve positive growth rates compared to creating larger clearings which are favoured by ungulates. Increased mammalian herbivory in canopy gaps or improved light levels has been reported in other studies (e.g. Howe, 1990). Although tōtara is not that palatable, Forbes et al. (2016a) noted that it can be attractive at times to deer browsing especially when the nutrient contents of its young shoots are seasonally high.

In contrast to gap creation, ring-barking was not effective in supporting the growth of tōtara. The gradual removal of canopy trees by ring-barking did not have a significant effect on tōtara growth because only a portion of the treated trees died, and after six years dead trees remained standing with intact branches resulting in insignificant increases in light transmission. In other studies, it took a minimum of six months for ring-barked trees to die (e.g. Romell et al., 2009), which in some instances created larger gaps and higher light transmission than gaps created by selective felling. In the case of kānuka, further ring-barking may be necessary due to its stringy bark characteristics, which appears to have prevented some ring-barked trees from dying.

Overall, the results of this study are consistent with existing knowledge on the potential of canopy gaps for restoration in seral forests that have established after farming abandonment. As expected, significant improvements in light environments were observed in artificial gaps, thus resulting in better growth performance of the light-demanding tōtara. These results indicated that small-scale canopy gaps can provide favourable growing conditions for tōtara in dense seral stands, with seedling growth being comparable to that from large canopy gaps, which have the disadvantage of attracting browsing ungulates. The results suggest that improving total light availability to 30%, which is about 10% increase only with respect to the intact kānuka canopy, would be sufficient to sustain tōtara growth similar to that found in other temperate and tropical forests (e.g. Coates & Burton, 1999; Ramos & del Amo, 1992). However, careful matching of the light environment and species' shade tolerance is also important to optimize seedling growth. Ring-barking was not as effective as artificial gaps because in our trial only a portion of the treated trees died, while dead ring-barked trees remained standing with intact branches which still cast considerable shade. This result differs from previous studies which showed that ring-barking can be more effective than artificial gaps (Romell et al., 2008). The current study found greatest variability in growth and lower seedling survival from the forest edge sites, which could be due to the higher susceptibility of tōtara to herbivory at the forest edge from introduced mammals. Thus, forest edge planting can be less successful in restoration sites where mammalian herbivory is a common problem.

6. CHAPTER SIX

Establishment of nursery grown mountain beech (*Fuscospora cliffortioides*) seedlings under regenerating shrub communities with canopy manipulations

6.1. ABSTRACT

In post-disturbance grasslands in New Zealand shrubs can serve as nurse plants. However, while many canopy trees may establish under a shrub canopy, shade may restrict seedling establishment. This study assessed the potential of shrubs and canopy manipulations in restoring mature forest species in a stressful environment. Mountain beech seedlings were planted in October 2015 and December 2016 in post-disturbance grasslands in New Zealand. Growth and survival were monitored over three growing seasons in five canopy treatments: open grassland, mānuka (*Leptospermum scoparium*) shrubland with intact canopy, mixed-species shrubland with intact canopy, artificial gaps in mānuka shrubland; and the grassland edge of the mixed-species shrubland. Understorey light transmission and canopy openness were quantified during the first growing season using hemispherical photos. Canopy manipulations caused significant differences in the light availability and canopy openness among treatments. The study observed that seedlings tend to perform better in the mānuka shrub with gap and mixed-species shrub canopies (intact and edge treatments), perhaps due to moderate canopy openness in these treatments compared to open grasslands and intact mānuka canopy. Growth and survival were positively associated with moderate log(light) levels, which correspond to light conditions in manuka with gaps and intact mixed-species shrubs and are likely to represent the net effects of these treatments. The results demonstrated that early-successional shrubs should be managed as nurse plants to control the effect of overshading and facilitate the growth and survival of canopy species in a stressful environment.

Key words: artificial gap, canopy species, *Fuscospora cliffortioides*, nurse plant, post-disturbance grassland, restoration planting

6.2. INTRODUCTION

Degraded shrublands found in abandoned pasture and logged-over forest can be important sites for restoration but often require active human intervention to reinitiate successional processes towards the desired state (Hobbs & Norton, 1996). One effective intervention to facilitate forest recovery in degraded ecosystems, which are often constrained by lack of seed sources or dispersal, is the planting of native plants (van Wieren, 2006). Restoration planting can benefit from early-successional shrubs acting as nurse plants (Tian & Wang, 2015; Yang et al., 2010), as their facilitative effects are increasingly recognized as being more pervasive than their competitive effects. This has been highlighted in stressful habitats (Flores & Jurado, 2003; Gómez-Aparicio et al., 2004) as well as on moderate environments (Holmgren & Scheffer, 2010). Results from abandoned pastures colonized by shrubs, for instance, suggest positive effects of shrubs on tree seedling establishment compared to open grassland ecosystems (e.g. Aide et al., 1995).

The complexity and unpredictability of competition and facilitation processes in degraded early-successional communities have been a major consideration in recent research about their use as a nurse crop in restoration projects. Many early-successional communities in a wide range of ecosystems have been found to have variable effects on different stages of seedling establishment, including the location and identity of nurse vegetation and target species involved (Armas & Pugnaire, 2005; Gómez-Aparicio et al., 2004; Holl, 2002). For instance, Jensen et al. (2012) observed positive effects of shrubs on growth of oaks (*Quercus robur*) in the first two years after planting but in the third year, oak seedling biomass accumulation was reduced. Such unpredictable effects on seedling establishment by early-successional vegetation are common in temperate and tropical degraded environments (cf. Berkowitz et al., 1995; Holl, 2002) and can be caused by differences in height and canopy structure of these low-growing early-successional communities (Berkowitz et al., 1995).

Other research (e.g. Holl, 1998; Meilleur et al., 1994) has suggested that post-disturbance communities, especially shrublands, can be strong inhibitors of plant establishment and may undermine the success of forest restoration projects. Interestingly, however, amongst possible nurse vegetation, shrub communities are assumed to provide stronger facilitative effects than other growth forms in degraded environments (Gómez-Aparicio, 2009). The transitional nature of the nurse-protégé relationship using shrubs where the beneficiary tree

species may outlive the nurse shrubs and persist independently for the rest of its growth (Callaway, 1995) is an added advantage if restoration of late-successional species is the end goal.

In South Island degraded montane environments, early-successional shrubs and perennial grass species (e.g. tussock) have widely invaded post-disturbance grasslands (Norton et al., 2018; Wardle, 1991). Although some of these communities are likely to support late-successional species (Reay & Norton, 1999b), native canopy forming species often fail to establish in degraded grasslands due to intense competition, harsh climate condition (e.g. frost, drought), high herbivory problem, and the absence of ectomycorrhizal fungal associations (Sessions & Kelly, 2000; Standish et al., 2008). Thus, many mature forest species including *Fuscospora* often regenerate in shrubland canopies such as mānuka (*Leptospermum scoparium*) stands for shade and ectomycorrhizal fungal associations (Burrows & Lord, 1993). However, while late-successional canopy forming species may persist under shaded microsites, their growth and survival under heavy shade is usually poor (Ogden, 1985), suggesting the importance of canopy manipulations to facilitate their active growth and establishment in shrubland canopies. A few nurse-based restoration studies in the tropics (e.g. Holl, 1998; Yang et al., 2013) have also recommended the use of manipulative interventions (e.g. artificial gaps) to reduce the effect of shrub canopy overshadowing or competition with target species, although this may vary with species or plant-plant interactions (Callaway, 1998). The limited studies on canopy manipulations on early-successional temperate stands makes it difficult to implement gap-based restoration projects in degraded environment as some late-successional species can be less responsive to canopy interventions (e.g. Dodson et al., 2012).

The purpose of this study was to examine the facilitative potential of early-successional shrub communities with canopy manipulations on the growth and survival of a late-successional canopy forming species, mountain beech (*Fuscospora cliffortioides*, Nothofagaceae), as a case study to identify viable options to implement restoration projects in degraded New Zealand South Island high country. Specifically, I asked: (1) how significant is the nurse vegetation in the establishment and survival of late-successional canopy forming species in post-disturbance grassland? (2) Do canopy manipulations of nurse shrub canopies help create favourable growing conditions for late-successional canopy forming species?

6.3. METHODS

6.3.1. Experimental design

A total of 210 one-year-old potted nursery-raised seedlings of mountain beech grown from locally sourced seed were used in the study. The experiment was set up in October 2015 and involved five treatments, seven seedlings per treatment, and six sites replicates. The experimental treatments were: open grassland (O), mānuka shrubland with intact canopy (LS), mixed-species shrubland with intact canopy (MS), artificial gaps in mānuka shrubland (LSG; four mānuka stems cut at ground level to create an immediate canopy opening of around 1 m radius); and the grassland edge of the mixed-species shrubland (MSE).

The seven seedlings of each treatment were individually planted at seven systematically located spots. The study used seven clumps of intact mixed-species shrubland that were about 10 m away from each other and each clump was planted with one mountain beech seedling in the interior to represent the intact mixed-species shrub treatment; and another seedling planted at the grassland edge of the mixed-species shrub for the mixed-species shrub edge treatment. The seven mānuka clumps in the study were circa 100 m away from the closest mixed-species shrub treatment with 10 - 20 m between mānuka clumps. Each mānuka clump was planted with two mountain beech seedlings, i.e. one at the centre of a canopy gap cut in the mānuka shrub for the artificial gap treatment, and the second 1-2 m away from the edge of the gap for the intact mānuka shrub treatment. Seedlings planted at the open grassland treatment were 5-10 m away from the closest mānuka or mixed-species shrubland clump. All these treatments were replicated six times at six different locations across the study area. These locations were at least 500 m distant from each other, and experienced similar environmental conditions of aspect (137.83 ± 5.29^0 to 198.33 ± 18.51^0 ; $\chi^2 = 5.56$, $p=0.235$) and slope (7.67 ± 1.58^0 to 8.83 ± 2.01^0 ; $\chi^2 = 0.16$, $p=0.997$).

The mixed-species shrubland comprised small shrubs dominated by hebe (*Hebe brachysiphon*), matagouri (*Discaria toumatou*), mingimingi (*Coprosma propinqua*), and korokio (*Corokia cotoneaster*). The average height of the mixed-species shrubland was 1.2 m, while the densely branched mānuka shrubland was 2.5 m tall on average. The open grassland was dominated by 20-30 cm tall native short tussocks *Festuca novae-zelandiae* and *Poa colensoi*.

During the first growing season (2015-2016), seedling survival particularly at the open grassland treatment was very low, thus a second batch of 210 mountain beech seedlings from the same source (and age) were established in December 2016 at the same sites to augment the number of seedlings per treatment/replicate in the study. These seedlings were planted at ca. 20 cm away from the first planted seedling in each treatment and their size was not big enough to result to competition between seedlings. Thus, at the end of the study, two sets or groups of data for seedling growth and survival were recorded and analysed separately, that is, the 30-month growth period for the first group of seedlings planted in October 2015 and the 16-month growth period for the second group of seedlings planted in December 2016 for a total of 420 seedlings. The mountain beech seedlings in the first batch were circa 0.16 – 20 cm at planting, while the second batch were about 30 – 36 cm.

6.3.2. Measurements

All transplanted seedlings were individually tagged to facilitate measurements. All seedlings in the first and second planting were watered only once, immediately after transplanting, and their heights measured to establish an initial seedling height. Monitoring of seedling growth and survival commenced in the month following planting and at approximately monthly intervals until April 2018. Seedling heights were measured from substrate level at the base of the stem to the topmost bud. Seedlings were considered dead if their stems were brittle and leaves had gone brown or if they could not be found at the site. Any shoot die-back observed was considered intrinsic seedling growth response among treatments to the harsh condition of the area, with the highest live bud used for measurements.

Seedling relative height growth and percent survival by treatments were calculated using the data in the growing months by year (February, April, and October) over the duration of the study. The planting sites were characterized in terms of slope, aspect, understorey light levels, and canopy openness at each treatment. The terrain slope (in degrees) and seedling exposure (aspect, in degrees) were assessed using a clinometer and compass. Hemispherical photographs were used to quantify light levels and canopy openness among treatments (Fig. 2). The hemispherical photographs (i.e. one photo per replicate and treatment) were taken during overcast skies in March 2016 using a digital camera (Nikon D3100) fitted with a Sigma 4.5 mm circular fisheye lens. The camera was set up just above the height of each seedling and

was oriented to magnetic north. A bubble level was used to level the camera before taking the hemispherical photos. The understory light transmittance (percent light transmitted and total transmitted PAR or photosynthetically active radiation, $\text{mol m}^{-2} \text{ day}^{-1}$) from each seedling canopy cover per treatment and replicate and the canopy openness were analysed from the hemispherical photos using Gap Light Analyzer computer software (GLA version 2; Frazer et al., 1999). The growing season was specified from 1 September to 31 March in the GLA modelling to match the estimated local plant growth patterns.

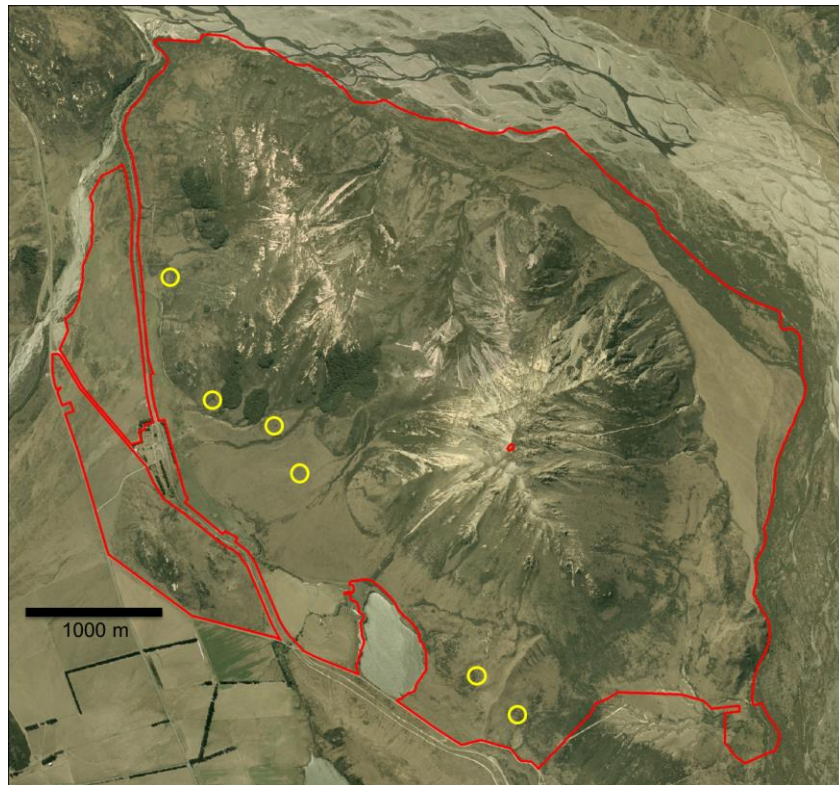


Figure 18. Location of the six site replicates (denoted by yellow circles) for the mountain beech restoration trial within the Cass Mountain Research Area (CMRA), Cass, Canterbury, eastern South Island high country, New Zealand.

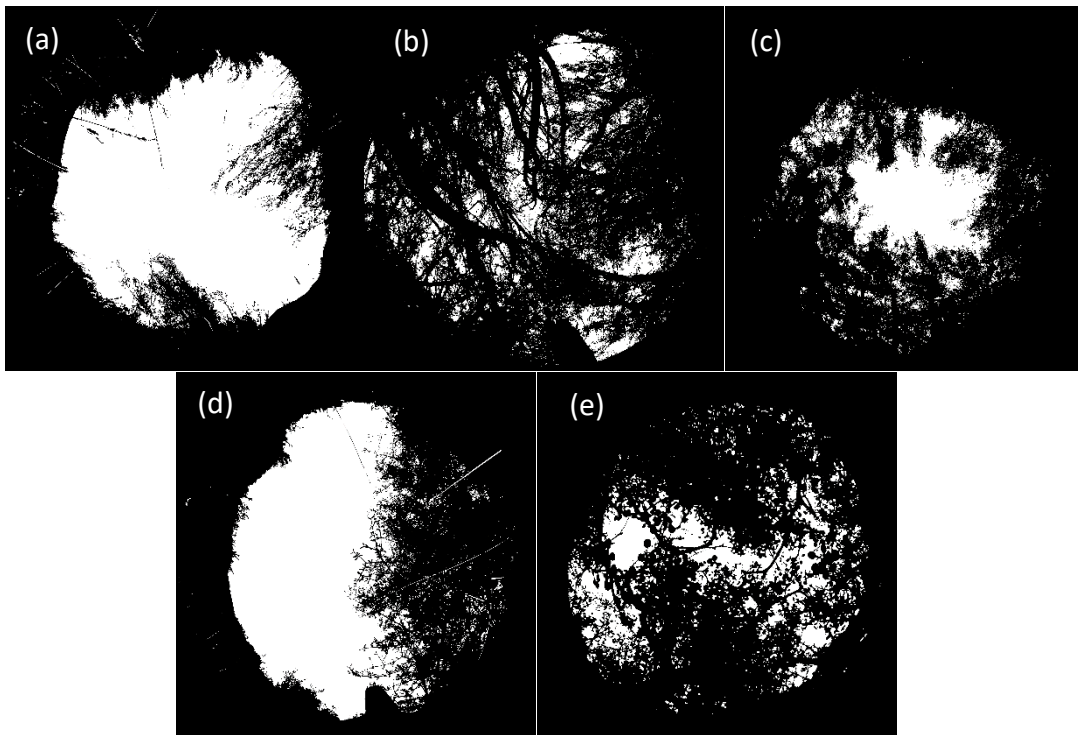


Figure 19. Representative hemispherical photos of the canopies of the five nurse vegetation treatments taken at seedling height: (a) open grassland, (b) intact manuka shrub, (c) manuka shrub with artificial gap, (d) edge of mixed-species shrub, and (e) intact mixed-species shrub.

6.3.3. Data manipulation and analyses

All statistical analyses were performed using R software (R Core Team, 2018). Differences in site physical variables, terrain slope and aspect were assessed using non-parametric tests on ranks. Kruskal-Wallis rank-sum test was used to assess the differences in terrain slope among seedling plots between the nurse vegetation treatments. Differences in slope aspect among seedling plots between treatments were assessed using the Wallraff test of angular distances (circular package; Agostinelli & Lund, 2017), which is equivalent to the Kruskal–Wallis rank-sum test. For the analyses of canopy openness and total transmitted PAR ($\text{mol m}^{-2} \text{ day}^{-1}$) differences among seedling plots between treatments, mixed models were used to account for variation associated with treatment replicates (random effects) since each nurse shrub represents a random cluster of vegetation that can be found everywhere in the study site. Differences in percentage canopy openness among treatments were determined using the glmer function in lme4 package (Bates et al., 2015) applying the binomial family and default logit link. Differences in the log transformed total PAR data among treatments were examined using the lmer model in lme4 package. Significance of treatment effects in the light and canopy openness models was assessed using a Wald chi-squared test (applying the Anova function) in car package (Fox & Weisberg, 2011).

Mean growth and survivorship of the seven plants were calculated per treatment across the six site replicates to facilitate the analyses. One-way analysis of variance (ANOVA) was used to assess the differences among treatments of the log-transformed initial height data. The succeeding seedling growth rate (relative height growth, RHG) and percent survival among treatments were assessed using mixed models to account for issues on temporal pseudo-replication with the site replicates as random effects. The relative height growth of seedlings was computed as the difference between the seedling height at different measurement periods (HT2) and seedling height at planting (HT1), expressed as a proportion of HT1: $\text{RHG} = (\text{HT2} - \text{HT1})/\text{HT1}$. The percent survival was calculated as the proportion of seedlings planted at the onset of the experiment and were still alive in succeeding measurements. The analyses of RHG and survival rates of mountain beech seedlings among treatments were carried out for each measurement period of each group of seedlings (i.e. seedlings planted in October 2015 and seedlings planted in December 2016). The RHG data were fitted using the lmer function in lme4 package applying the maximum likelihood. Mixed models with binomial distribution and default log link (glmer function in lme4 package) were used to define the relationships between

the survival rates and treatments. When there were complete separation issues, i.e. unusually large Wald standard errors and various warnings with glmer, the survival rates were fitted using the Bayesian GLMMs with Laplace approximation method of the R blme package (Chung et al., 2013). To test the significance of the parameter in each model, a Wald chi-squared test in car package was carried out. *Post hoc* tests of the significant treatment effects in the mixed models were conducted using the general linear hypothesis (glht) function in the multcomp package (Hothorn et al., 2008).

The relationship between the per annum scaled seedling heights (cm year⁻¹) and the log-transformed total transmitted PAR was fitted using simple linear regression and polynomial regression models. The models were compared using the R anova function and *compareLM* function in rcompanion package (Mangiafico, 2018). The *compareLM* function provides a table of fit statistics including the Akaike's Information Criteria (AIC) and r-squared value. The significant model with the lowest AIC was selected as the best model fit. For the relationship between the per annum scaled seedling survivorship (%) and log-transformed total transmitted PAR, simple and polynomial terms in logistic regression were fitted. The best model was selected via AIC estimate and the R stat.anova likelihood ratio test. The pseudo-r-squared of the logistic regression models was estimated using the *nagelkerke* function in rcompanion package (Mangiafico, 2018).

6.4. RESULTS

6.4.1. Canopy openness and light transmittance among treatments

Significant differences occurred among treatments in terms of the proportion of canopy openness ($W^2_{[4]} = 457.15$, $P < 0.001$) and light availability at seedling height ($W^2_{[4]} = 534.54$, $P < 0.001$) (Fig. 20). As expected, the open grassland sites had the highest percent canopy openness with 72.1 ± 3.0 % compared to other treatments. Among the shrub treatments, mixed-species shrub edge (52.6 ± 3.9 %) had a more open canopy than the intact mānuka shrub (17.8 ± 0.9 %), intact mixed-species shrub (28.5 ± 3.9 %), and mānuka shrub with gaps (25.8 ± 3.8 %). The log normal transformed transmitted PAR was also highest in the open grassland with 1.57 ± 0.02 mol m⁻² d⁻¹ compared to other treatments ($W^2_{[4]} = 207.03$, $P < 0.001$): mixed-species shrub edge (1.42 ± 0.04 mol m⁻² d⁻¹), mānuka shrub with gaps (1.20 ± 0.06 mol m⁻² d⁻¹), intact

mixed-species shrub ($1.13 \pm 0.07 \text{ mol m}^{-2} \text{ d}^{-1}$), and intact mānuka shrub ($1.0 \pm 0.04 \text{ mol m}^{-2} \text{ d}^{-1}$). Both the mānuka shrub with gap and intact mixed-species shrub had comparable proportions of canopy openness and total transmitted PAR.

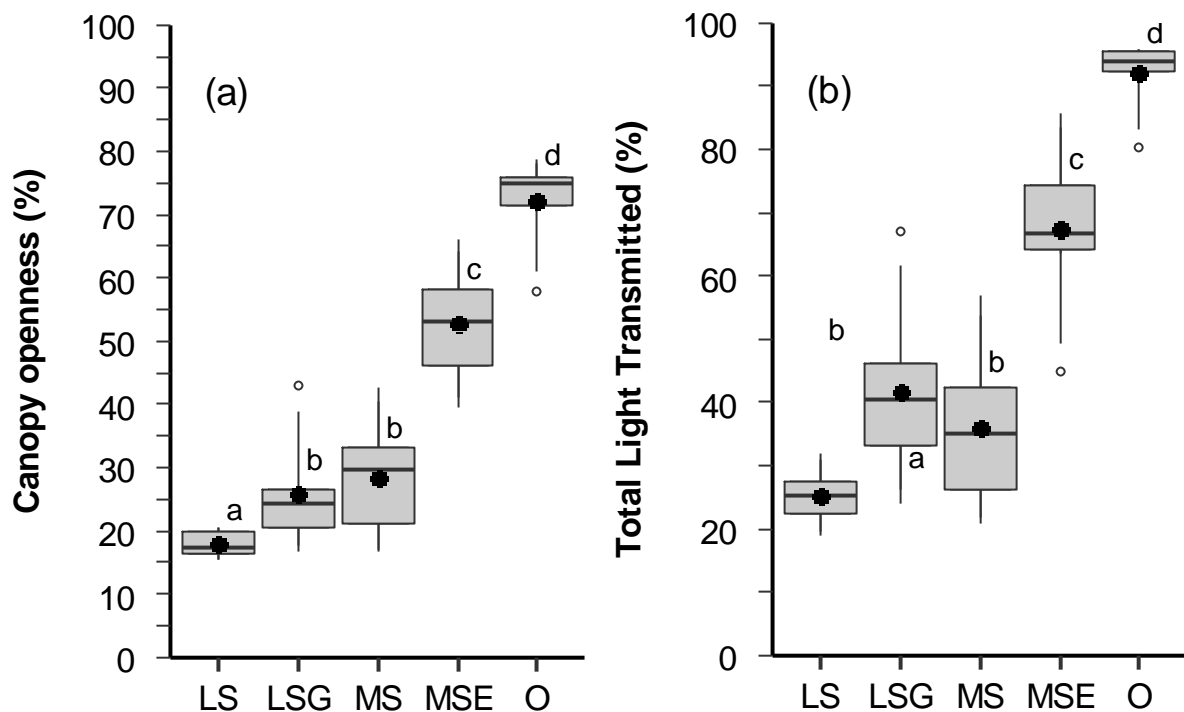


Figure 20. (a) Mean percent canopy openness and (b) log transformed mean total transmitted PAR of the five treatments (LS = intact manuka shrub, LSG = manuka shrub with artificial gap, MS = mixed-species shrub, MSE = mixed-species shrub edge, and O = open grassland). Box-and-whisker plots with the same letters indicate no significant difference, while plots with different letters indicate significant differences at $P < 0.05$. The filled point inside the box-and-whisker plot represent the mean value, while the unfilled points outside the box-and-whisker plot are the outliers.

6.4.2. Seedling height growth

Initial absolute height (cm) of mountain beech seedlings did not differ significantly across treatments in both batches of transplanted seedlings: seedlings planted in October 2015 ($F_{[4,25]} = 0.193$, $P=0.940$) and December 2016 ($F_{[4,25]} = 0.7055$, $P=0.596$). The mean initial height of seedlings planted in October 2015 and December 2016 was 20.2 ± 0.4 cm and 36.7 ± 1.0 cm, respectively.

6.4.2.1. Seedlings planted in October 2015 (30-month growing period)

Relative height growth (RHG) of seedlings planted in October 2015 differed significantly among treatments during the first 12 months after treatment: 4 months (February 2016, $W^2_{(4)} = 22.30$, $P<0.001$), 6 months (April 2016, $W^2_{(4)} = 16.69$, $P=0.002$), and 12 months (October 2016, $W^2_{(4)} = 13.30$, $P=0.01$) (Fig. 21a). At the fourth month, seedlings planted under the mānuka shrub with artificial gap, mixed-species shrub edge, and intact mixed-species shrub grew significantly faster compared to seedlings planted under the intact mānuka shrub and in the open grassland sites. By six and 12 months, seedling RHG remained significantly higher in the mānuka shrub with artificial gap, intact mixed-species shrub, and mixed-species shrub edge treatment. However, at these times, growth rates were comparable between the mixed-species shrub edge and open grassland site treatment, and between open grassland site and intact mānuka shrub treatment perhaps due to the observed decline in seedling growth rates among these treatments.

In the second year (in 2017), the treatments did not show significant effects on seedling growth rate, particularly at 16 months (February 2017, $W^2_{(4)} = 8.90$, $P=0.064$), 18 months (April 2017, $W^2_{(4)} = 8.40$, $P=0.078$), and 24 months (October 2017, $W^2_{(4)} = 8.76$, $P=0.068$) after planting. By the third year, seedling growth varied significantly among treatments particularly at 28 months (February 2018, $W^2_{(4)} = 13.11$, $P=0.011$) and 30 months later (April 2018, $W^2_{(4)} = 12.38$, $P=0.015$) with the mānuka shrub with artificial gap providing the more favourable condition for growth of planted mountain beech seedlings, although this was statistically similar ($P>0.05$) with those in the intact and edge sites of the mixed-species shrubs. The seedling RHG by treatment after 30 months were: 1.02 ± 0.14 RHG or 7.63 ± 0.96 cm year⁻¹ (mānuka shrub with artificial gap), 0.87 ± 0.08 RHG or 6.58 ± 0.72 cm year⁻¹ (intact mixed-species shrub), 0.81 ± 0.12 RHG or 6.30 ± 0.68 cm year⁻¹ (edge of mixed-species shrub), 0.52

± 0.12 RHG or 3.56 ± 0.88 cm year⁻¹ (intact mānuka shrub), and 0.42 ± 0.24 RHG or 4.26 ± 1.20 cm year⁻¹ (open grassland).

There was a significant association between the per annum scaled seedling height growth and the log transformed total transmitted PAR after the 30-month growing period: $\hat{Y} = -47.3 + 85.3 \log(x) - 33.2 \log(x^2)$, $F_{(2,23)} = 8.76$, $P = 0.002$, $R^2 = 0.43$. The model showed a better height growth (cm year⁻¹) at log PAR values approximately between 1.1 and 1.4 mol m⁻² d⁻¹ (Fig. 22a).

6.4.2.2. Seedlings planted in December 2016 (16-month growing period)

Relative height growth (RHG) of mountain beech seedlings planted in December 2016 did not vary significantly among treatments in the first growing season (in 2017) after planting: two months (February 2017, $W^2_{(4)} = 2.47$, $P = 0.65$), four months (April 2017, $W^2_{(4)} = 2.43$, $P = 0.66$), and 12 months (October 2017, $W^2_{(4)} = 4.43$, $P = 0.35$) (Fig. 21b). The significant effects of the treatments were observed in the following growing season (in 2018) or 14 months (February 2018, $W^2_{(4)} = 10.15$, $P = 0.04$) and 16 months later (April 2018, $W^2_{(4)} = 12.99$, $P = 0.01$). The three treatments (i.e. intact mixed-species shrub, mixed-species shrub edge, and mānuka shrub with artificial gap) remained more favourable for the growth of mountain beech seedlings, although in such a short growing period (compared to the seedlings planted in October 2015) the significant difference ($P < 0.05$) in height growth 14 and 16 months later was visible only between the intact mixed-species shrub and the open grassland site. The height growth of seedlings by treatment after 16 months were: 0.25 ± 0.06 RHG or 5.85 ± 1.55 cm year⁻¹ (intact mixed-species shrub), 0.21 ± 0.06 RHG or 4.51 ± 1.82 cm year⁻¹ (mixed-species shrub edge), 0.13 ± 0.03 RHG or 3.28 ± 0.72 cm year⁻¹ (mānuka shrub with artificial gap), 0.12 ± 0.06 RHG or 4.50 ± 1.45 cm year⁻¹ (open grassland), and 0.02 ± 0.04 RHG or 0.92 ± 1.36 cm year⁻¹ (intact mānuka shrub).

There was no significant association found between the per annum scaled seedling height growth and the log transformed total transmitted PAR after the 16-month growing period: $\hat{Y} = 172.7 - 428.5 \log(x) + 350.4 \log(x^2) - 92.7 \log(x^3)$, $F_{(3,26)} = 1.47$, $P = 0.246$, $R^2 = 0.15$ (Fig. 22b).

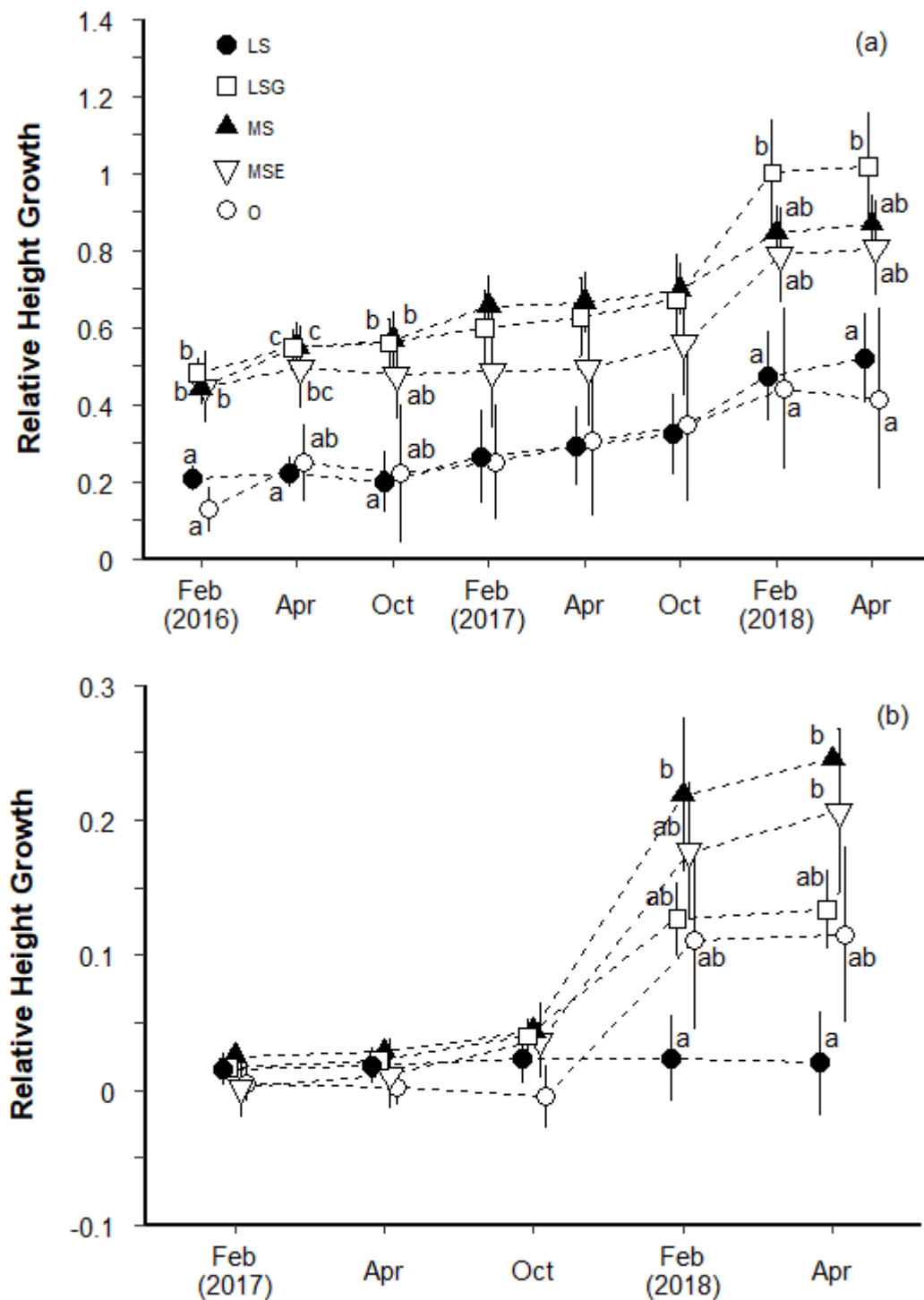


Figure 21. Relative height growth of mountain beech seedlings under the five nurse vegetation treatments (LS = intact manuka shrub, LSG = manuka shrub with artificial gap, MS = mixed-species shrub, MSE = mixed-species shrub edge, and O = open grassland). (a) Seedlings planted in October 2015, and (b) seedlings planted in December 2016. Significant differences ($P < 0.05$) between treatments are indicated with different letters next to the treatment symbols. Error bars represent \pm SE.

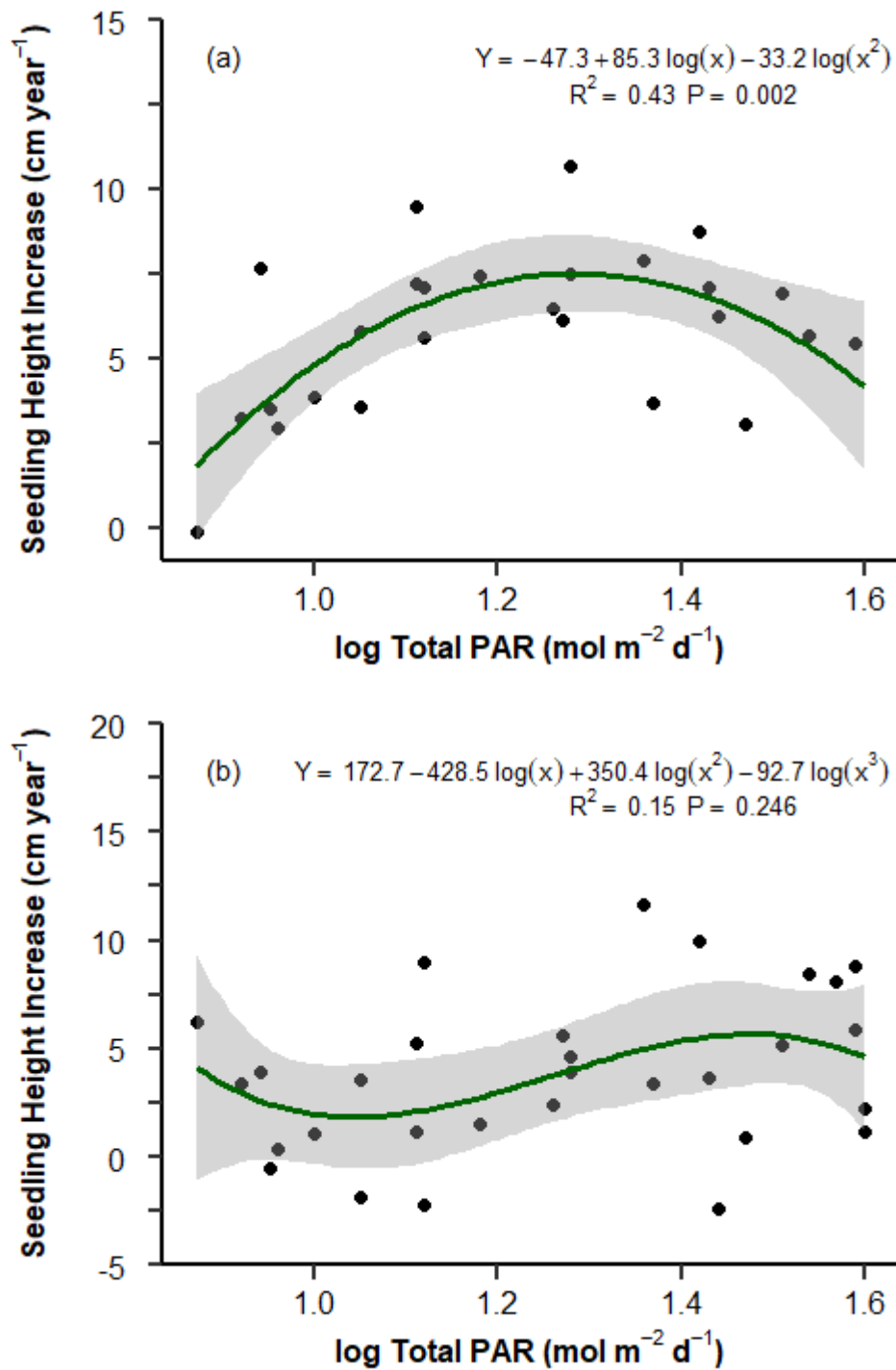


Figure 22. Relationship between the per annum scaled seedling height growth and total transmitted PAR measured at seedling height at the five nurse vegetation treatments: (a) seedlings planted in October 2015 ($n = 30$), and (b) seedlings planted in December 2016 ($n = 30$). The shaded region around the regression line is the confidence interval (0.95).

6.4.3. Seedling survival

6.4.3.1. Seedlings planted in October 2015 (30-month growing period)

The survival rates of the mountain beech seedlings planted in October 2015 varied significantly among treatments throughout the measurement period ($P < 0.001$) (Fig. 23a). The significant variations in the survival rate were largely due to the lowest survival recorded in the open grassland compared to other treatments throughout the 30-month growing period. Although seedling survival was also lower at the edge of mixed-species shrub, this was not statistically different ($P > 0.05$) at some point with other shrub treatments, especially with the intact mānuka shrub and intact mixed-species shrub. Survival rate was relatively higher under the mānuka shrub with artificial gap, but this was statistically comparable ($P > 0.05$) to the seedling survival rate under the mixed-species shrub and intact mānuka shrub throughout the duration of the study. The mean percent seedling survival \pm SE (or mean percent survival per year) of mountain beech by treatment after the 30-month growing period ($W^2_{(4)} = 50.82$, $P < 0.001$), were: 95.2 ± 3.0 % (38.1 ± 1.2 % year⁻¹) for mānuka shrub with artificial gap, 88.1 ± 5.7 % (35.2 ± 2.3 % year⁻¹) for the intact mixed-species shrub, 73.8 ± 7.8 % (29.5 ± 3.1 % year⁻¹) for the intact mānuka shrub, 64.3 ± 11.5 % (25.7 ± 4.6 % year⁻¹) for the mixed-species shrub edge, and 11.9 ± 9.3 % (4.8 ± 3.7 % year⁻¹) for the open grassland site.

A highly significant association was found between the mountain beech seedling survival rate and log transformed total transmitted PAR after the 30-month growing period: $\hat{Y} = 32.7 - 97.9 \log(x) + 93.3 \log(x^2) - 28.9 \log(x^3)$, $\chi^2_{(1)} = 26.4$, $P < 0.001$, pseudo $R^2 = 0.56$). The relationship indicated better survival rates at log PAR between ca 1.1 and 1.4 mol m⁻² d⁻¹ (Fig. 24a).

6.4.3.2. Seedlings planted in December 2016 (16-month growing period)

Significant variation in the survival rate of mountain beech seedlings planted in December 2016 was observed 14 months (February 2018, $W^2_{(4)} = 21.29$, $P < 0.001$) and 16 months following planting (April 2018, $W^2_{(4)} = 23.11$, $P < 0.001$) (Fig. 23b). Although a different pattern was observed compared to the first group of seedlings, the highest survival was also observed in the mānuka shrub with artificial gap, while the lowest was recorded in the open grassland. There were also no significant differences in the survival rate among the

intact mānuka shrub, mixed-species shrub, and mixed-species shrub edge treatments. However, unlike the earlier planted seedlings, survival in the mixed-species shrub edge treatment did not differ significantly with those in the mānuka shrub with artificial gap and a significant difference was observed between the latter treatment and the intact mānuka shrub after 14 and 16 months. The mean survival rate (\pm SE) of mountain beech seedlings by treatment after the 16-month growing period, were: 100.0 ± 0.0 % (75.0 ± 0.0 % year⁻¹) for mānuka shrub with artificial gap, 92.9 ± 4.9 % (69.6 ± 3.7 % year⁻¹) for the intact mixed-species shrub, 90.5 ± 7.1 % (67.9 ± 5.3 % year⁻¹) for the mixed-species shrub edge, 76.2 ± 7.9 % (57.1 ± 5.9 % year⁻¹) for the intact mānuka shrub, and 59.5 ± 11.3 % (44.6 ± 8.5 % year⁻¹) for the open grassland site.

A strong significant association was also found between the mountain beech seedling survival rate and log transformed total transmitted PAR after the 16-month growing period: $\hat{Y} = 8.2 - 30.4 \log(x) + 34.4 \log(x^2) - 11.7 \log(x^3)$, $\chi^2_{(1)} = -6.68$, $P = 0.009$, pseudo $R^2 = 0.28$). The model indicated better survival rates at log PAR between ca. 1.1 and 1.4 mol m⁻² d⁻¹ (Fig. 24b).

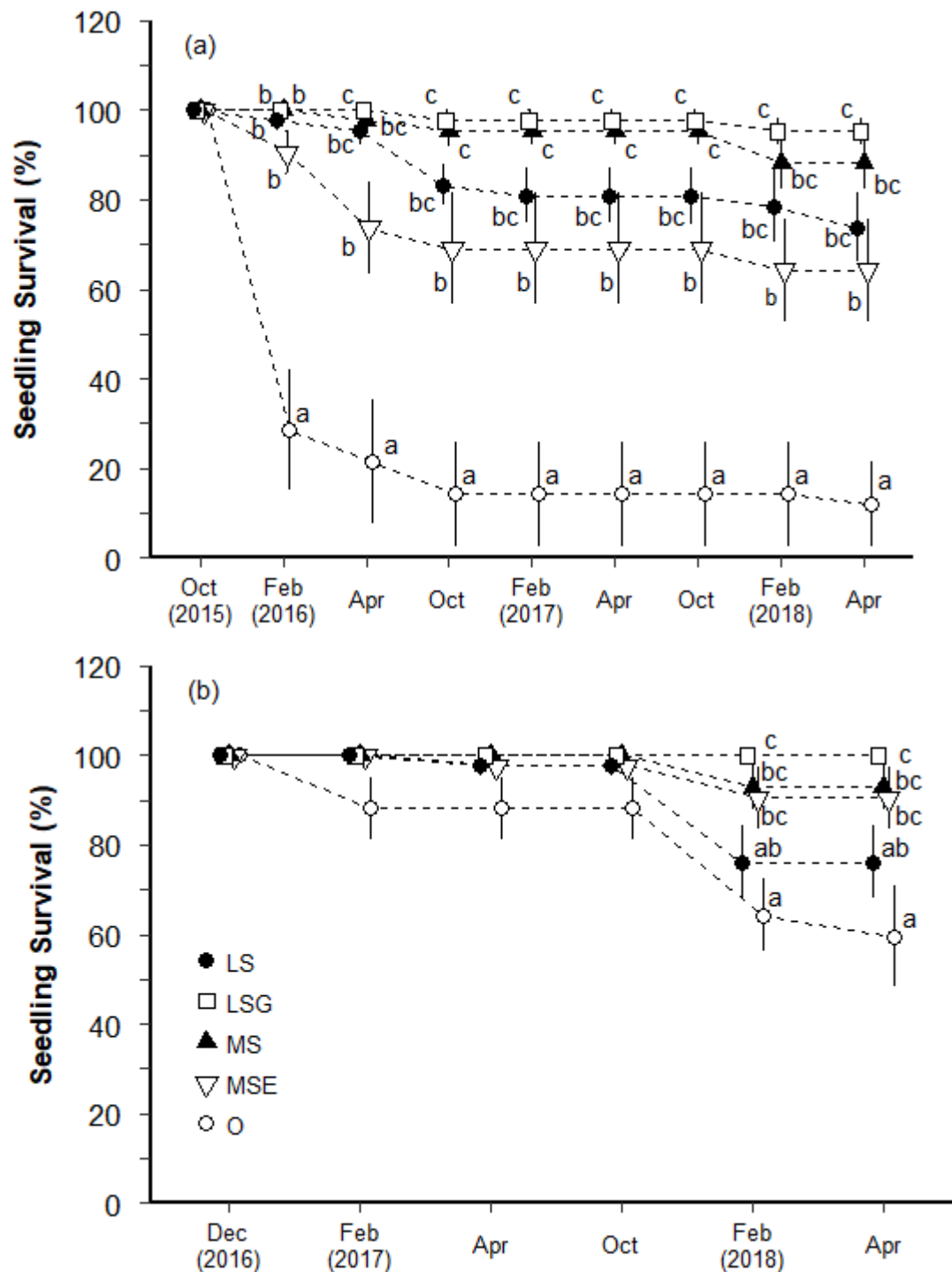


Figure 23. Percent survival of mountain beech seedlings under the five nurse vegetation treatments (LSG = manuka shrub with artificial gap, LS = intact manuka shrub, MS = mixed-species shrub, MSE = mixed-species shrub edge, and O = open grassland). (a) Seedlings planted in October 2015, and (b) seedlings planted in December 2016. Significant differences ($P < 0.05$) between treatments are indicated with different letters next to the treatment symbols. Error bars represent \pm SE.

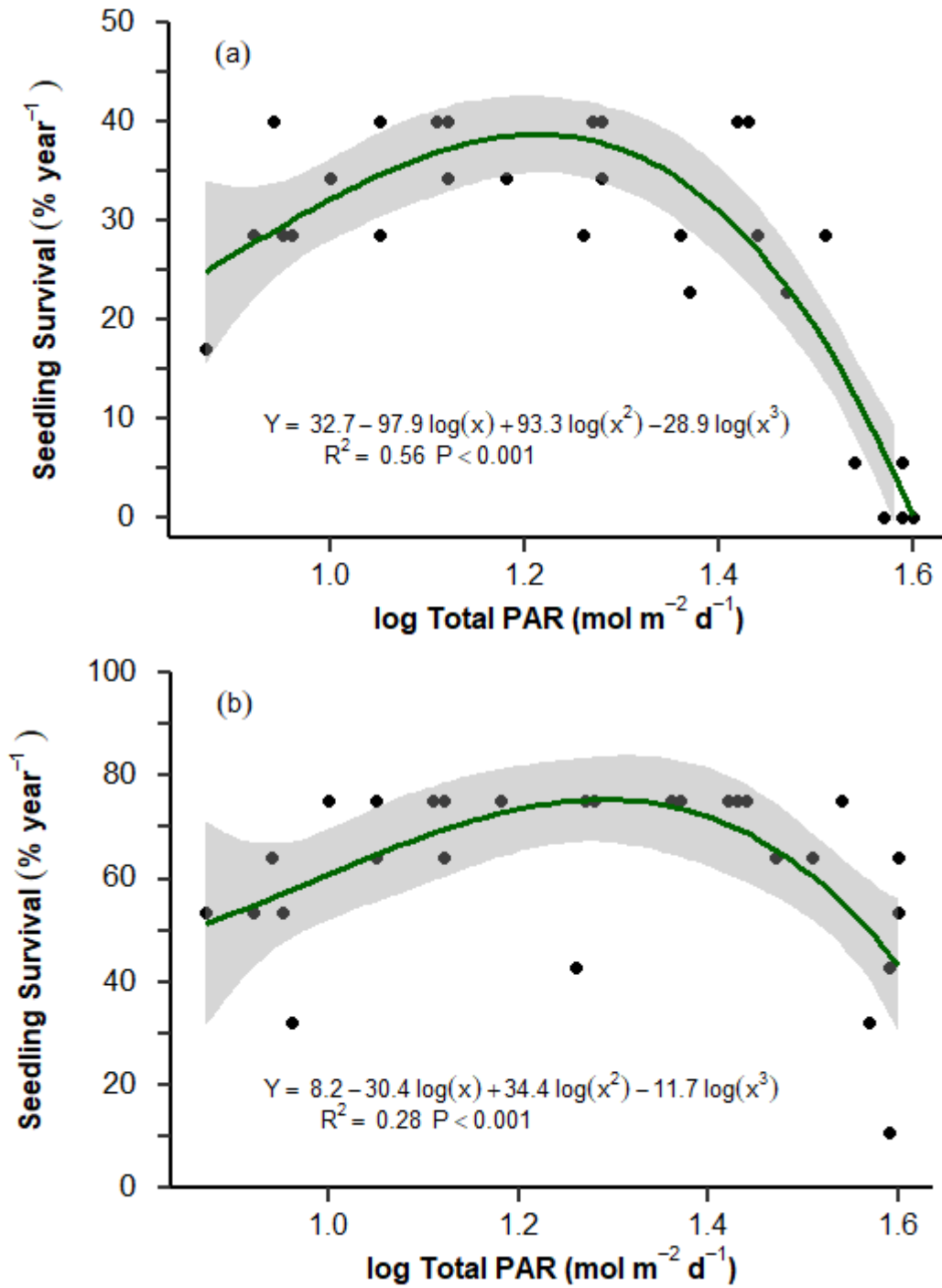


Figure 24. Relationship between the per annum scaled percent seedling survival and total transmitted PAR measured at the seedling height at the five nurse vegetation treatments: (a) seedlings planted in October 2015 (n = 30), and (b) seedlings planted in December 2016 (n = 30). The shaded region around the regression line is the confidence interval (0.95).

6.5. DISCUSSION

Both grasslands and early-successional shrublands can inhibit forest tree seedling establishment and survival and will require management interventions to reduce above-ground competition and facilitate the success of restoration projects (Holl, 1998). In this study, canopy interventions in early-successional shrubs have caused significant differences in light availability and canopy density among treatments, which had significant effects on the growth and survival of mountain beech seedlings. While this effect was not consistent throughout the duration of the study, which could be due to the short duration of the study or the intermittent effect of canopy manipulations over time (Romell et al., 2008), the results suggest that mountain beech seedlings perform better in mānuka shrub with gap and mixed-species shrub canopies (intact and edge treatments) than under dense mānuka or in the open, perhaps due to the moderate canopy openness at these treatments (20-50 %) compared to open grasslands (<18 %) and intact mānuka canopy (>72 %). These results support similar studies in stressful conditions (e.g. Puerta-Pinero et al., 2007; Rey-Benayas, 1998) with survival and growth of some canopy species being favourable under moderate shade or intermediate light levels.

6.5.1. Seedling growth and survival

The mean seedling height growth of mountain beech over the 30-month growing period ranged from 6.30 ± 0.68 to 7.63 ± 0.96 cm yr⁻¹ within the mānuka shrub with gap and mixed-species shrubs (intact and edge sites) and was relatively higher than in open grasslands (4.26 ± 1.20 cm yr⁻¹) and intact mānuka canopy treatments (3.56 ± 0.88 cm yr⁻¹). In the second batch (16-month growing period), seedlings also had better growth performance in the mixed-species shrubs and mānuka shrub with gap than in open grasslands and intact mānuka treatments suggesting that the light-demanding mountain beech benefit positively from shrub canopies with moderate shade conditions. The growth rates in this study are, however, lower compared to height growth (>45 cm year⁻¹) recorded for naturally regenerating mountain beech seedlings under moderate forest shades or natural canopy gaps (Ledgard & Baker, 1988) and of the seed-sown mountain beech within regenerating shrub communities in drought-prone eastern areas of the South Island, which had an average of ca. 10.53 to 13.16 cm yr⁻¹ after about 19-20 years from seeding (Ledgard & Davis, 2004). Such differences are typical for many late-successional canopy species due to their low acclimation ability especially during the early transplanted

stage (Kenzo et al., 2008), although the duration of our study was too short for such comparison and the number of seedlings used may have been too small to fully understand their growth responses to different canopy treatments. However, the seedling RHG results in our study indicate that growth can accelerate in the long-term under moderate shade conditions such as in mānuka shrub with gaps and/or mixed-species shrubs.

In terms of survival, the presence of shrubs was generally favourable to mountain beech seedlings irrespective of canopy manipulation as shown by the higher mean survival rates (64-100 %) in the shrub treatments compared to open grassland (11-59 %). Similar results have been observed in the second planted cohort of mountain beech seedlings. These findings provide support to earlier assumption that survival facilitation by shrubs can dominate in harsh environments than growth facilitation especially for late-successional canopy trees (Gómez-Aparicio, 2009). The results are also comparable to seedling survival of canopy forming species in other degraded systems under shrub communities with different manipulative interventions (e.g. Cogliastro et al., 2006; Yates et al., 2000), suggesting the importance of nurse shrubs on seedling survival in open grasslands where radiation, winter desiccation, and summer water deficits can be intense. However, these constraints on seedling growth do not necessarily preclude the potential of grassland communities to function as nurse plants (Filazzola & Lortie, 2014) as some perennial and annual grass species (e.g. tussocks) can have comparable positive effects with shrubs (Anthelme et al., 2014; Maestre et al., 2001). In our study, there were instances that seedlings in the open grassland had comparable survival and growth with other shrub treatments indicative of the dynamic nature of nurse-protégé interactions in stressful environment where the intensity of nurse effects (positive and negative) at different stages of plant growth may change depending on the prevailing environmental conditions, e.g. seasonal water availability (Armas & Pugnaire, 2005). Such comparable performance of seedlings, however, could also be due to the death of least vigorous mountain beech seedlings in the open grassland treatment, thus leaving only the larger ones for data analysis that makes interpretation of the results more difficult.

Nonetheless, shade-driven facilitation by shrubs on tree seedling establishment has been demonstrated in our study similar to restoration experiments in other stressful natural systems (e.g. Beaudet & Messier, 2002; Urretavizcaya & Defossé, 2013). Shade is considered the main mechanism of facilitation of nurse vegetation in harsh environments (Castro et al., 2002; de Toledo Castanho & Prado, 2014) through its ameliorative effects especially against

extreme temperatures, which often trigger photoinhibition or desiccation of seedlings (Gómez-Aparicio et al., 2006; Liu et al., 2007). Even in benign environments, facilitation through shading is important for seedling establishment as species in this condition tend to be sensitive to periods of stressful conditions (Holmgren & Scheffer, 2010).

6.5.2. Net effects of shrub canopy manipulation on seedling growth and survival

The present study demonstrates the importance of controlling shade to match the shade tolerance trait of target species. For instance, the study observed better growth and survival of mountain beech seedlings in moderate light condition, especially between 1.1 and 1.4 moles $\text{m}^{-2} \text{d}^{-1}$, but light levels lower than 1.1 and higher than 1.4 moles $\text{m}^{-2} \text{d}^{-1}$ appeared to slow seedling growth and reduce survival rates. Competition between the nurse plant and planted seedlings is likely the dominant interaction at lower light condition ($< 1.1 \text{ mol m}^{-2} \text{d}^{-1}$) and as the light level increases further ($> 1.4 \text{ mol m}^{-2} \text{d}^{-1}$) physical stress (e.g. high radiation, winter desiccation) is likely more intense. Previous studies indicate that while mountain beech is known to grow on a wide range of habitats than many other New Zealand tree species (Wardle, 1974), it is highly vulnerable to dry open environment and competition (especially for light) in the early stages of establishment (Wardle, 1984), suggesting the importance of controlling shade and light to facilitate seedling establishment. The 1.1 to 1.4 $\text{mol m}^{-2} \text{d}^{-1}$ light level corresponds to the light levels observed in the mānuka shrub with gap and intact mixed species shrub and are likely to represent the net effects or the balance between the positive and negative effects of these treatments (cf. Armas & Pugnaire, 2005). These net effects are however below the light compensation point ($1.66 \text{ mol m}^{-2} \text{d}^{-1}$) reported by Lusk and Jorgensen (2013) for light-demanding Nothofagaceae species regenerating under the rainforest canopies in North Island, New Zealand, suggesting that mountain beech can maximize growth under moderate shade condition. This result also highlights the importance of nurse shrubs with moderate shades for late-successional canopy forming species restoration in post-disturbance grasslands because, although late-successional canopy species can be light demanding, they do not establish well in high light environment (Wiser et al., 1997) and will require some amount of shade and light for active growth (Ledgard & Baker, 1988).

Aside from the provision of shade, the seedlings may have also benefit from the protective effect of shrub against herbivores, which is known as an indirect mechanism of facilitation by shrubs (Baumeister & Callaway, 2006; Callaway, 1995; Smit et al., 2006).

Mortality due to herbivory by ungulates was not evident in the study despite the prevalence of introduced mammals (e.g. deer, pigs, possums, and hares) in the study area and some indications of disturbance on a few seedlings (e.g. chewing of the seedling aluminum tags especially those in the open grassland). However, it was possible that red deer population in the study site is at low levels to be a threat in this restoration trial (cf. Husheer et al., 2006a), and unlikely to spend much time in open sites.

6.5.3. Implications when managing post-disturbance shrublands for forest restoration project

This study has demonstrated the potential of minimal canopy intervention and moderate shade conditions to facilitate the growth and survival of transplanted late-successional and light demanding mountain beech species in early successional shrubland. This approach could be an important option in designing restoration projects for mature forest species in degraded high country and post-disturbance grassland colonized by early-successional shrubs, which have been reported and demonstrated in this study to have the potential to limit seedling growth and survival largely due to overshadowing effects. The overshadowing effects by shrub communities, along with other land degradation issues (e.g. habitat invasion) associated with the dominance of shrub communities in post-disturbance grasslands and open woodlands were reported as the basis of extensive shrub removal programs elsewhere (e.g. Australia; Eldridge & Soliveres, 2015). While shrub communities can be barriers to the success of restoration projects (Holl, 1998; Meilleur et al., 1994; Putz & Canham, 1992), the results of this study suggest that they should be managed as nurse plant in forest restoration projects to match the shade-tolerance trait of the target species and facilitate their establishment in stressful environments. The present study showed that: (1), using early-successional shrubs as nurse plants is a better option for the restoration of late-successional canopy species than planting them in the open grassland; (2) the provision of shade by nurse shrubs is significant to the survival of target species in harsh environment; but, (3) controlling the shade of nurse shrubs through canopy manipulations can provide favourable growing condition compared to planting in the open grassland and dense shrub canopy where seedlings could suffer from winter or drought-related desiccation and intense competition, respectively. Long-term monitoring is however recommended as nurse-protégé interactions may change in direction and intensity in the long-term, which may have important implications to the success of mature forest restoration projects in degraded habitats. There is also concern about the intermittent effect of canopy manipulations on the restoration

of shade-intolerant or late-successional canopy species as the process of gap closure could affect seedling establishment over time (Romell et al., 2008). This aspect needs to be considered in future studies especially whether maintaining canopy gaps is necessary until the target species are able to grow into the canopy or outgrow the nurse shrub.

7. CHAPTER SEVEN

SYNTHESIS

The overall objective of this thesis was to explore options to establish native forest vegetation especially later-successional canopy tree species into early-successional forest communities in degraded eastern South Island, New Zealand. This chapter synthesizes the main findings of this thesis, discuss their implications to forest restoration, and provide some future research direction for forest restoration projects in degraded successional environments.

At present, there is still a considerable knowledge gap on restoration prescriptions for indigenous woody species or canopy species in many degraded grasslands and shrublands including in New Zealand, despite of the decline or absence of these species in their original habitats and in regenerating forest fragments (Norton et al., 2018). There is a wide consensus that the dominance of one or few species in early successional vegetation can alter the trajectory of succession or arrest the regeneration of later-successional or less-tolerant woody species (Aide et al., 1995; Norton et al., 2018; Royo & Carson, 2006). Thus, in the context of managing early-successional vegetation for forest restoration, understanding successional change and the impacts of management interventions are critical to guide a degraded system towards the desired state as variability in vegetation attributes, species-specific responses, and prevailing filters have important implications to the success of restoration project.

7.1. REGENERATION IN SERAL INTACT COMMUNITIES AND UNDER ARTIFICIAL CANOPY GAPS

The aim of Chapter 3 in this thesis was to examine the succession of regenerating forest in abandoned pastureland by utilizing long-term data from permanent vegetation plots to describe the changes in species composition, density, and growth of native woody species over time. This chapter provided evidence that in the absence of active intervention, succession in early-successional communities such as kānuka can be arrested or delayed. While widespread herbivory by ungulates in New Zealand is usually identified as a major limitation to successful recovery of mature forests in degraded environments, and thus, the substantial scientific works to eradicate or control them have been carried out in the past (Norton, 2009; Wilson et al.,

2006); the findings of Chapter 3 suggest that low light condition within regenerating stands such as kānuka is also an important factor to consider when managing early-successional communities for forest restoration. A key finding in this chapter was that the dominance of kānuka can restrict the growth and recruitment processes especially of less shade-tolerant species as demonstrated by the lower stem density, basal area, and the increasing mortality rates over time of other emerging tree species in the overstorey. These effects were likely confounded by the dominance of more shade-tolerant species like māhoe and *Coprosma* species in the understorey in both density and growth parameters, which could be ascribed also for the increased mortality and low recruitment rates of other species in the understorey.

In the absence of active intervention (e.g. artificial canopy gaps), it is highly likely that succession of woody species within the regenerating kānuka will remain arrested for many years, similar to other early-successional communities in degraded environment in New Zealand and elsewhere (Acácio et al., 2007; Curt et al., 2009; Denslow, 1980; Dodd & Power, 2007; Prach et al., 2001; Richardson et al., 2014; Whitney, 1996). The results in Chapter 3 indicate the high possibility of shade-tolerant māhoe to replace or co-dominate with the kānuka canopy, which could result in the maintenance of the relatively closed-canopy or low light-condition within the kānuka stand. Hence, a deliberate disturbance of canopies to create a favourable understorey light condition is considered a key intervention requirement for structuring forest ecosystems, providing regeneration niche for canopy trees, and controlling the competitive dominance of one or a few species (Denslow, 1980; Roberts & Gilliam, 1995; Tilman, 1994). However, canopy species may be inferior competitors and that successional pioneers or other species may have a competitive advantage to maintain their population or dominate even in gap environments (Grime, 1973; Oliver, 1980; Royo & Carson, 2006), although this aspect remains rarely tested empirically (Suding, 2001).

In succeeding chapters of this thesis, I proposed that artificial gaps are likely to be important for facilitating natural regeneration and restoration of canopy species in New Zealand's seral communities that are usually being protected for succession to mature forest by removing degrading factors such as livestock grazing (Norton et al., 2018). Canopy intervention through artificial gaps has the potential to not only reduce the intensity of competition in dense communities but also provide opportunities for less tolerant canopy species to persist or coexist with more tolerant counterparts (Suding, 2001). Surprisingly, there is still a limited application of artificial canopy gaps in restoration projects in New Zealand,

although gap environments are critical for New Zealand native canopy species as their successful regeneration in forest understories have been observed in areas with elevated light conditions (e.g. treefall gaps, windthrow, snow breakage, logged-over forests, among others) (Allen & Wardle, 1985; Baxter & Norton, 1989; Ogden, 1985, 1988; Ogden et al., 1991; Runkle et al., 1995; Stewart et al., 1991; Stewart & Veblen, 1982). Recent use of artificial gaps in New Zealand has been in restoration plantings within exotic stands that showed to accelerate in the establishment of canopy species (e.g. Forbes, 2017; Forbes et al., 2016a; Forbes et al., 2016b).

Consequently, in Chapter 4, the importance of artificial gaps on the natural regeneration and establishment of woody species was assessed in dense patches of regenerating kānuka forests. Gap creation was found to be related to the increase in the number of species and density of woody regeneration that included a mixture of shade-tolerant and intolerant woody species indicative of the decline in the intensity of competition or the improved competitive ability of shade-intolerant woody species in gap environments as suggested in previous studies by Suding (2001). However, in the current study, there was no significant effect detected with respect to the interaction of time and gap treatments on species recruitment suggesting that initial succession can be slow even under artificial canopy gaps as the dominance of *Melicytus ramiflorus* (māhoe) in the understorey may have neutralized the woody species turnover and recruitment processes. Nonetheless, survival and growth of woody regeneration were significantly greater in canopy gaps than beneath the intact canopy despite the higher proportions of ground vegetation and browsing incidence by ungulates in gap treatments. The tendency of woody seedlings to grow better in canopy gaps may have provided them the competitive ability and browsing tolerance to offset survival and growth disadvantages, thus, the opportunity for coexistence among woody species with different shade-tolerance traits in gap environments. In addition, the immediate occurrence of some canopy species in canopy gaps, although sporadically, highlight the potential of canopy gaps to facilitate the regeneration of canopy species even those that have been suppressed for years in the soil seed bank.

In Chapter 5, the significance of different canopy treatments (artificial gaps, ring-barking, and forest edge planting) on the survival and early growth of light-demanding tōtara (*Podocarpus totara*, Podocarpaceae) was tested within the early-successional kānuka forest. The limited studies on different canopy manipulations on early-successional temperate forest restoration underscore the importance of understanding their effects on the light environment

of such ecosystems and their viability on shade-intolerant late-successional species restoration as outcomes may vary with species and disturbance regimes involved (Caplat & Anand, 2009). Results highlighted the effectiveness of artificial gaps over other methods in accelerating the growth of planted tōtara. The improvement in light transmission in this study was significantly related to artificial gaps, which had available light levels of 33 % of open sky conditions compared to other methods (less than 23 %). The result is comparable to the 30% total light transmission under large, naturally formed, canopy gaps in a dense mixed forest in central North Island, New Zealand, that was found to result in the best growth of tōtara seedlings in a natural setting (Ebbett & Ogden, 1998). In an 8-year Mexican study involving shade-intolerant and shade-tolerant tropical trees, Ramos and del Amo (1992) reported a consistent growth improvement and highest survival of all planted seedlings in a canopy treatment with 37% light transmission but highly variable seedling growth response in canopies with 68% and 17% irradiance. Thus, the findings in the current study demonstrate that moderate understorey light transmission provided by gap treatments would be enough as seedlings under gaps grew consistently taller and faster over time under artificial gaps.

Finally, Chapter 6 was conducted to examine the facilitative potential of different early-successional shrubland communities and minimal canopy manipulations on the growth and survival of a mature forest species, mountain beech (*Fuscospora cliffortioides*, Nothofagaceae), as a case study to identify viable options to implement restoration projects in degraded grassland environments. One of the key findings in this chapter was that seedling growth and survival of transplanted seedlings of mountain beech were significantly associated with moderate light levels (ca. 1.1 to 1.4 mol m⁻² d⁻¹ light levels or 20-40% canopy openness) that were associated with gap treatments in the taller shrub communities of mānuka (*Leptospermum scoparium*) and moderate canopy openness in low-growing mixed-species shrubs. The results indicate that canopy species such as mountain beech can maximize growth under moderate shade condition suggesting that minimal canopy interventions are important for mature forest species restoration in post-disturbance grasslands and shrublands because, although canopy species can be light demanding, they do not establish well in larger canopy openings or higher light environment (Ogden, 1985; Wiser et al., 1997) and will require some amount of shade and light for active growth (Ledgard & Baker, 1988). Although the study found inconsistent nurse-protégé interactions over time, the result suggests that dense early-successional shrubland can be managed as nurse plant to facilitate the initial growth and survival of canopy species in stressful environment. Seedling mortality due to herbivory by

ungulates was not evident in this study despite the prevalence of introduced mammals (e.g. pigs, possums, and hares) in the study area and some indications of disturbance on a few seedlings especially those in the open grassland.

In summary, gap creation is likely to be an important tool for restoring less tolerant and later-successional canopy species in early-successional communities both through providing ideal and safe sites for survival and active growth of light-demanding species and through natural establishment of other future canopy trees into the gaps. This thesis provided a unique opportunity to understand the viability of artificial gaps in a degraded successional environment wherein regeneration of less tolerant species could be limited by intense competition with ground vegetation and the occurrence of herbivory, which are rarely empirically observed.

7.2. IMPLICATIONS TO RESTORATION IN DEGRADED EARLY-SUCCESSIONAL COMMUNITIES

The results of this study are consistent with existing knowledge on the potential of canopy gaps for restoration in seral stands that have established after farming abandonment and other disturbances (e.g. fire). As expected, significant improvements in light environments in seral communities' understories were associated with artificial gaps resulting in better establishment of native woody species and light-demanding canopy trees, which are often assumed to be inferior competitors compared to more dominant and shade-tolerant counterparts in shaded understories. As demonstrated in this thesis, small-scale canopy gaps can provide favourable growing conditions for canopy species including the mitigation of the intensity of competition and impacts of herbivory by ungulates, and the provision of opportunities for co-existence among native woody species with different shade tolerance traits.

These restoration benefits from canopy interventions are relevant to the management goals in the Canterbury region that include conservation of native biodiversity and restoration of representative habitats and ecosystems that have been lost or severely degraded (Biodiversity Strategy Advisory Group, 2008). These targets would require more than just the removal of degrading factors (e.g. grazing) but the integration of more active management interventions such as canopy manipulations and restoration planting in degraded forest fragments and regenerating communities. Removal of degrading factors and allowing degraded

lands to naturally regenerate have been important themes in the past restoration programs in New Zealand (Norton et al., 2018), but the continued decline or changes in species configurations of many early-successional communities such as grassland (Duncan et al., 2001; Norton & Young, 2016b) and the slow mature forest recovery in remnants and regenerating forests (Dodd & Power, 2007; Richardson et al., 2014; Smale et al., 2005) as also demonstrated in this thesis, suggest that successful conservation also depends on active measures that can provide favorable conditions for active growth and positive co-existence of many native canopy species especially in highly degraded and disturbed conditions. Successions of canopy species in degraded areas are usually restricted by the dominance of one or few species in both overstorey and understorey structures even after removal or control of degrading factors. For instance, results from the long-term assessment of succession in regenerating kānuka forest in a restoration project in Tiromoana Bush showed that even after 15 years of grazing exclusion succession within the kānuka-dominated forest stand a state of arrested or delayed succession characterized by the absence of significant improvement in species compositional structure, high mortality rates, low recruitment rates, and the prolonged dominance of kānuka and māhoe in the area in terms of density and basal area. In contrast, the gap-based restoration trials, natural succession, and restoration planting, within the kānuka-dominated forest in Tiromoana Bush demonstrated an improved succession and establishment of target woody species, respectively. In the tōtara restoration trial, for instance, the influence of gap treatments on seedling growth remained significant after six years, suggesting that gaps should be maintained to accelerate restoration within the dense kānuka stands.

However, while succession can benefit from canopy intervention, it is important to note in the gap-based regeneration trial that woody species regeneration can be slow even in gap environments especially in degraded seral communities with inadequate seed sources or with seed dispersal limitation. Although this aspect was not examined in this thesis, the importance of this filter in New Zealand degraded environments and fragmented landscapes is well recognized and are expected to limit local seed rain of many canopy species including mutualistic relationships as significant numbers (ca. >50%) of native species in New Zealand are bird dispersed (Beveridge, 1973; Canham et al., 2014; Kelly et al., 2010; Norton, 2009; Norton & Kelly, 1988; Sullivan & Kelly, 2000). In this situation, active restoration plantings under artificial gaps using native canopy species would be a viable option to overcome seed dispersal limitations and maximize the restoration benefits associated with canopy intervention. However, in sites where herbivory is a problem, the results of this thesis suggest

that small-scale gaps are sufficient to improve understorey light conditions and achieve positive growth rates of target species as herbivory can reduce the benefits of elevated light environments especially in areas with larger clearings (e.g. Forbes et al., 2016a; Howe, 1990), which are favoured by ungulates.

The results from this thesis are also expected to have applications elsewhere as the dominance of early-successional communities such as grassland and shrubland in stressful or degraded conditions are typical over large areas in tropical and subtropical environments such as in Australia (Eldridge & Soliveres, 2015; Tongway & Ludwig, 1990), North and Central America (Barger et al., 2011; Portillo-Quintero & Sánchez-Azofeifa, 2010), and Africa (Huntley & Walker, 2012). A few nurse-based restoration studies in the tropics (e.g. Holl, 1998; Yang et al., 2013) have also acknowledged the importance of canopy manipulative interventions to reduce the effect of shrub canopy over-shading or competition with target species. For instance, the concern on over-shading effects, along with other land degradation issues (e.g. habitat invasion), associated with the dominance of shrub communities in post-disturbance grasslands and open woodlands were reported as the basis of extensive shrub removal programs in Australia (Eldridge & Soliveres, 2015). While shrub communities can be barriers to the success of restoration projects (Holl, 1998; Meilleur et al., 1994; Putz & Canham, 1992), the results of this thesis suggest that they can be managed as nurse plant in forest restoration projects to match the shade-tolerance trait of the target species and facilitate growth and survival of mature forest species especially in stressful or harsh environments.

7.3. FUTURE RESEARCH

The results of this thesis point to the following two main areas for future research.

First, it is important to consider whether the positive effects of canopy interventions in this thesis are also general to regenerating communities across a wider geographic area. It must be recognized that the components of this research were conducted within a relatively small geographic location and have focused on relatively few patches of successional communities or a few representative canopy species (i.e. tōtara and mountain beech) for restoration. Early-successional communities in a wide range of ecosystems can have variable effects on different stages of seedling establishment and can be caused by differences in terms of environmental gradients, location, identity of regenerating vegetation, target species involved (Aerts et al., 2007; Armas & Pugnaire, 2005; Callaway et al., 1996; Cavard et al., 2011; Gómez-Aparicio et al., 2004; Holl, 2002; Jensen et al., 2012; Maestre et al., 2009; Putz & Canham, 1992) including differences in height and canopy structure of regenerating communities (Berkowitz et al., 1995) that may entail different prescriptions from a management perspective. For instance, differences in canopy structure can affect the potential of canopy interventions especially in terms of the quality of light transmission in the understorey environment (Clebsch & Busing, 1989) and thus the dynamics of woody regeneration or target species performance in response to canopy disturbance. In other studies, it has been shown that different disturbance regimes can also produce different outcomes (e.g. species composition) in different successional communities (Caplat & Anand, 2009; Romell et al., 2008). Thus, future research should consider the potential of different canopy interventions on a wider range of ecosystems at a larger spatial scale as some important canopy species may require certain disturbance regime to establish and/or survive (Brokaw, 1987; Buchanan & Hart, 2012; Sapkota & Odén, 2009; Zhu et al., 2003).

The intensity of plant-plant interactions (competition and facilitation) is also expected to change along environmental gradients (e.g. wet to dry, infertile to neutral or more infertile habitat) (Armas et al., 2011; Holmgren et al., 1997; Pugnaire & Luque, 2001; Putz & Canham, 1992), which underlined the relevance of the growing number of nurse-protégé studies to better predict the success of restoration projects especially along stress-gradient (Flores & Jurado, 2003; Filazzola & Lortie, 2014). Future research should examine the response of successions along environmental gradients (especially from dry to wet) combined with different distances

from seed sources, as differential dispersal ability can affect species recruitment processes profoundly (Cain et al., 2000; Gonzales & Nakashizuka, 2010; Nagaike et al., 2012). In the case of important mature forest species (e.g. tōtara, matai), for instance, abundant regeneration were observed in higher rainfall environment (Lusk et al., 2015; McSweeney, 1982; Miller & Wells, 2003; Norton, 1991) but drivers of their succession in drier condition are still poorly understood despite being associated with drier sites.

The importance of aboveground competition as observed in this research also warrants consideration of understorey disturbance particularly to control the density of dominating or persistent understorey species like māhoe. Understorey disturbance has been demonstrated to benefit tree succession or planted seedling establishment in other successional communities with dense understorey layers (e.g. Dupuy & Chazdon, 2008; Forbes et al., 2016b; Holl, 1998).

Second, long-term research is required to account fully for the potential of artificial canopy gaps to sustain the growth and survival of canopy species in degraded early-successional communities. This is needed because the regeneration or growth response to canopy disturbance by woody species can be slow in the early years or transplanted stage, while the rate of gap closure of some successional communities is usually faster in the early period (e.g. up to 11-16 years) following canopy gap creation (Lu et al., 2015). This may affect the density and rate of succession or establishment of target woody species over time. Thus, future gap-based restoration research should consider the rate of gap closure in regenerating communities at broader temporal and spatial scale to account for their effects on canopy species establishment especially that many native canopy species in New Zealand are slow growing and might require sequential gap events to reach the canopy (Ogden et al., 1991).

In addition, in the current research undertaken here, there were indications of inconsistencies over time in the plant-plant interactions under the different shrub canopy treatments in the mountain beech restoration trial suggesting that the competitive and facilitative effects by successional shrub as nurse plant on canopy species restoration may change in direction and intensity in the long-term. Such inconsistencies may represent the complexity and unpredictability of competition and facilitation processes in degraded early-successional communities (Berkowitz et al., 1995; Callaway & Walker, 1997; Holl, 2002) that should be considered in restoration projects, as this may have important implications to the

sustainability of gap-based restorations, especially in stressful conditions, at these times of changing climate.

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9. APPENDICES

APPENDIX A. Species composition and distribution of native woody regeneration beneath the intact kānuka canopy and canopy gaps in Tiromoana Bush, Kate Valley, eastern South Island, New Zealand over 28 months (2.3 years).

Code*	Scientific Name	Canopy				Gap			
		Density	Relative	Relative	IV	Density	Relative	Relative	
		(stem ha ⁻¹)	Density (%)	Freq (%)		(stem ha ⁻¹)	Density (%)	Freq (%)	IV
December 2016 (12 months)									
Aser	<i>Aristotelia serrata</i>	< 0.00	1.30	< 0.00	1.30	156.25	0.37	1.19	1.56
Cluc	<i>Coprosma lucida</i>	0.00	0.00	0.00	0.00	781.25	1.07	3.57	4.64
Cpro	<i>Coprosma propinqua</i>	12343.75	42.86	24.44	67.31	10468.75	18.18	13.10	31.28
Crha	<i>Coprosma rhamnoides</i>	4531.25	19.24	17.78	37.02	7187.50	11.86	14.29	26.14
Crot	<i>Coprosma rotundifolia</i>	2812.50	8.79	11.11	19.90	4218.75	7.74	7.14	14.88
Cser	<i>Carpodetus serratus</i>	0.00	0.00	0.00	0.00	4687.50	6.63	7.14	13.77
Fexc	<i>Fuchsia excorticata</i>	0.00	0.00	0.00	0.00	156.25	0.15	1.19	1.34
Mlae	<i>Myoporum laetum</i>	1562.50	6.95	6.67	13.61	6093.75	10.06	7.14	17.20
Mram	<i>Melicytus ramiflorus</i>	2031.25	8.49	11.11	19.60	17656.25	24.20	17.86	42.06
Parb	<i>Pseudopanax arboreus</i>	1093.75	6.66	13.33	19.99	9218.75	14.50	16.67	31.16
Pcor	<i>Pennantia corymbosa</i>	0.00	0.00	0.00	0.00	625.00	0.87	2.38	3.25
Pcra	<i>Pseudopanax crassifolius</i>	781.25	2.89	6.67	9.56	1718.75	3.48	5.95	9.44
Pten	<i>Pittosporum tenuifolium</i>	625.00	2.83	8.89	11.72	468.75	0.90	2.38	3.28
Total		25781	100	100	200	63438	100	100	200

February 2017 (14 months)									
Aser	<i>Aristotelia serrata</i>	< 0.00	1.30	< 0.00	1.30	156.25	0.35	1.11	1.46
Cluc	<i>Coprosma lucida</i>	0.00	0.00	0.00	0.00	1093.75	1.35	4.44	5.79
Cpro	<i>Coprosma propinqua</i>	13593.75	43.00	23.91	66.91	13593.75	18.59	13.33	31.93
Crha	<i>Coprosma rhamnoides</i>	5156.25	20.47	19.57	40.03	7812.50	10.71	14.44	25.15
Crot	<i>Coprosma rotundifolia</i>	3125.00	8.56	10.87	19.43	6093.75	6.94	5.56	12.50
Cser	<i>Carpodetus serratus</i>	0.00	0.00	0.00	0.00	6250.00	7.85	8.89	16.74
Fexc	<i>Fuchsia excorticata</i>	0.00	0.00	0.00	0.00	156.25	0.14	1.11	1.25
Hlan	<i>Helichrysum lanceolatum</i>	0.00	0.00	0.00	0.00	312.50	0.60	2.22	2.82
Mlae	<i>Myoporum laetum</i>	1562.50	6.95	6.52	13.47	5937.50	8.72	6.67	15.38
Mram	<i>Melicytus ramiflorus</i>	2031.25	8.19	10.87	19.06	26406.25	27.01	16.67	43.68
Parb	<i>Pseudopanax arboreus</i>	1093.75	6.55	13.04	19.59	9531.25	13.12	15.56	28.67
Pcor	<i>Pennantia corymbosa</i>	0.00	0.00	0.00	0.00	625.00	0.76	2.22	2.98
Pcra	<i>Pseudopanax crassifolius</i>	781.25	2.28	6.52	8.80	1718.75	3.01	5.56	8.57
Pten	<i>Pittosporum tenuifolium</i>	625.00	2.72	8.70	11.41	468.75	0.86	2.22	3.08
Total		27969	100	100	200	80156	100	100	200
April 2017 (16 months)									
Aser	<i>Aristotelia serrata</i>	< 0.00	1.52	< 0.00	1.52	156.25	0.37	1.09	1.45
Cluc	<i>Coprosma lucida</i>	156.25	0.27	2.13	2.40	937.50	1.26	4.35	5.61
Cpro	<i>Coprosma propinqua</i>	12343.75	43.14	23.40	66.55	12656.25	17.78	13.04	30.82
Crha	<i>Coprosma rhamnoides</i>	5312.50	20.10	17.02	37.12	8281.25	11.71	14.13	25.84
Crot	<i>Coprosma rotundifolia</i>	3437.50	9.03	12.77	21.79	7187.50	6.71	7.61	14.32
Cser	<i>Carpodetus serratus</i>	0.00	0.00	0.00	0.00	5781.25	6.46	9.78	16.24

Fexc	<i>Fuchsia excorticata</i>	0.00	0.00	0.00	0.00	156.25	0.13	1.09	1.21
Hlan	<i>Helichrysum lanceolatum</i>	0.00	0.00	0.00	0.00	312.50	0.52	2.17	2.69
Mlae	<i>Myoporum laetum</i>	1093.75	5.94	6.38	12.32	4687.50	6.81	6.52	13.34
Mram	<i>Melicytus ramiflorus</i>	2031.25	7.65	10.64	18.29	35937.50	30.01	15.22	45.23
Parb	<i>Pseudopanax arboreus</i>	1250.00	7.27	12.77	20.04	9843.75	13.68	15.22	28.90
Pcor	<i>Pennantia corymbosa</i>	0.00	0.00	0.00	0.00	625.00	0.62	2.17	2.79
Pcra	<i>Pseudopanax crassifolius</i>	781.25	1.98	6.38	8.37	1875.00	2.82	5.43	8.25
Pten	<i>Pittosporum tenuifolium</i>	625.00	3.10	8.51	11.62	468.75	1.13	2.17	3.30
Total		27031	100	100	200	88906	100	100	200
September 2017 (21 months)									
Aser	<i>Aristotelia serrata</i>	< 0.00	1.39	< 0.00	1.39	156.25	0.35	1.10	1.45
Cluc	<i>Coprosma lucida</i>	156.25	0.30	2.22	2.52	625.00	0.90	3.30	4.20
Cpro	<i>Coprosma propinqua</i>	11250.00	40.23	24.44	64.68	10625.00	15.78	13.19	28.96
Crha	<i>Coprosma rhamnoides</i>	4062.50	24.06	20.00	44.06	7656.25	11.16	14.29	25.44
Crot	<i>Coprosma rotundifolia</i>	3281.25	11.00	13.33	24.33	7656.25	7.48	8.79	16.27
Cser	<i>Carpodetus serratus</i>	0.00	0.00	0.00	0.00	6562.50	7.77	12.09	19.85
Fexc	<i>Fuchsia excorticata</i>	0.00	0.00	0.00	0.00	156.25	0.14	1.10	1.23
Hlan	<i>Helichrysum lanceolatum</i>	0.00	0.00	0.00	0.00	312.50	0.50	2.20	2.70
Mlae	<i>Myoporum laetum</i>	1093.75	5.44	6.67	12.11	4843.75	6.68	6.59	13.27
Mram	<i>Melicytus ramiflorus</i>	1718.75	7.25	11.11	18.36	38125.00	31.05	14.29	45.34
Parb	<i>Pseudopanax arboreus</i>	1093.75	6.70	11.11	17.81	10156.25	14.04	13.19	27.22
Pcor	<i>Pennantia corymbosa</i>	0.00	0.00	0.00	0.00	1250.00	0.93	3.30	4.22
Pcra	<i>Pseudopanax crassifolius</i>	468.75	1.28	4.44	5.72	1406.25	2.14	4.40	6.54

Pten	<i>Pittosporum tenuifolium</i>	468.75	2.35	6.67	9.01	468.75	1.09	2.20	3.28
Total		23594	100	100	200	90000	100	100	200
April 2018 (28 months)									
Aser	<i>Aristotelia serrata</i>	< 0.00	0.70	< 0.00	0.70	312.50	0.54	1.83	2.38
Cluc	<i>Coprosma lucida</i>	156.25	0.28	1.89	2.16	1562.50	1.75	4.59	6.34
Cpro	<i>Coprosma propinqua</i>	13437.50	39.01	20.75	59.76	11093.75	13.62	12.84	26.47
Crha	<i>Coprosma rhamnoides</i>	4218.75	14.10	13.21	27.30	6406.25	8.27	11.93	20.20
Crot	<i>Coprosma rotundifolia</i>	4218.75	13.53	13.21	26.74	9531.25	9.64	9.17	18.81
Cser	<i>Carpodetus serratus</i>	0.00	0.00	0.00	0.00	6406.25	9.94	10.09	20.04
Fexc	<i>Fuchsia excorticata</i>	0.00	0.00	0.00	0.00	156.25	0.11	0.92	1.03
Hlan	<i>Helichrysum lanceolatum</i>	0.00	0.00	0.00	0.00	312.50	0.46	1.83	2.30
Mlae	<i>Myoporum laetum</i>	1718.75	5.28	7.55	12.83	4062.50	4.34	6.42	10.76
Mram	<i>Melicytus ramiflorus</i>	4218.75	11.50	15.09	26.59	43750.00	33.69	12.84	46.54
Parb	<i>Pseudopanax arboreus</i>	3437.50	11.55	15.09	26.64	10937.50	12.12	12.84	24.96
Pcor	<i>Pennantia corymbosa</i>	156.25	0.32	1.89	2.21	2500.00	2.37	5.50	7.87
Pcra	<i>Pseudopanax crassifolius</i>	937.50	2.13	5.66	7.79	1562.50	1.92	5.50	7.42
Pten	<i>Pittosporum tenuifolium</i>	468.75	1.61	5.66	7.27	937.50	1.22	3.67	4.89
Total		32969	100	100	200	99531	100	100	200

Shrubs (Aser, Cluc, Cpro, Crha, Crot, Hlan); Trees (Cser, Fexc, Mlae, Mram, Parb, Pcor, Pcra, Pten).

APPENDIX B. Percent cumulative contribution (Cum.) of each species to the overall dissimilarity between canopy treatments. Species are presented in order of their percent cumulative contribution with the first five species as the most influential discriminating between treatments based on the SIMPER analysis. The significance of the difference in density between treatments is also presented.

Code	Species	Mean density (m ² /ha)		Dis.	SD	Cum. (%)
		Canopy	Gap			
Mram	<i>Melicytus ramiflorus</i>	2,406	32,375	0.22	0.19	28.76***
Cpro	<i>Coprosma propinqua</i>	12,594	11,688	0.14	0.12	46.89
Parb	<i>Pseudopanax arboreus</i>	1,594	9,938	0.09	0.08	58.49***
Crha	<i>Coprosma rhamnoides</i>	4,656	7,469	0.08	0.09	68.92
Crot	<i>Coprosma rotundifolia</i>	3,375	6,936	0.07	0.08	78.05
Cser	<i>Carpodetus serratus</i>	0	5938	0.06	0.09	85.34***
Mlae	<i>Myoporum laetum</i>	1406	5125.	0.05	0.09	92.57***
Pcra	<i>Pseudopanax crassifolius</i>	750	1657	0.02	0.03	95.38***
Pten	<i>Pittosporum tenuifolium</i>	563	563	0.01	0.02	96.77
Cluc	<i>Coprosma lucida</i>	94	1000	0.01	0.02	98.03***
Pcor	<i>Pennantia corymbosa</i>	31	1125	0.01	0.02	99.13***
Hlan	<i>Helichrysum lanceolatum</i>	0	250	0.003	0.01	99.51***
Aser	<i>Aristotelia serrata</i>	0	188	0.003	0.01	99.86***
Fexc	<i>Fuchsia excorticata</i>	0	156	0.001	0.004	1.00***

SD = standard deviation of contribution. Asterisk (*) indicates significance: * P<0.05, ** P<0.01, *** P<0.001.

APPENDIX C. Tulod, A. M., Norton, D. A., & Sealey, C. (2019). Canopy manipulation as a tool for restoring mature forest conifers under an early-successional angiosperm canopy. *Restoration Ecology*, 27(1), 31-37.doi.org/10.1111/rec.12707