Enrichment planting of late-successional plant species within restored urban forests

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Monique Mae Hall

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Abstract

Successful ecological restoration of early-successional forests should result in highly biodiverse, stable, self-perpetuating ecosystems. This often requires active intervention to transition them to a late-successional state. However, little research has explored specific conditions required for introducing late-successional plant species into urban forests undergoing restoration, especially for different plant functional guilds. This research gap is addressed in this thesis by exploring restored urban forest development with a focus on identifying optimal environmental conditions for re-introducing juveniles of three late-successional species from different functional guilds in Aotearoa New Zealand. Late-successional plant species can have narrow microclimate tolerances and these conditions, e.g., humidity and air temperature, may only be present at certain stages of forest development.

To explore these microclimatic tolerances, three model enrichment plant species were planted and monitored for survival and growth, while recording key abiotic environmental conditions, these included: an epiphyte (*Griselinia lucida*, akapuka), an understorey shrub (*Piper excelsum*, kawakawa) and a large canopy tree (*Dacrydium cupressinum*, rimu). Plants were introduced into 27 forest patches in three North Island cities (Hamilton, New Plymouth and Napier) spanning a chronosequence of 5–47 years since initial forest restoration planting began. This chronosequence design allowed observation of enrichment species' responses under differing stages of forest development. Linear regression models were used to see how canopy openness, air and soil temperature, relative humidity and non-native herbaceous weed cover within the restored urban forest sites affected the growth and survival of the three model enrichment plant species.

After one year, juvenile enrichment plant survival was 75.5% (*G. lucida*), 100% (*P. excelsum*), and 75% (*D. cupressinum*). As forests developed, the canopies closed, buffering the understorey from the external macroclimate to create a microclimate below. When the forest canopy reached 10.88 years old, there was a significant threshold where canopy closure rates slowed, markedly restricting light reaching the forest floor. Relative humidity fluctuations in the understorey stabilised at 33.86 years of forest age, when the canopy was about 80% closed.

The late-successional plant species from different functional guilds responded differently to changing understorey environmental conditions, driven by the developing forest canopy.

Griselinia lucida growth increased under more open canopies, suggesting a primary dependence on light availability. In contrast, *P. excelsum* growth increased under more closed canopies with higher relative humidity. *Dacrydium cupressinum* showed alternate biomass allocation responses to different understorey conditions. Under cooler and wider fluctuations in air temperature, plants were shorter with wider stems. However, under stable, warmer air temperatures, plants grew taller with narrower stems. Further, *D. cupressinum* growth seemed somewhat uncoupled from canopy cover and responded instead to competition with forest floor plants like non-native herbaceous weeds.

This thesis broadens understanding of enrichment planting approaches for late-successional plant species in forests undergoing restoration. During restoration planning, the requirements of plants' functional guilds should be considered. Re-introduction of *G. lucida* should be higher within the canopies of older, taller forests. *Piper excelsum* should be planted under closed canopies. *Dacrydium cupressinum* juveniles should be planted within warm, stable temperatures with little non-native plant competition. These conditions generally occur ~10+ years following initial forest restoration planting. These research results highlight the importance of considering timing and thresholds in forest development and the environmental constraints of different plant guilds to ensure successful, biodiverse and long-lived urban forest restoration.

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There is a whakataukī that says, "*Ehara taku toa i te toa takitahi, engari he toa takitini*" which means, "*My success is not mine alone but from the strength of many*". And this expresses how I have felt throughout the enriching journey of my master’s and this thesis.

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Here's to our future!!!

“So, how do you learn to understand what the trees are saying?

It is mostly a matter of quietly and humbly getting to know the forest, listening carefully, watching closely, noticing little details, all the while building up a sense of really belonging, becoming part of the family of Tāne”

- Pa Ropata (Rob McGowan)

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CHAPTER 1

Introduction

1.1 Chapter outline

This introductory chapter provides the background and context of the thesis. Relevant ecological restoration literature is reviewed first followed by autecological information on the focal species and profiles for each of the three North Island cities where the research was undertaken. The research questions and objectives of the thesis are then specified, and the structure of the remainder of the thesis is outlined.

1.2 Background

Ecology is the study of interactions between organisms and their environments (Chapin *et al.*, 2011; Smith & Smith, 2015). Ecologists study ecosystems at various spatial and temporal scales to understand the processes behind how and why a community of organisms is structured in a particular way (Chapin *et al.*, 2011). Ecological principles and theories can, therefore, be used to reconstruct and restore disturbed ecosystems (Smith & Smith, 2015; Society for Ecological Restoration Australasia, 2018).

Restoration ecology is an applied science discipline nested within ecology which focuses on the study of restoring ecosystems following human-induced damage, typically intending to imitate the environment's original state and reinstate ecological function (Hobbs & Norton, 1996; Palmer *et al.*, 1997; Society for Ecological Restoration, 2004). The focus of restoration ecology is on specific ecosystems which known ecological principles apply to, such as lakes, rivers, wetlands, grasslands and forests from tropical to temperate to alpine (Smith & Smith, 2015). Each ecosystem is unique and complex, with differing amounts of disturbance, and therefore the scale of ecological restoration required varies and the approach may differ drastically. Restoration ecology occurs on a continuum of scales, from re-introducing a species to re-establishing a whole community (Hobbs & Norton, 1996; Smith & Smith, 2015). As a science, restoration ecology developed to formalise the sometimes ad hoc approach to restoring ecosystems, which are currently being destroyed on an unprecedented level worldwide (Society for Ecological Restoration, 2004). Restoration ecology can contribute to expanding larger ecological theory by understanding how to re-assemble ecosystems and provides the ideas on methodology to support the practice of ecological restoration (Society for Ecological Restoration, 2004).

Ecological restoration is the practice of undertaking restoration work (Society for Ecological Restoration, 2004). Restoring damaged ecosystems is vital on many levels: conserving endangered species (Benayas *et al.*, 2009), improving water and air quality (Pataki *et al.*, 2011), providing recreational environments, providing for hunting and fishing (Brancalion *et al.*, 2014; Wehi & Lord, 2017), flood control (Nilsson *et al.*, 2018), provision of food (Cilliers *et al.*, 2018), for human health and well-being (Sandifer *et al.*, 2015) and employment (BenDor *et al.*, 2015). The practice of ecological restoration is similar to the stewardship methodologies used for centuries by indigenous cultures as they have co-evolved with their ecosystems (Uprety *et al.*, 2012).

Significant knowledge gaps still exist within restoration ecology, especially in some new areas such as the restoration of urban forest ecosystems (Acosta *et al.*, 2018). Only 2% of research led since 1990 was within urban ecosystems (Acosta *et al.*, 2018), even though 55% of the world's population live within urban settlements (United Nations, 2018). Further, the studied urban ecosystems are rarely those that are being restored or indeed reconstructed from severely degraded states with little to none of the original vegetation present, i.e., mowed urban parkland (Wallace & Clarkson, 2019). For practical reasons, this restoration versus reconstruction is an essential distinction, as highly degraded environments will often have had previous land uses which may affect reconstruction success. Here, the term restoration is used generally to mean reconstruction of urban forest ecosystems from a highly degraded state.

Urban ecosystems are complex and differ from rural ecosystems in several key aspects (Elmqvist *et al.*, 2013). Within cities, temperatures are higher than in nearby rural settings, i.e., the 'urban heat island' effect (Zipper *et al.*, 2016; Ziter *et al.*, 2019). Higher temperatures are attributed to the increased area of impervious surfaces such as metal, concrete and asphalt, which retain the heat (Ziter *et al.*, 2019). These warmer temperatures can cause stress on vegetation from the altered water and energy cycling (Zipper *et al.*, 2016). Within cities, the urban heat island effect can be countered by creating forest cover to lower temperatures (Zipper *et al.*, 2016). However, the native land cover in urban areas is typically of small extent (Hejkal *et al.*, 2017; Piana *et al.*, 2019) and therefore cannot provide this and manifold other benefits to the full possible extent. Another common issue in urban ecosystems is the reduced landscape connectivity due to intensified urban development, which causes native land cover fragmentation and isolation (Piana *et al.*, 2019). Small fragmented patches are subject to dispersal barriers such as movement for less-mobile fauna with a narrow range of ideal habitats and lessening seed dispersal (Hejkal *et al.*, 2017), both resulting in restriction of gene flow (Schlaepfer *et al.*, 2018).

City ecosystems are further disrupted because of their innate proximity to high human population densities (Piana *et al.*, 2019). Urbanisation causes light pollution (Farnworth *et al.*, 2018) and other environmental pollution (an array of pollutants, from heavy metals to an overload of nutrients in waterways) (Fergusson *et al.*, 1980) and the introduction of non-native and potentially invasive floral and faunal species (Piana *et al.*, 2019). Urban forest ecosystems may require more maintenance due to the increased invasion of introduced non-native plant species from nearby properties (Wallace *et al.*, 2017) and these other disturbances, but their care produces many benefits.

Restoring native ecosystems in cities has multifaceted benefits for urban dwellers. Experiencing a connection with nature reduces mental distress, anxiety and depression, and lowers the prevalence of physical disease (Standish *et al.*, 2013; Barton, 2017; Taylor *et al.*, 2018). For example, a positive correlation exists between how much nature people view from home or work and their wellbeing (Taylor *et al.*, 2018). Furthermore, as the biodiversity in cities increases, so do the psychological benefits to humans (Fuller *et al.*, 2007) and social support of nature for cultural importance (e.g., indigenous worldviews) (Wehi & Lord, 2017). The amount and size of greenspace (areas of urban forests, parks, street trees etc.) in cities are positively associated with the aforementioned psychological benefits (Beninde *et al.*, 2015; Houlden *et al.*, 2018).

Larger areas of urban greenspace also aid in sustaining biodiversity (Lepczyk *et al.*, 2017; Threlfall *et al.*, 2017). If forest cover is cumulatively <20% of the landscape, the habitat is considering to be detrimentally fragmented for the survival of species, and to ensure native flora and fauna species do not cross the extinction threshold, >10% of the land area must be protected (Rybicki & Hanski, 2013). The urban landscape typically contains highly fragmented forest areas which can be connected using corridors to form metapopulations (Rybicki & Hanski, 2013). Metapopulations allow plant and animal dispersal so urban forests can naturally regenerate. To maximise benefits from forest restoration efforts, the goal should be to recreate a self-sufficient environment to as great an extent as possible (Hobbs & Norton, 1996; Society for Ecological Restoration, 2004).

Ecological succession is the process of ecosystem development following a disturbance, typically beginning as the presence of early-successional (i.e., pioneer) plant species facilitate changes in their immediate environment to make way for mid and late-successional species (Connell & Slatyer, 1977; Bazzaz, 1979). Under evolutionary selection theory, late-successional species are *K*-strategists (long-lived, slow-growing, only somewhat resilient to abiotic and biotic pressures). This is opposed to *r*-strategist species (short-lived, high reproduction with many offspring, smaller in size, very resilient to abiotic and biotic pressures) which are generally considered early-successional species (Smith & Smith, 2015). Early-successional forests typically start comprised mostly of early-successional species, terrestrial in nature, together growing rapidly and creating a new microclimate beneath their canopies which creates conditions conducive to the establishment of mid-successional flora and fauna (Fig. 1.1) (Connell & Slatyer, 1977; Bazzaz, 1979; Smith & Smith, 2015). Mid-successional forests develop further to facilitate the establishment of late-successional species (Fig. 1.1). Late-successional forest plant species may be ground-dwelling, epiphytic, or parasitic, but all preferentially establish and grow in more mature forests. This is because late-successional species typically are *K*-strategists and have more specialised ecological niches due partially to environmental constraints (Forbes *et al.*, 2020).

Figure 1.1: Ecological forest succession through time, from early, through mid, to a late-succession forest. The *r*-strategist plant species present during early-succession ameliorate conditions to be suitable for the mid-successional plant species to establish and grow, and eventually the *K*-strategist plant species which are long-lived late-successional plant species. Achieving the late-successional stage is vital to promote forest stability and provide maximum biodiversity support and ecosystem services.

Forests undergoing restoration should shift predictably across different abiotic and biotic thresholds as forest development proceeds and succession occurs (Wallace *et al.*, 2017). One of these thresholds is found during the reduction in light availability due to canopy closure. As forests age the trees' collective basal area increases and canopy openness decreases (Fig. 1.2) (Reaburn, 2014; Suganuma & Durigan, 2015; Wallace *et al.*, 2017). Photosynthetic flexibility is typically lower for late-successional species; therefore, the environmental conditions under which these species can survive are narrower than those required by early-successional species, creating a biotic threshold for late-successional species to be present (Bazzaz & Carlson, 1982). Canopy closure seems a key forest development threshold, as it triggers changes in a number of other forest ecosystem properties, such as causing a reduction in the early-successional non-native herbaceous weed cover (Fig. 1.2) (Wallace *et al.*, 2017). Canopy formation also provides a buffer to the regional macroclimate conditions, creating an understorey microclimate which has dampened daily swings in humidity and temperature (Valladares *et al.*, 2016; Wallace *et al.*, 2017). As the canopy openness, microclimate fluctuations, and herbaceous weed cover decrease, the native tree seedling regeneration and epiphyte density can increase (Shoo *et al.*, 2016; Wallace *et al.*, 2017). This threshold in canopy cover creates a critical threshold in forest development dynamics more generally (Fig. 1.2). These critical threshold responses are essential to understand because they signal when late-successional plants can be introduced into the forest with the best chance of survival (saving both money and time). With higher survival rates, restoration practitioners will reduce costs of replacing dead individuals, and save time because the late-successional plants will be introduced at the earliest practicable chance, accelerating the forest's succession towards a self-perpetuating urban forest and reducing weed management.

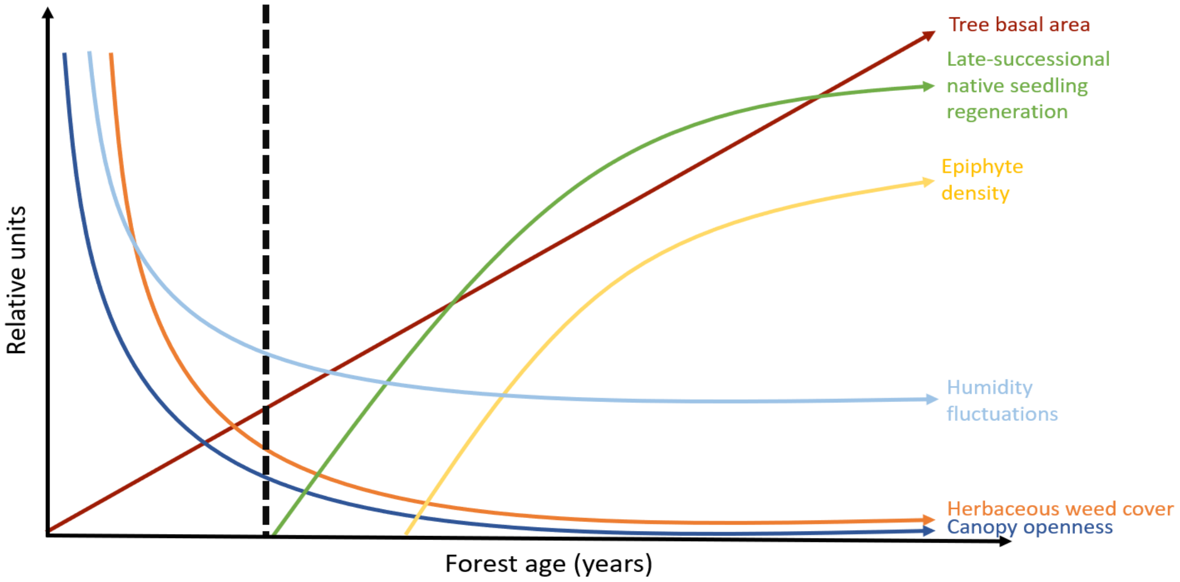


Figure 1.2: Trajectories in the recovery of forest ecosystem properties' during canopy development after initial restoration plantings. There is a critical threshold where a series of significant events co-occur (dashed black line). First, tree basal area increases, then the canopy openness, herbaceous weed cover and humidity fluctuations all decrease, facilitating suitable conditions for late-successional native seedling regeneration and increases in the epiphyte density (adapted from Wallace *et al*., 2017).

Ecological theory such as succession theory is vital for understanding the applied science of restoration ecology to understand how to manage forests to mimic natural dynamics (Palmer *et al.*, 1997). Accelerating succession with active ecological restoration within an urban forest means the forest can reach a late-successional, more stable status sooner (Palmer *et al.*, 1997). Measurements of successful restoration can be the establishment of mature-phase late-successional plants (Suganuma & Durigan, 2015) and epiphytes (Bryan, 2011; Oishi & Doei, 2015; Wallace *et al.*, 2017; Forbes *et al.*, 2020).

Late-successional plant species fall into a variety of different guilds, regardless of their taxonomic group (Simberloff & Dayan, 1991). These species may be within the same functional guild, yet have different ecological niches (Wilson, 1999). Ecological niches are the environmental conditions, spatial positions and resources (nutrients, food, water, etc.) that a species requires to survive (Smith & Smith, 2015). The requirements of each late-successional species, as well as biotic competition and related forces, will therefore create differentiation of different realised ecological niches and location within forest structure: an epiphyte in the canopy, a shrub in the understorey, or a seedling on the forest floor destined to grow into a canopy tree. Part of how species from different guilds define their niche occurs through competition and is termed resource partitioning (Poorter *et al.*, 2012). This may broadly occur between species in a community (interspecific), or partitioning may occur between individuals of the same species (intraspecific). The energy within an ecosystem is also manipulated within individual organisms themselves. The 'resource-ratio hypothesis' explores the concept of biomass allocation, how different species will divide their growth differently depending on the most limiting resource (Tilman, 1985; Domisch *et al.*, 2002; Poorter *et al.*, 2012; Smith & Smith, 2015). Depending on the competition for light, space, nutrients and water, the growth of the plant will show different amounts of biomass allocation to plant height, stem diameter, root growth and leaf size and abundance (Tilman, 1985; Poorter *et al.*, 2012). The biomass allocations between early, mid and late-successional plant species vary due to how the sunlight is intercepted, as late-successional species have longer-lived leaves that require more biomass allocation (higher leaf mass ratios) than early-successional species (Galia Selaya *et al.*, 2008). As a result of these interplaying forces, late-successional forests are typically complex and have a more extensive range of habitat niches than early-successional forests as species diversity and species richness increase (Smith & Smith, 2015), and an increased variety of ages and sizes between organisms (Bazzaz, 1979).

Late-successional plant species are essential to include in forest restoration management because they increase ecosystem biodiversity, stability (Ducey *et al.*, 2013) and create a wide range of habitats for other species (Lindenmayer, 2017). They also provide long-term carbon sequestration, lowering the effects of climate change (Luyssaert *et al.*, 2008; Gao *et al.*, 2011). Ecological restoration best practice suggests that active introduction of *K*-strategist, late-successional plant species is needed to help the forest ecosystem develop well long-term (Forbes *et al.*, 2020), especially in cities due to the high level of disturbance and fragmentation.

As disturbances are more likely in urban forests, we need an urban perspective on ecological succession in these forests (Johnson & Handel, 2016). Research in Auckland found there is sometimes no sign of natural succession occurring in restored urban forests at all (Pothercary, 2012). This is unfortunate, as forest succession is essential to complete restoration projects, but can be facilitated by managed interventions such as enrichment planting. In cities, succession often does not happen spontaneously, so we must conduct enrichment plantings in the urban areas we are restoring (Overdyck & Clarkson, 2012; Piana *et al.*, 2019).

Enrichment planting is the addition or re-introduction of absent late-successional species to an ecosystem (Karam *et al.*, 2012; Forbes *et al.*, 2020). Enrichment species must be carefully selected and planted under appropriate conditions so they will survive to offer ecosystem services and ecological benefits like food for native fauna. Re-introduction of late-successional species to an ecosystem facilitates or speeds up the process of establishment, as the early-successional plants have already gone through their natural thinning (Labatore, 2017) and conditions have become suitable for sensitive early germination and seedling phases of the next generation of forest plants in the understorey. Sometimes enrichment planting may be the sole way late-successional species are re-introduced into urban forests because it is difficult for late-successional tree species to arrive (Overdyck & Clarkson, 2012) and germinate in restored urban forests naturally (Busbridge, 2020).

There are several reasons why late-successional native Aotearoa New Zealand forest species fail to spontaneously re-establish in city forests. For one, seeds often persist for only a few years in the seed bank, additionally, forest fragmentation creates islands of forest too far apart for the majority of seed rain to traverse between (Clarkson *et al.*, 2007; Overdyck & Clarkson, 2012). Even if seeds can arrive, germination location can make a difference in survival. For example, an investigation in a lowland forest context between the differences in spontaneous germination and active planting of late-successional tree species showed better survival for planted *Dacrydium cupressinum* trees (James, 1998). Seedlings which germinated naturally had a 28% rate of survival and grew at 4 cm per year, compared to an 85% survival rate of manually planted seedlings, growing at 16 cm per year (James, 1998). James' (1998) method of using planting versus natural seedling germination illustrates that when the environmental conditions are carefully selected to suit species' tolerances, enrichment plants will thrive. Furthermore, the growth stage of enrichment plants (seedling, sapling, adult) influences the sensitivity to environmental conditions (Busbridge, 2020).

The size of the enrichment plants being introduced into a forest can determine establishment and growth success (Smale & Kimberley, 1986; Kunstler *et al.*, 2009; Busbridge, 2020). At different stages of growth, late-successional species have different light requirements and tolerances (Kunstler *et al.*, 2009; Busbridge, 2020). This is influenced by the forest patch size, which determines if the centre of the forest is affected by the edge effects, such as different light levels (Murcia, 1995; Chacón & Armesto, 2005; Busbridge, 2020). As urban forests are often small and fragmented, edge effects can infiltrate through the entire forest patch (Piana *et al.*, 2019). Mid to late-successional seedlings being introduced into restored urban forests are sensitive to edge effects, but appear to become more tolerant in their sapling phase (Niinemets, 2010; Busbridge, 2020), and were able to establish and grow where seedlings could not. This is apparent when observing larger forest patch sizes as they have different interior microclimate conditions and a greater abundance of mid to late-successional species' seedlings (Busbridge, 2020).

In Aotearoa New Zealand, the increased edge to size ratio typical of small forest patches also increases the risk of seed predation and plant browse by introduced mammals that native plants did not co-evolve alongside (Dodd *et al.*, 2011). For example, introduced invasive mammalian species in Aotearoa New Zealand browse significantly more at the edge of forests than the interior (Bach & Kelly, 2004). Without co-evolution, native flora lack defence mechanisms, resulting in introduced mammals being detrimental to the native forest as they feed heavily on the seeds and plant buds (Dodd *et al.*, 2011). Introduced mammalian species are also present in cities, although, across different cities the invasive species' abundance and presence vary (N. Fitzgerald, personal communication, November 21, 2019). Introduced mammalian species may present additional difficulties for the natural establishment of sensitive late-successional species' seedlings in small urban forests consisting of mostly edge habitat (N. Fitzgerald, personal communication, November 21, 2019).

Within urban contexts, forest restoration science and practice rarely include late-successional species, especially specialist guilds such as epiphytes (other noted underrepresented non-tree guilds include ground ferns and climbers) (Reaburn, 2014; Spicer *et al.*, 2020). Epiphytes grow on other plants, making them innately late-successional, and each epiphyte species varies in required growing sites and environmental constraints (Zotz & Hietz, 2001). Epiphytes appear last in forest development, e.g., a study in restored tropical rainforests found that epiphyte richness and density did not reach an equivalent amount to that of undisturbed reference forests even 85 years after a disturbance (Martin *et al.*, 2013). To maximise successful establishment while introducing epiphytes and other specialist guild late-successional plants, we need to better understand their niches and interactions with their ecosystems.

1.3 Research background

This research focuses on improving understanding of the best conditions for enrichment planting of juvenile late-successional plant species in urban forests undergoing restoration from scratch (i.e., no original vegetation present when restoration began). The experimental design uses plots in each of 27 urban forest patches occurring in a planted chronosequence from 5–47 years since being planted from scratch. The chronosequence method of observing ecosystem successional change allows for space to be substituted for time, to compare forests at differing stages of growth (Walker *et al.*, 2010; Piana *et al.*, 2019). The design allows for a quantitative approach to pinpointing what niche requirements, like physiological tolerances and priority resource needs (e.g., microclimate conditions and stages of forest development), are most important for late-successional enrichment species from different guilds. The chronosequence approach also allows for the identification of thresholds in forest development that indicate when these optimal conditions for late-successional species introduction occur.

Three model late-successional species from different guilds were chosen for experimental planting into the urban forest restoration plots: the epiphyte *Griselinia lucida* (J. R. Forst. & G. Forst.) (akapuka), the understorey shrub *Piper excelsum* subspecies *excelsum* (G. Forst.) (kawakawa) and the long-lived canopy tree *Dacrydium cupressinum* (Sol. Ex G. Forst.) (rimu). Experimental *G. lucida* individuals were germinated in May 2016, and *P. excelsum* and *D. cupressinum* individuals were germinated in May 2017. Experimental individuals for all three species were planted into the established research plots in June 2018, thus, they were one and two-year-old seedlings at planting. By introducing these species into forests at different stages of forest development along the planting chronosequence, we can better understand how the stage of forest development determines the environmental constraints on the establishment of enrichment plantings of various guilds.

<u>*Model late-successional enrichment species background*</u>

Griselinia lucida

Griselinia lucida (Griseliniaceae) is a late-successional evergreen shrub, most commonly occurring as an epiphyte (Fig. 1.3A) (Bryan *et al.*, 2011). It is primarily found growing in the crown of host trees, extending roots to the ground if nutrient or water availability is scarce (Fig. 1.3A) (Bryan *et al.*, 2011). The species is endemic to Aotearoa New Zealand and is distributed mainly on the west coast of both the North and South Islands, and can be found inland on the North Island, likely due to the warmer temperatures (Bryan *et al.*, 2011). Natural dispersal is reliant on birds as the flesh of the fruit needs to be removed via digestion by birds to trigger seed germination physiologically. Additionally, seeds are then deposited in the bird's faeces in appropriate new germination locations on host trees (Burns & Dawson, 2005; Bryan *et al.*, 2011).

Griselinia lucida is an excellent example of how plants respond to resource limitations by investing energy for different functions, trading-off between growth, reproduction and defence (Grime, 1977). Epiphytes generally invest more energy into smaller, coriaceous, long-lived foliage, compared to terrestrial species, in order to combat water deficits and still grow efficiently (Bader *et al.*, 2009; Zotz, 2016). As a result, *G. lucida* is surprisingly resistant to drought, being an epiphyte with roots that are somewhat exposed in minimal arboreal detritus (Ogden, 1976). When comparing congeners in different guilds: *G. lucida* is adapted to be epiphytic, while *G. littoralis* is a terrestrially bound shrub. When under drought conditions, the epiphytic *G. lucida* invests energy into leaf elasticity, rendering it capable of postponing desiccation under drought conditions and slowing growth rates (Bryan, 2011). Conversely, the terrestrial *G. littoralis* is not able to reach the low levels of water potential *G. lucida* attains and is slower to recover (Bryan, 2011). For *G. lucida* to live in the canopy and capitalise on the greater light availability there, energy capture is traded-off for investment in drought stress strategies to withstand fluctuations in the water supply.

Generally, epiphytes (including *G. lucida*) require a fairly well developed forest canopy and relatively high, stable humidity levels to establish and thrive (Bryan, 2011). The urban forest edge effects sometimes cause a lack of microclimate stability that epiphytes often require. Additionally, epiphytes (including *G. lucida*, Bryan *et al.*, 2011) thrive on larger host tree individuals (Burns & Dawson, 2005; Hirata *et al.*, 2008; Woods & DeWalt, 2013), requiring forests to be of a certain age to provide both the right-sized trees and stable microclimate conditions. Measurements across the natural distribution of *G. lucida* indicate it requires mean annual temperatures between 14-16°C, the mean solar radiation of 13 MJ/day/m^2, a rainfall to evapotranspiration ratio of 3.9-4.5 and mean vapour pressure deficits of <0.5 kPa (Bryan *et al.*, 2011).

Griselinia lucida was chosen for this study because it is seemingly resilient to fairly harsh conditions like drought and desiccation, which are present in younger forests and city forests. It is also an ecologically important species in its provision of habitat and role in mediating canopy microclimate (Stanton *et al.*, 2014). Study sites for this thesis are all situated where *G. lucida* would have once been distributed, thus, where the forests provide for its niche requirements. However, *G. lucida* has not often been re-introduced into restored urban forests via enrichment planting (e.g., Bryan's, 2011 thesis reported finding Hamilton had no *G. lucida* in restored urban sites (n = 20) and New Plymouth had 13 individuals total in restored urban sites (n = 3); Bryan *et al.*, 2011). Re-introducing *G. lucida* as an epiphyte into urban forests is important for increasing biodiversity as it provides resources for native fauna and contributes to abiotic processes such as water and nutrient cycling (Bryan *et al.*, 2011).

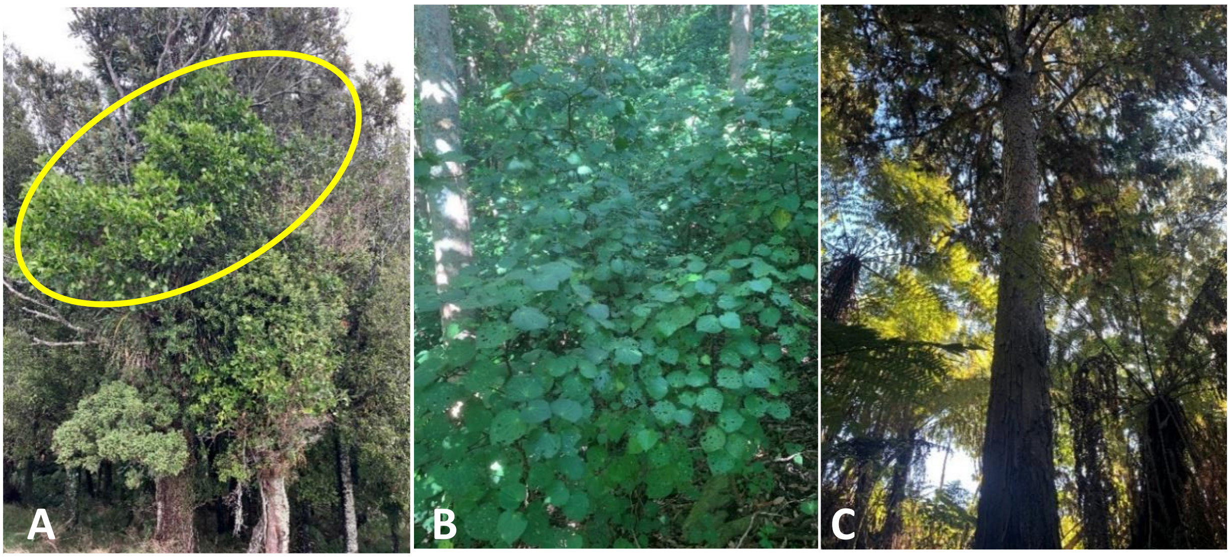


Figure 1.3: A) A sun-exposed adult *Griselinia lucida* shrub specimen perched in a large host tree, highlighted by the yellow outline, B) a mostly-shaded understorey *Piper excelsum* shrub, and C) an adult *Dacrydium cupressinum* canopy tree with an understorey of tree ferns.

Piper excelsum subspecies excelsum

Piper excelsum (Piperaceae) is a late-successional evergreen understorey terrestrial shrub (Fig. 1.3B) (de Lange, 2019). Endemic to Aotearoa New Zealand, it grows in coastal to lowland forests across the entire North Island and about half-way down the South Island to Ōkārito and Banks Peninsula (de Lange, 2019). *Piper excelsum* is frost tender (Mohi, 2001; de Lange, 2019). Species from the diverse genus *Piper* include pantropical understorey shrubs that are similar to *P. excelsum*, as well as other functional guilds like herbs and lianas (Jaramillo & Manos, 2001). Most *Piper* species, including the closely related *P. methysticum* (Jaramillo & Manos, 2001), grow in warm, humid conditions at low elevations (Dyer & Palmer, 2004), suggesting the genus is sensitive to frost and requires protection from the canopy.

Birds and lizards eat the fruits of *P. excelsum*, and birds disperse the *P. excelsum* seeds through their excrement (Te Motu Kairangi, n.d.). This illustrates one of the roles of *P. excelsum* in the environment, as a food resource for native fauna, but it is also important for humans. *Piper excelsum* has immense cultural significance and represents a widely recognized Rongoā Māori plant (traditional herbal medicine used for holistic healing), with an array of medicinal uses due to the natural bioactive compounds in the leaves (Russell & Fenemore, 1973; Ahuriri-Driscoll, 2014).

Piper excelsum was chosen for this study because it is a common and ecologically important understorey component in many native Aotearoa New Zealand forests and is also known to be sensitive to microclimate conditions. Little is known about which microclimate conditions affect *P. excelsum* the most, and therefore, when in the course of forest development, it can be most effectively introduced through enrichment planting. The distribution of *P. excelsum* is widespread across Aotearoa New Zealand, including the areas where the research sites for this thesis are located. *Piper excelsum* is seldom included in planting plans for forest restoration, depending on the planned length of restoration work in a project, as it has poor survival if planted during the initial planting stages in exposed circumstances. However, it is still essential to include in ecological restoration plantings due to both its ecological and cultural significance. If included in urban forest restoration, it could provide a resource for people practising Ronogā Maori in local urban communities. *Piper excelsum* could also provide a dense understorey shade cover which aids in suppressing the herbaceous weeds, thus encouraging regeneration of other late-successional species which are shade-tolerant.

Dacrydium cupressinum

Dacrydium cupressinum (Podocarpaceae) is a late-successional long-lived evergreen Podocarp tree (Fig. 1.3C) (Norton *et al.*, 1988). The drooping branches are often visible as an emergent canopy tree within coastal to lowland forests across all of Aotearoa New Zealand (Fig. 1.3C) (Norton *et al.*, 1988). The optimum temperature for *D. cupressinum* net photosynthesis is 27°C (Hawkins & Sweet, 1989). The optimal temperature is relatively high (for Aotearoa New Zealand plant species) but is thought to be an evolutionary selection pressure maintained from when Aotearoa New Zealand had tropical climatic conditions from the Miocene, ~23 million years ago (Hawkins & Sweet, 1989). However, the mean annual temperature in the natural distribution in *D. cupressinum* is much lower now, at 12.4°C (Leathwick, 1995), indeed *D. cupressinum* is capable of surviving intense ground frosts of temperatures below 0°C (Leathwick & Mitchell, 1992). Within the current natural distribution of *D. cupressinum,* the solar radiation is typically about 8.7 MJ/day/M^2, and the rainfall to evapotranspiration ratio is around 5.1 (Leathwick, 1995).

Birds disperse seeds of *D. cupressinum* and by eating the fruit they will remove the fleshy receptacle from the exterior, making germination possible (Norton *et al.*, 1988). In fact, *D. cupressinum* plays an integral part in the breeding lifecycle of the critically endangered endemic kākāpō (*Strigops habroptilus*) bird (Cottam *et al.*, 2006). Every few years *D. cupressinum* populations have mast fruiting seasons, producing a massive amount of fruit concurrently. The *D. cupressinum* mast season drives the kākāpō breeding season success because the chicks are nearly exclusively fed on *D. cupressinum* fruit (Cottam *et al.*, 2006).

Dacrydium cupressinum was chosen for this study because it is a late-successional tree that, once mature, is a true hallmark of an established forest. As an adult, it can tolerate full sunlight conditions but grows best under partial shade (Norton *et al.*, 1988). This thesis investigates its sensitivity to microclimatic conditions within planted, developing forests. In naturally occurring forests within its range, *D. cupressinum* is a dominant tree found to have a wide variety of associations with other organisms and, as a canopy or emergent tree, influences the abiotic conditions within the forest (Norton *et al.*, 1988). Furthermore, it provides food to native fauna and habitat to perching plants, such as epiphytes (Burns & Dawson, 2005; Cottam *et al.*, 2006). As a large tree of the forest, it impacts the abiotic processes within forests by acting as a wind barrier and providing shade (Norton *et al.*, 1988).

Research city backgrounds

This research was a part of the larger People, Cities & Nature research programme, funded by a New Zealand Ministry of Business, Innovation and Employment grant (MBIE UOWX1601). The research plots used were part of a pre-established urban forest plot network from that programme.

Research was conducted in planted native forests undergoing restoration in three North Island cities in Aotearoa New Zealand; Hamilton (Waikato region), New Plymouth (Taranaki region), and Napier (Hawke's Bay region).

Before human settlement, the native temperate rainforest in Aotearoa New Zealand covered 75% of the land, but after clearing for agriculture and urbanisation, it is now reduced to approximately 23% cover (Nicholls, 1980; Star, 2002). Early Polynesian settlers (circa 1300) began to alter Aotearoa New Zealand's flora and fauna through hunting and gathering food, as well as through the introduction of predatory mammals – kurī (extinct Polynesian dog, *Canis lupus familiaris*) and kiore (Polynesian rat, *Rattus exulans*) (Bradford, 2008; Keane, 2008). The first permanent European settlers arrived in Aotearoa New Zealand (circa 1825), bringing 55 mammal species between then and the present day, 32 of which have become established (Courchamp *et al.*, 2003). Along with these introduced species, European settlers caused large-scale landscape change through logging, burning, mining and urbanisation.

Hamilton

Hamilton is also known as Kirikiriroa ('long stretch of gravel'), as Māori first called it from the Tainui waka (canoe) when arriving approximately 700-800 years ago. Hamilton is situated inland on the Waikato River and historically was a hotspot for local Māori tribes to live due to the productive soils and the ease of transport along the flat terrain and the river. The European colonisers later named it Hamilton in 1864, and this followed with the destruction of the temperate rainforests and wetlands characteristic to the area for agriculture. Hamilton was ideal for urbanisation as the urban centre has a mild temperate climate with moderate rainfall. The wetlands were drained to make the land more suitable for urbanisation, causing declines in local biodiversity (Swarbrick, 2015). By 2015, Hamilton became the second-fastest-growing population centre in Aotearoa New Zealand after the largest city, Auckland, with a large student population of ~40,000 students attending the city's tertiary institutions (Swarbrick, 2015).

Today Hamilton retains only 2.1% (11,000 ha) native vegetation (Clarkson *et al.*, 2007), the lowest percentage cover for any Aotearoa New Zealand city. This is largely a consequence of the gentle terrain and productive soils, which encouraged the wide-scale clearing for agriculture and now conversion to urban and suburban areas. The temperatures in Hamilton are mild, and the rainfall is relatively consistent (Fig. 1.4A). Main landforms include low rolling hills, alluvial plains, gullies and peatlands. Hamilton has four natural lakes, all peat lakes that formed after drainage activities, and more than 750 ha of branching gullies (7% of the land cover), which drain to the Waikato River running through the centre of the city (Cornes *et al.*, 2012). Some noteworthy restoration work has already occurred in Hamilton, namely The Gully Restoration Programme (began in 2000) to encourage gully restoration on private and public land (Clarkson & McQueen, 2004). Additionally, in 2004, 60 ha of public land was dedicated to the restoration of native habitat and named Waiwhakareke Natural Heritage Park (Wallace & Clarkson, 2019).

New Plymouth

New Plymouth, or Ngāmotu ('the islands') as it was called by the arrival of the Māori waka named Aotea in the 15th century (Wells, 1878), is situated on the west coast of the North Island, at the base of Mount Taranaki. The expanse New Plymouth now exists on was the site of numerous Māori villages (pā) over hundreds of years because the land was a fertile temperate rain forest, and the terrain was gentle (Lambert, 2016). The area was colonised by Europeans around 1842 and named 'New Plymouth'. After that, from the mid to late 1800s, followed many major land wars between local Māori and the European colonists. A lot of the native forest was burned and cleared during the wars to make way for rail (Lambert, 2016). Through the 1900s and until the current day, the economy of New Plymouth is fuelled by agriculture and petroleum and gas mining (Lambert, 2016).

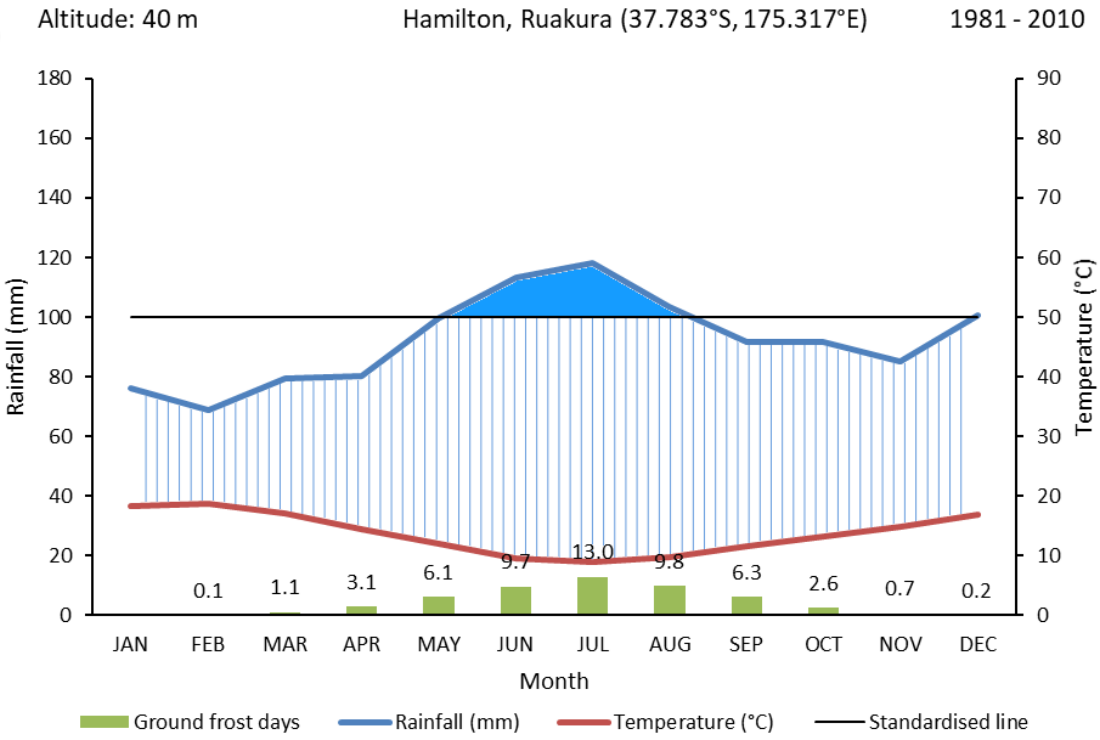
Today, New Plymouth has 8.5% native vegetation cover, which is the highest percentage native land cover of any Aotearoa New Zealand city, and is a consequence of initial reserve plans as urbanisation began (Clarkson *et al.*, 2007). The temperatures in New Plymouth are mild, and rainfall is high, fluctuating throughout the year with relatively long periods of excess water availability (Fig. 1.4B). Main landforms include rolling hills and gullies, and there are many original bush remnants of high-quality that had been protected which are now part of the built-up city matrix. Early town planning for New Plymouth allowed for a town belt (an area surrounding the city to remain vegetated). Unfortunately, this land was re-allocated for agriculture. Nevertheless, the Taranaki Scenery Preservation Society (established in 1891), was active through to the mid-1900s and was responsible for the protection of many significant bush areas (Cyclopedia Company Limited, 1908). As the city grew, these important reserves were incorporated into the developed city matrix (Clarkson et al., 2007b). Fostered by horticulturalists Victor Davies and James Duncan, a world-renowned plant supplier, the enthusiasm for native vegetation planting from citizens in New Plymouth from 1910 continues to the present day (Fryer, 1998).

Napier

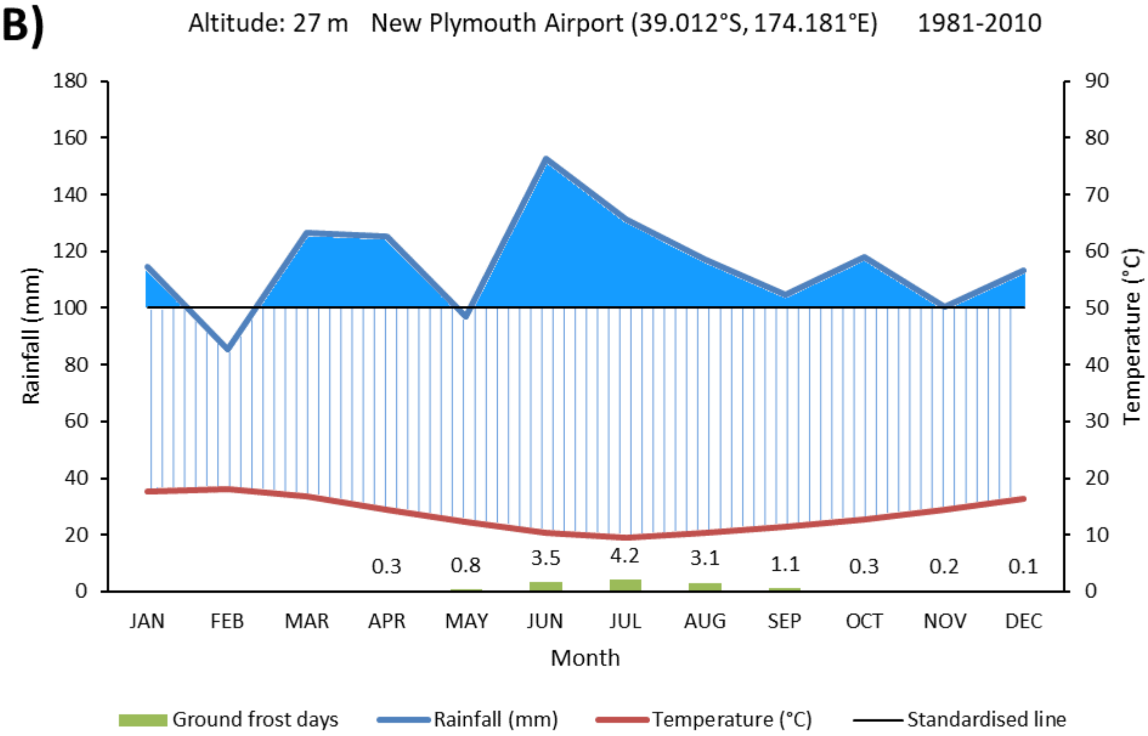
Napier is also known as Ahuriri ('fierce waters'), as local Māori first called it after a chief had cut a channel into the lagoon because the entrance was blocked (Pollock, 2015). It is located on the east coast of the North Island, which is typically much drier than the west coast where New Plymouth is. Māori sustainably cultivated Ahuriri before European colonisation until the city of Napier was founded in that area in 1855. Thereafter, landscape modification and cultivation exponentially increased (Pollock, 2015). Napier was one of Aotearoa New Zealand's first ports due to the development in the region (Pollock, 2015). Extensive native forests were removed to exploit flat terrain for agriculture, horticulture and viticulture, alongside the urbanisation (Hashiba *et al.*, 2014). The urbanised areas were drained, and non-native invasive plants and animals have been major causes of the decline in native biodiversity (Hashiba *et al.*, 2014).

Today, Napier has 5.1% native vegetation, mostly comprised of wetland and nearly none of it within the central urban zone (Clarkson *et al.*, 2007). The temperatures are mild to warm, and the rainfall is low throughout the year, peaking in July (Fig. 1.4C). Main landforms include lowland hill country, coastal and alluvial plains (Hashiba *et al.*, 2014). Some alluvial plain areas were raised as much as 2.4 m above sea level after a major earthquake in 1931 (Pollock, 2015). Much of Napier has had little conservation focus, other than within several patches of remnant bush further afield in the Hawke's Bay region (Hawke's Bay Regional Council, n.d.). Recently, local restoration groups in and around Napier have begun estuary and coastal restoration including Cape Sanctuary just north of Napier in 2006 (with the installation of predator-proof fencing) (Hashiba *et al.*, 2014). Additionally, Dolbel Reserve began forest restoration in 1991 with 18 ha of lowland hill area in Napier (mostly native forests, with some exotic plantings) (Rotary Club of Taradale, n.d.). Also, the Ahuriri Estuary Restoration Group began restoring 40 ha of the estuary in Napier, in 2003 (Hashiba *et al.*, 2014; Hawke's Bay Regional Council, n.d.).

A)


Altitude: 40 m
Hamilton, Ruakura (37.783°S, 175.317°E)
1981 - 2010
Rainfall (mm)
180
160
140
120
100
80
60
40
20
0
Temperature (°C)
90
80
70
60
50
40
30
20
10
0
0.1
1.1
3.1
6.1
9.7
13.0
9.8
6.3
2.6
0.7
0.2
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
Month
Ground frost days
Rainfall (mm)
Temperature (°C)
Standardised line

B)


Altitude: 27 m
New Plymouth Airport (39.012°S, 174.181°E)
1981-2010
Rainfall (mm)
180
160
140
120
100
80
60
40
20
0
Temperature (°C)
90
80
70
60
50
40
30
20
10
0
0.3
0.8
3.5
4.2
3.1
1.1
0.3
0.2
0.1
JAN
FEB
MAR
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Month
Ground frost days
Rainfall (mm)
Temperature (°C)
Standardised line

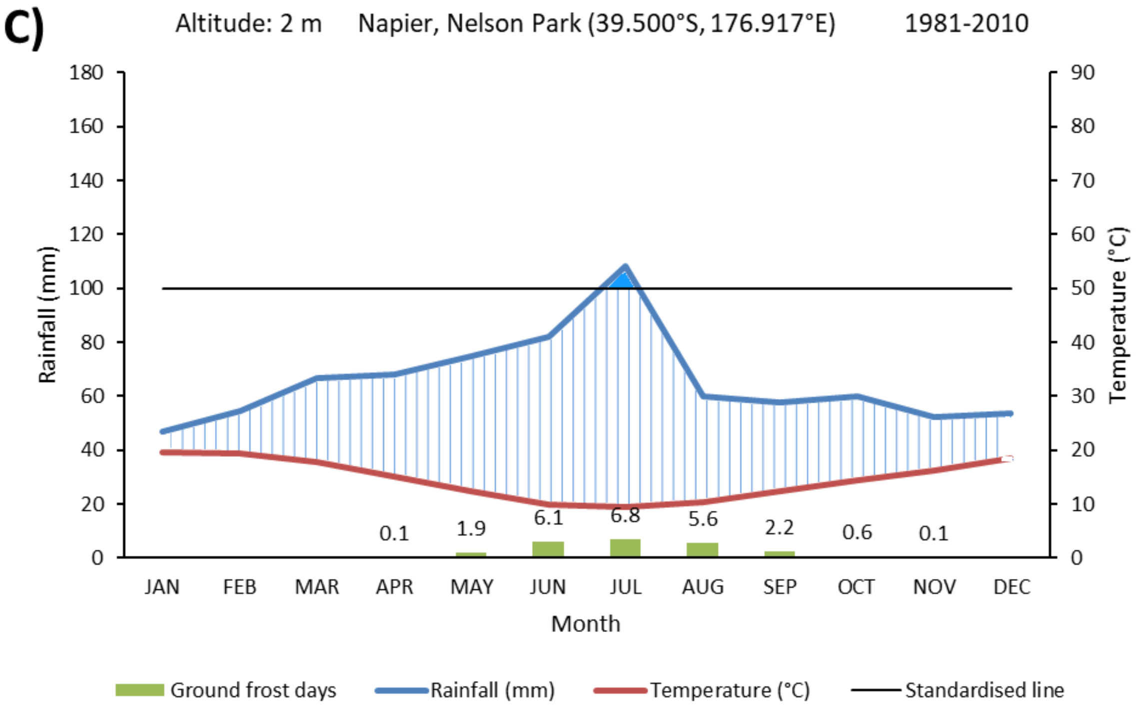


Figure 1.4: Climate diagrams (adapted from Walter and Leith (1967)) for Hamilton, New Plymouth and Napier, including the average monthly rainfall (mm) (blue line), average monthly air temperature (°C) (red line) and the monthly average number of ground frost days (days with a recording of 0°C at ground level) (green bars) using data from 1981-2010. To indicate the wet season blue vertical lines are drawn, with the months of rainfall >100 mm indicated with solid blue. A) Hamilton's mean annual temperature is 14.6°C (minimum: 8.9°C in July, maximum: 18.8°C in February), the mean annual precipitation is 1108.2 mm (minimum: 68.7 mm in February, maximum: 118.2 mm in July), and there are on average 52.8 ground frost days (minimum: 0.0 in January, maximum: 13.0 in July, 11 months with frost), B) New Plymouth's mean annual temperature is 13.7°C (minimum: 9.5°C in July, maximum: 18.0°C in February), the mean annual precipitation is 1385.9 mm (minimum: 85.4 mm in February, maximum: 152.6 mm in July), and there are on average 13.5 ground frost days (minimum: 0.0 in January February and March, maximum: 4.2 in July, 9 months with frost), C) Napier's mean annual temperature is 14.6°C (minimum: 9.4°C in July, maximum: 19.5°C in January), the mean annual precipitation is 784.8 mm (minimum: 46.8 mm in January, maximum: 108.3 mm in July), and on average there are 25.7 ground frost days (minimum: 0.0 in January February, March and December, maximum: 6.8 in July, 8 months with frost) (data from NIWA, 2020). The climatic conditions in New Plymouth of moderate temperatures, high rainfall and few frost days could be preferred by two of the model species seedlings, as the epiphytic *Griselinia lucida* requires available water as its roots are not yet terrestrial, the understorey shrub, *Piper excelsum*, is frost tender and prefers moist soil, and *Dacrydium cupressinum* could prefer the climatic conditions in Napier, as the temperatures are higher. The climate in New Plymouth has a wet season all-year-round, where Napier has little excess water availability, especially in the summer months. Hamilton has a relatively moderate climate and wet season compared to New Plymouth and Napier.

1.4 Research questions and objectives

Specifically, research questions in this thesis are: 1) How does growth of three late-successional plant species (*G. lucida, P. excelsum* and *D. cupressinum)* from different guilds (epiphyte, understorey shrub and canopy tree) respond to differing degrees of restored urban forest canopy development, 2) What are the main forest understorey conditions limiting survival and growth of these three late-successional plant species during the juvenile growth stage and 3) at what points during forest development are there detectable thresholds that can determine optimal conditions for successful late-successional species establishment?

Regarding question one, I hypothesised that the three late-successional species from different guilds would likely react differently to forest canopy development even though they are all late-successional plant species that would typically occur in mature forests with closed canopies. For example, *G. lucida* grows best where it is exposed to patches of relatively open canopy because it requires high light conditions. However, young *P. excelsum* and *D. cupressinum* grow best under relatively closed, developed canopies because they can tolerate low light conditions and prefer the buffering of climatic extremes that occurs there. Therefore, an objective of this thesis research is to measure forest canopy openness across a planted forest chronosequence and analyse growth responses of the three late-successional species.

Regarding question two, it is likely the growth rates of the enrichment plant species respond to greater air temperature fluctuations and higher relative humidity. For example, *G. lucida* will prefer being attached to the trunks of smaller host trees in newly planted forests, as they typically provide a more open canopy, and hence more access to light though with little protection from fluctuations in air temperature and humidity. This is because smaller trees and their associated canopy openness will mimic the higher points of the canopy in a mature forest where *G. lucida* would typically occur. *Piper excelsum* and *D. cupressinum* should grow best when the air temperatures are warmer, and perhaps more stable. It is also likely that these two terrestrial plants, *P. excelsum* and *D. cupressinum* will display more growth under closed canopies because the lower light levels cause senescence of non-native herbaceous weeds, which are often strong competitors with young native plants. Therefore, an objective of this thesis research is to identify the microclimatic conditions that affect the growth of the three model enrichment plant species the most, and measure non-native weed cover.

Regarding question three, it is likely there are critical abiotic thresholds such as where light levels reaching the forest floor drop sharply, or the understorey microclimatic conditions suddenly fluctuate less at a point in forest canopy development. Based on other research (Wallace *et al.*, 2017), it is possible there is a threshold around ten years since initial forest restoration plantings are conducted where canopy closure crosses a critical threshold causing the microclimatic conditions to stabilise and therefore become more amenable for sensitive juvenile late-successional plant species.

The results of this research provide management recommendations regarding the planning stages of enrichment planting for urban forest restoration projects in Aotearoa New Zealand and globally. The purpose is to hasten native tree establishment in the early stages of forest development to build a self-perpetuating forest in the long term.

1.5 Thesis overview

The remainder of the thesis is comprised of three chapters which focus on answering the research questions posed above:

- Chapter 2: describes the study sites and their forest composition, data collection methods, plot set up and installation of the experimental species. This is followed by data preparation methodology and the justification of the different statistical methods employed.
- Chapter 3: systematically describes the results obtained from the analyses for the urban forest research sites, also the three model enrichment plant species and in relation to key environmental parameters.
- Chapter 4: interprets and discusses the results within a broader context of urban forest restoration, with regard to the ecology of each of the model enrichment species. It provides some implications and future research ideas for how the practice ecological restoration may include these findings to improve best practice and a summary of the entire thesis.

The research, data analysis and writing were all my own and were conducted under the supervision of Dr Kiri Joy Wallace and Professor Bruce D. Clarkson from the University of Waikato.

CHAPTER 2

Methods

2.1 Study sites

Research was conducted on the North Island of Aotearoa New Zealand. Data were collected from 27 restored urban forest patches in three cities (nine sites in each city) (Fig. 2.1; Appendix Table A.1). Hamilton (37.7870° S, 175.2793° E; population ~166,000) has 2.1% native vegetation cover within 5 km of the city centre, New Plymouth (39.0556° S, 174.0752° E; population ~74,000) has 8.5% native vegetation cover within 5 km of the city centre, and Napier (39.4928° S, 176.9120° E; population ~63,000) has 5.1% native vegetation cover within 5 km of the city centre (Clarkson *et al.*, 2007).

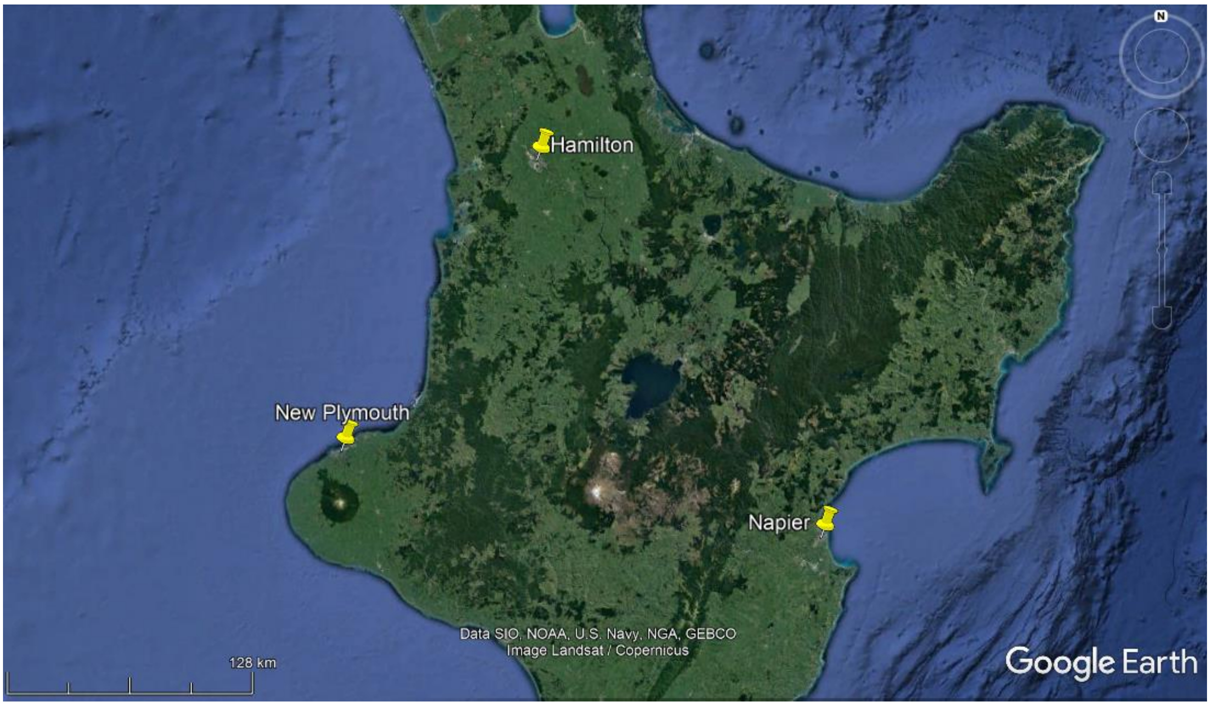


Figure 2.1: The central area of the North Island of Aotearoa New Zealand. The yellow pins indicate locations of the three study cities, Hamilton, New Plymouth and Napier (Google Earth).

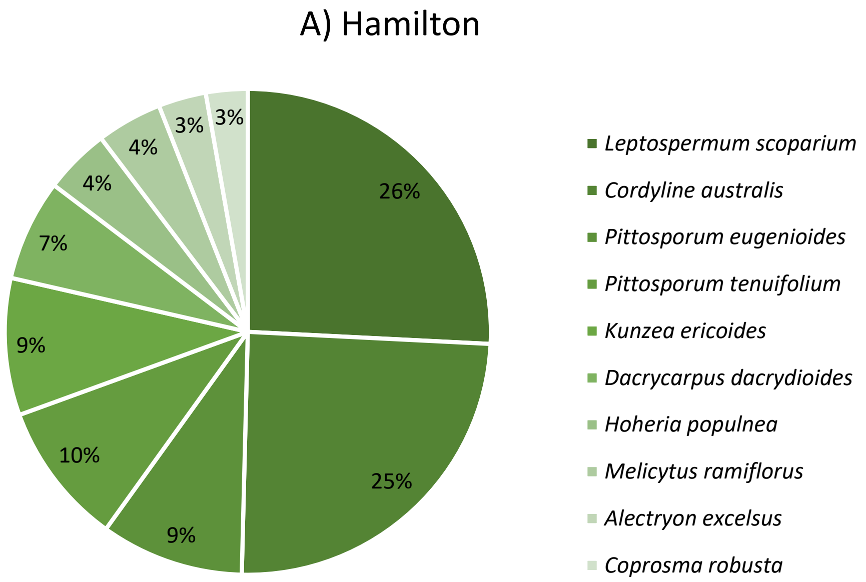
During the period of plant establishment and microclimate data collection (1 July 2018 – 30 June 2019), the total rainfall in Hamilton was 983.80 mm, the mean daily temperature ranged from 8.37-19.89°C, and there were 29 frost days (NIWA, 2019). New Plymouth had a total rainfall of 1215.60 mm, the mean daily temperature ranged from 10.14-18.37°C, and there were four frost days (NIWA, 2019). Napier had a total rainfall of 741.60 mm, the mean daily temperature ranged from 10.01-20.06°C, and there were ten frost days (NIWA, 2019).

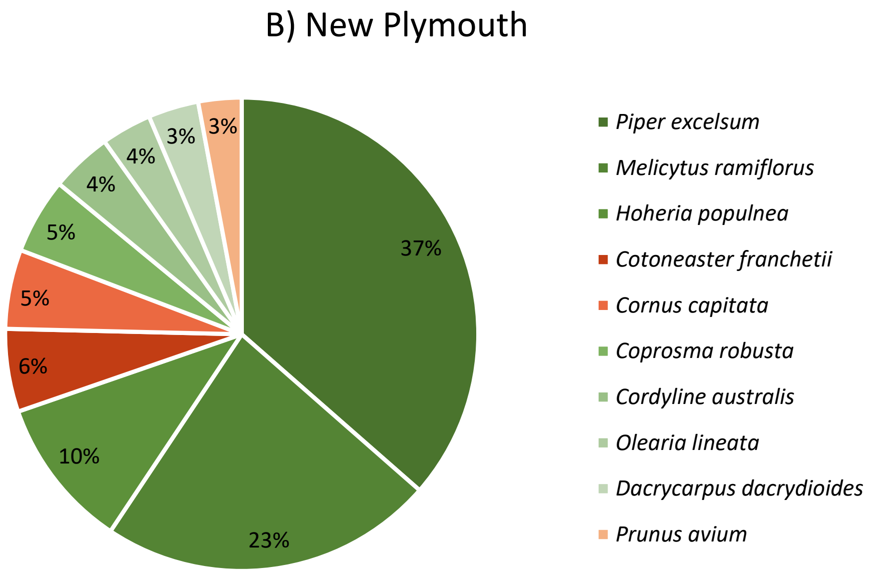
Each of the forest patches containing research plots were restored from scratch with one initial large cohort of planting. These forest sites were chosen for research purposes to form a chronosequence from 5 to 47 years since this initial planting. The research forests in Hamilton ranged from 7–39 years, New Plymouth from 5–47 years and Napier ranged from 7–38 years since initial planting. The forest patches used as research sites were generally required to be located within the city boundaries or the built-up city matrix and had to be large enough to contain a 20 x 10 m plot which could not include streams or seepages. Most forest patches were larger than the research plot (Appendix Table A.1). We formed relationships with each of the landowners (primarily city councils) and gained permission for data collection to occur.

The descriptive analysis results below illustrated the forest canopy compositions at the study sites when the research for this thesis occurred (Table 2.1). The composition is grouped by each city and shows the ten most abundant tree species (Fig. 2.2).

Table 2.1: Total abundance and species richness of individual adult trees (diameter at breast height DBH ≥ 2.5 cm) from the People, Cities & Nature research programme planted restored urban forest plots (200 m^2 per plot) within Hamilton (n = 9), New Plymouth (n = 9) and Napier (n = 9).

	Hamilton	**New Plymouth**	**Napier**
Tree total abundance (native: exotic)	294 (289: 5)	538 (472: 66)	313 (306: 7)
Tree species richness (native: exotic)	30 (28: 2)	46 (38: 8)	36 (32: 4)


A) Hamilton
26%
25%
9%
10%
9%
7%
4%
4%
3%
3%
Leptospermum scoparium
Cordyline australis
Pittosporum eugenioides
Pittosporum tenuifolium
Kunzea ericoides
Dacrycarpus dacrydioides
Hoheria populnea
Melicytus ramiflorus
Alectryon excelsus
Coprosma robusta


B) New Plymouth
37%
23%
10%
6%
5%
5%
4%
4%
3%
3%
Piper excelsum
Melicytus ramiflorus
Hoheria populnea
Cotoneaster franchetii
Cornus capitata
Coprosma robusta
Cordyline australis
Olearia lineata
Dacrycarpus dacrydioides
Prunus avium

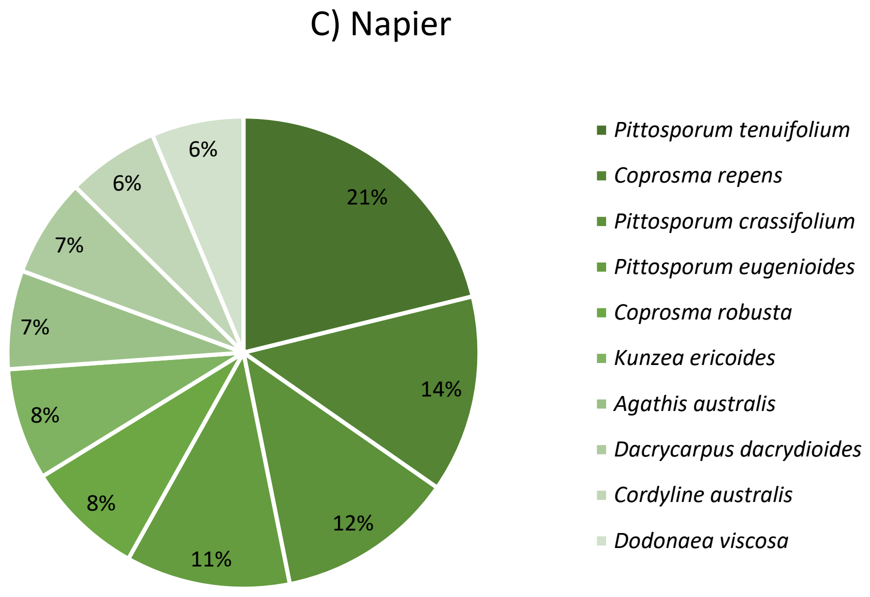


Figure 2.2: Breakdown of the ten most abundant adult tree (diameter at breast height DBH ≥ 2.5 cm) species within the People, Cities & Nature restored forest plots from each of the three cities used in this research. A) Hamilton plots had forest canopies comprised of 97% early-successional species and 3% mid-successional species, B) New Plymouth plots had forest canopies comprised of 63% early-successional species and 37% late-successional species, C) Napier plots had forest canopies comprised of 93% early-successional species and 7% late-successional species. Red hues indicate non-native tree species, green shades indicate native species. Successional status generally followed Busbridge (2020). Forest plots differed in age since planting from 5-47 years.

2.2 Data collection

Plant species

Six enrichment plants were planted in each plot: two epiphytes (*Griselinia lucida*, Akapuka), two understorey shrubs (*Piper excelsum*, Kawakawa) and two canopy trees (*Dacrydium cupressinum*, Rimu).

These species were chosen for this research project because they are all late-successional plants and are native to the regions where this project took place. The two terrestrial species (tree and shrub) were chosen as good candidates for the research because they are generally tolerant of a range of topographies, which was necessary as the restored forest patches where they were planted vary somewhat in topography (some gullies, some hilltops), however, no plots were situated on slopes of 10° or more. The plants were all sourced from the same nursery and had germinated at the same time (within each species). Therefore, experimental individuals within each species were the same age as each other at planting. The nursery also had collected the seeds used for germination of each species from generally the same areas as each other (in some cases the same tree), so we could be relatively sure of genetic similarity within species.

Plant growth measurements and planting

The initial measurements of the physical size of these seedlings were collected immediately prior to planting. Each plant had a metal tag with a unique number on it attached with a cable tie loosely around the stem base for identification purposes. Each individual's height was measured to its highest naturally occurring point in centimetres, whether to the tip of a leaf or a bent-over stem, etc. The stem diameter of all three species was measured in millimetres using waterproof callipers across the widest part of the base directly adjacent to the soil surface. If the plant was multi-stemmed at ground level, each stem (>2 mm) was measured separately and values for all stems were summed to represent a value for the individual plant's stem width. Total leaf number was counted using a tally clicker to count all green leaves that were >50% intact. Only the *P. excelsum* and *G. lucida* individuals' leaf numbers were counted because *D. cupressinum* leaves were too small for reliable counts. These data were recorded respectively to the individual plant's unique tagged number.

Plantings locations of the enrichment plants within each forest plot consisted of two individuals of the canopy tree and understorey shrub species being planted within ~4 m of the plot centre (Fig. 2.3). The two *D. cupressinum* canopy trees were located diagonally from each other, as were the two *P. excelsum* understorey shrubs (Fig 2.3). The epiphytic *G. lucida* were tied onto the southern side of two native trees with the largest basal area within each experimental plot, at 1.5 m from the ground (Fig. 2.3 & 2.4).

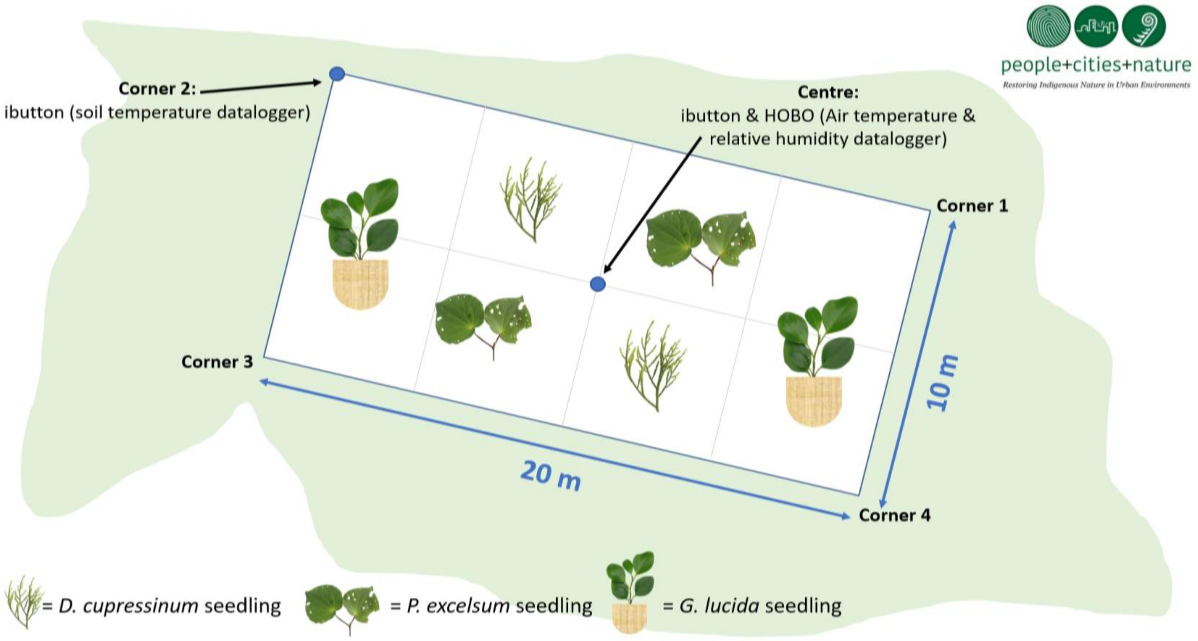


Figure 2.3: An example People, Cities & Nature research plot layout within a hypothetical restored forest patch (light green background), illustrating the placement of the late-successional plant species and the microclimate dataloggers used in this experiment. The two *Griselinia lucida* epiphytes were attached to the host tree within sphagnum moss baskets (shown in the hatched baskets), the two *Piper excelsum* seedlings were planted in the ground diagonally to the *Dacrydium cupressinum* seedlings from the centre of the research plot.

Figure 2.4: A *Griselinia lucida* epiphyte individual at its initial introduction to the forest plot in June 2018. It was attached to the chosen host tree with black cable ties and coconut husk wraps and was planted directly inside a sphagnum moss basket held together with twine (Photo courtesy K. Wallace).

A repeat of plant physical size data collection occurred in July 2019 (one year after planting into forest plots). Experimental plants were measured to their maximum height from the ground without manipulating the plant (even if overgrown by surrounding plants). The plant physical size measurement data was only collected if the plant was alive.

One year after planting, a rating out of five was given to each enrichment plant individual to quantify health status. The range was: ‘good’ health, ‘marginal’ and unsure whether the individual will survive, ‘poor’ because the plant had lost a majority of leaves or they were yellow or diseased, ‘standing dead’ as there were no green leaves, and ‘missing’ if the enrichment plant could not be found again. The survival rating of every enrichment plant was judged by one person to ensure consistency in data collection, as this is a somewhat subjective measure.

At one year after planting any apparent root growth of *G. lucida* was ascertained*,* including root growth length (mm) and direction of growth along the host tree trunk. Of the individuals which had visible root growth along their host trees, the length measurements were taken (with no manipulation) from the root tip to the base of where the root appeared from the epiphytic plant basket. The directions of possible root growth were classified as ‘up’ (skyward), ‘down’ (groundward), ‘left’ and ‘right’ from the position of standing face-on to where the *G. lucida* was attached to the host tree.

Abiotic measurements

Canopy openness (%) was measured at five points within each plot using a convex spherical densiometer (Convex model A; Forestry Suppliers, Jackson, Mississippi, USA). Readings were taken at each plot corner by standing one metre inside the plot facing outward, and the fifth reading in the plot centre. If a tree was in the way, the measurement was taken as close as possible to where the default position was for taking the measurement. The reading was taken while holding the densiometer with the palm facing skyward, at waist height with the arm at right angles to the body. Densiometer readings were taken at time zero (at enrichment species planting into the forest plots), six months after planting and 12 months after planting (final plot visit). An average of these 15 readings was calculated to represent each plot’s canopy openness (%) over the course of the year that the experimental plants were in the plots.

At each urban forest plot, one HOBO datalogger in a radiation shield was attached to the tree nearest to the plot centre. This datalogger measured atmospheric relative humidity (RH) and the air temperature (degrees Celsius) every four hours for the entire year after the experimental plants were planted in the plot (HOBO MX2301A weatherproof RH & temperature Bluetooth datalogger; Onset, Massachusetts, USA). This period was 1 July 2018 – 30 June 2019 within each plot (n = 27).

The soil temperature was measured using two thermochrons (iButton dataloggers model DS1921G-F5; Maxim Integrated, San Jose, California, USA) buried at 10 cm depth in each plot (one in the centre, one at corner 2 to capture variation within the plot, Fig. 2.3). Soil temperature (degrees Celsius) data were automatically obtained every four hours from 21 February 2019 – 7 July 2019. Data from the two iButton dataloggers were averaged together for a representative plot value, but in several plots a thermochron iButton failed to function the entire annual period and the data was lost. In these cases, the average was taken of the values from the one remaining functioning iButton.

The plot-level standard deviation (SD) and means for each of the microclimate variables (RH, air temperature and soil temperature) were calculated in Excel (Office 365; Microsoft, Redmond, Washington, USA) using all values measured in the timeframes stated above.

During the People, Cities & Nature plot establishment in 2018, vegetation surveys were conducted within each of these plots. These data included herbaceous weed percent cover (visually estimated within each plot) and adult tree basal area (DBH ≥2.5 cm), which were used as covariates to examine enrichment plant growth in this study, see Busbridge (2020) for those methods.

2.3 Data preparation and statistical analyses

Statistical analyses were carried out in R Studio version 3.4.3 (R Core Team 2018). Equal numbers of each plant species were planted across the 27 plots (n = 56), but the statistical analyses excluded individuals which were classified as 'missing' and 'standing dead' at the one-year data collection mark. Thus, final sample sizes were: *G. lucida* n = 37, *P. excelsum* n = 49 and *D. cupressinum* n = 33. A single *G. lucida* individual from the 'Waiwhakareke young' site was removed from the dataset prior to analysis as it fell from the host tree prior to data collection and was therefore deemed invalid for use in the analysis. The percentage of surviving enrichment species was calculated using the 'alive' individuals, divided by the total number of individuals initially planted, after excluding the 'missing' individuals. A relative growth rate (RGR) mean was calculated for each species using Microsoft Excel.

The plant growth variables measured in the field were used to calculate the RGR and the rate of leaf growth. Using plant stem diameter and height measurements, an RGR was calculated for each living experimental plant using:

$$\mathbf{RGR} = \frac{\left[\ln\left(D_2{}^2 * H_2\right) - \ln\left(D_1{}^2 * H_1\right)\right]}{(t_2 - t_1)}$$

where D_1 and D_2 are stem diameter at t_1 (date the plants were initially measured before planting) and t_2 (date of the plants' final measurement after one year) respectively. H_1 and H_2 are the plant heights at t_1 and t_2 in units of days, respectively (Martin *et al.*, 2011). An analysis of variance (ANOVA) was conducted for the RGR of each species to investigate whether city (i.e., regional climate or other differences) was a meaningful determinant of RGR and if not, then pooling plant growth responses across the cities enabled for further analyses.

A rate of leaf growth was also calculated for *G. lucida* and *P. excelsum* individuals using:

$$\textbf{Rate of leaf growth} = \frac{[\ln(L_2) - \ln(L_1)]}{(t_2 - t_1)}$$

where L_1 and L_2 are the number of leaves at t_1 (initial planting) and t_2 (final measurement), respectively.

The ensuing statistical analysis was divided into four main lines of investigation. The first investigated restored urban forest canopy openness, including how it was related to forest age and microclimate and its effects on growth of all three enrichment plant species. The next three lines of investigation more specifically explored the three enrichment species separately in how their growth was affected by restored forest conditions like the microclimate. Where data appeared non-normal, log transformations were applied and used in models initially, but ultimately were not shown in the results because they did not improve the model fits. Thus, all analyses were performed using untransformed data.

Investigation 1: Urban forest canopy openness

A bivariate plot and linear model of the data was inspected to investigate the relationship between forest age (years since planting) and canopy openness (%). The linear model was created using the lm() function in the R base package. Where there appeared to be a defining break (threshold) where the linear models changed slope, breakpoint analyses were done using the segmented() function in the 'segmented' package in R (Muggeo, 2017).

Investigation 2-4: Enrichment plant growth responses to restored conditions

For all three enrichment plant species, bivariate plots and linear models of the data were inspected using the lm() function in the R base package. The relationships between the plant growth variables (stem width, plant height, leaf number) and restored forest conditions (air temperature, relative humidity, soil temperature, herbaceous weed cover and canopy openness) were investigated. The models were evaluated based on significance ($\alpha = 0.05$).

Multiple linear regression was used in the final investigation of *D. cupressinum* to investigate its growth responses to the forest conditions using the lm() function in the 'tidyverse' package in R (Wickham *et al.*, 2019).

CHAPTER 3

Results

3.1 Enrichment species survival

After one year, of the enrichment species planted in forest research plots, *Piper excelsum* had a 100% survival rate, compared to *Griselinia lucida* and *Dacrydium cupressinum* which both had a ~75% survival rate (Table 3.1). There were more missing *D. cupressinum* individuals than the other enrichment species (Table 3.1).

Table 3.1: The number of live, dead and missing of each species by city. In the far right column, are the survival proportions for the three species of enrichment plants one year after planting in restored forest plots. The totals are the sums across all cities.

	Hamilton (live, dead, missing)	**New Plymouth (live, dead, missing)**	**Napier (live, dead, missing)**	**Total (live)**	**Total (dead)**	**Total (missing)**	**Survival (%)**
***Griselinia lucida* (Akapuka)**	14, 3, 1	12, 6, 0	14, 4, 0	40	13	1	75.5
***Piper excelsum* (Kawakawa)**	17, 0, 1	17, 0, 1	18, 0, 0	52	0	2	100.0
***Dacrydium cupressinum* (Rimu)**	9, 7, 2	15, 1, 2	12, 4, 2	36	12	6	75.0

When comparing relative growth rates (RGR) of *G. lucida* between cities, those in Hamilton were twice that of those in Napier (Table 3.2). *Dacrydium cupressinum* grew poorly in all of the cities (i.e., generally lost condition) (Table 3.2). The highest proportion of living individuals was *P. excelsum* in Napier, and the lowest was *D. cupressinum* in Hamilton (Table 3.2).

The ANOVA investigating differences in RGR between cities for each species did not show significant differences ($\alpha = 0.05$) (Table 3.2). Therefore, the data were pooled by species across all the cities for the rest of the analyses.

Table 3.2: Mean ± standard deviation (SD) of the relative growth rates (RGR; see Methods for calculation) of the three enrichment species surviving within each of the three cities one year after planting in the restored forest plots. The RGRs (mg g^{-1} day^{-1}) that are very small in number and values are presented showing five decimal places to retain meaning (e.g., *Dacrydium* cupressinum in New Plymouth and Napier). The sample size indicates how many individuals were 'alive', as a proportion of the individuals planted initially (which was n = 18 in each city). The *F*-statistic and *P*-value for comparing RGR by city within each species were found using ANOVA tests and resulted in no significant differences in RGR of any of the species by city.

	Hamilton	**New Plymouth**	**Napier**	***F*-statistic**	***P*-value**
***Griselinia lucida* (Akapuka)**	0.00090 ± 0.00144 (n = 14; 77.8%)	0.00154 ± 0.00234 (n = 12; 66.7%)	0.00045 ± 0.00127 (n = 14; 77.8%)	1.317	0.280
***Piper excelsum* (Kawakawa)**	0.00323 ± 0.00337 (n = 17; 94.4%)	0.00270 ± 0.00262 (n = 17; 94.4%)	0.00247 ± 0.00551 (n = 18; 100.0%)	0.162	0.851
***Dacrydium cupressinum* (Rimu)**	-0.00010 ± 0.00172 (n = 9; 50.0%)	-0.00004 ± 0.00127 (n = 15; 83.3%)	-0.00003 ± 0.00172 (n = 12; 66.7%)	0.008	0.993

3.2 Canopy openness

As forest age increases, there is a significant drop in canopy openness which is supported by a statistically significant negative linear relationship (Fig. 3.1A; *P* <0.001). Young forests have more open canopies than older forests, and an additional breakpoint analysis indicated there is a threshold at 10.88-years-old, before which, young forest canopies are closing more rapidly than those of the older forests (Fig. 3.1B; *P* = 0.002).

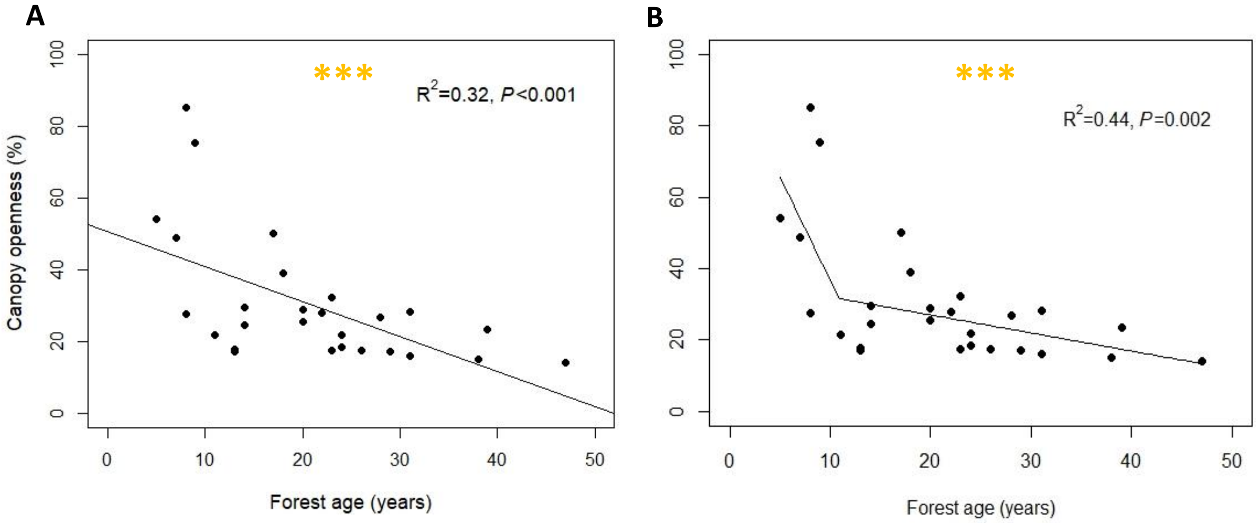


Figure 3.1: The relationship between forest age (years since planting) and canopy openness (%) in the restored urban forest plots in Hamilton, New Plymouth and Napier (n = 27). Each point represents the mean canopy openness for a given forest plot. A) contrasts a normal linear regression model with B) a linear regression model using break point analysis. The break point analysis improved model fit and also identified a significant threshold (i.e., change in slope) where canopy closure occurred at a slower rate after 10.88 years of forest age since planting. Significance codes: '***' <0.001, '**' <0.01, '*' <0.05, '.' <0.1, ' ' >1.

A more open canopy is associated with larger fluctuations in relative humidity (i.e., relative humidity's standard deviation (SD)) (Fig. 3.2), indicating that canopy presence mediates the forest understorey microclimate. The linear regression model shows a significant positive relationship between canopy openness and the standard deviation of relative humidity (Fig. 3.2A; *P* <0.001). The linear regression model that includes a breakpoint analysis shows that when the canopy reaches a threshold of being only 17.68% open, there is a steep drop in relative humidity fluctuations (Fig. 3.2B; *P* <0.001). A 33.86-year-old forest will have canopy openness of 17.68%.

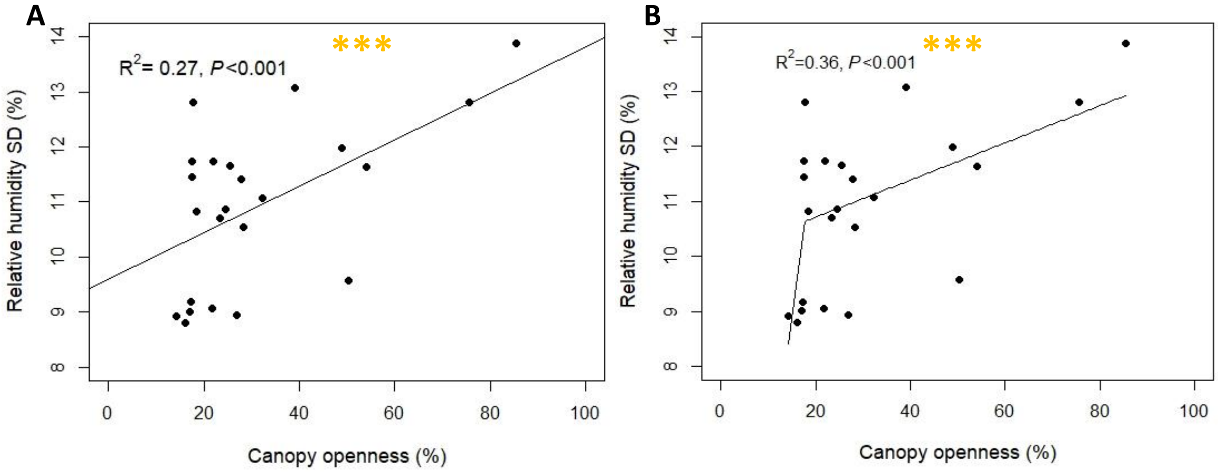


Figure 3.2: The relationship between the canopy openness and relative humidity fluctuations (standard deviation (SD)) in the restored urban forest plots in Hamilton, New Plymouth and Napier (n = 27). Each point is the mean canopy openness for a given plot. A) The linear regression model fit is improved with a B) breakpoint analysis which reveals a significant reduction in relative humidity fluctuations when canopy openness is 17.68%. Significance codes: '***' <0.001, '**' <0.01, '*' <0.05, '.' <0.1, ' ' >1.

The three late-successional enrichment species planted for this experiment had varying growth responses across differences in canopy openness as the forest aged. A linear regression model shows that *G. lucida*'s relative growth rate is significantly positively related to canopy openness (Fig. 3.3A; *P* = 0.038). In contrast, the growth rate of *P. excelsum* was significantly negatively affected by canopy openness (Fig. 3.3D; *P* = 0.029). *Dacrydium cupressinum* growth rate is not affected by the canopy openness at all (Fig. 3.3G; *P* = 0.964).

Change in stem width of *G. lucida* is positively related to canopy openness (Fig. 3.3B; *P* = 0.011), whereas the change in stem width of *P. excelsum* and *D. cupressinum* is not affected by the canopy openness at all (Fig. 3.3E; *P* = 0.406, Fig. 3.3H; *P* = 0.185).

The number of leaves of *G. lucida* was positively related to canopy openness (Fig. 3.3C; *P* = 0.018) whereas the number of leaves of *P. excelsum* is not affected by the canopy openness at all (Fig. 3.3F; *P* = 0.153). The scatter in the data resulted in a low R^2 for all model fits.

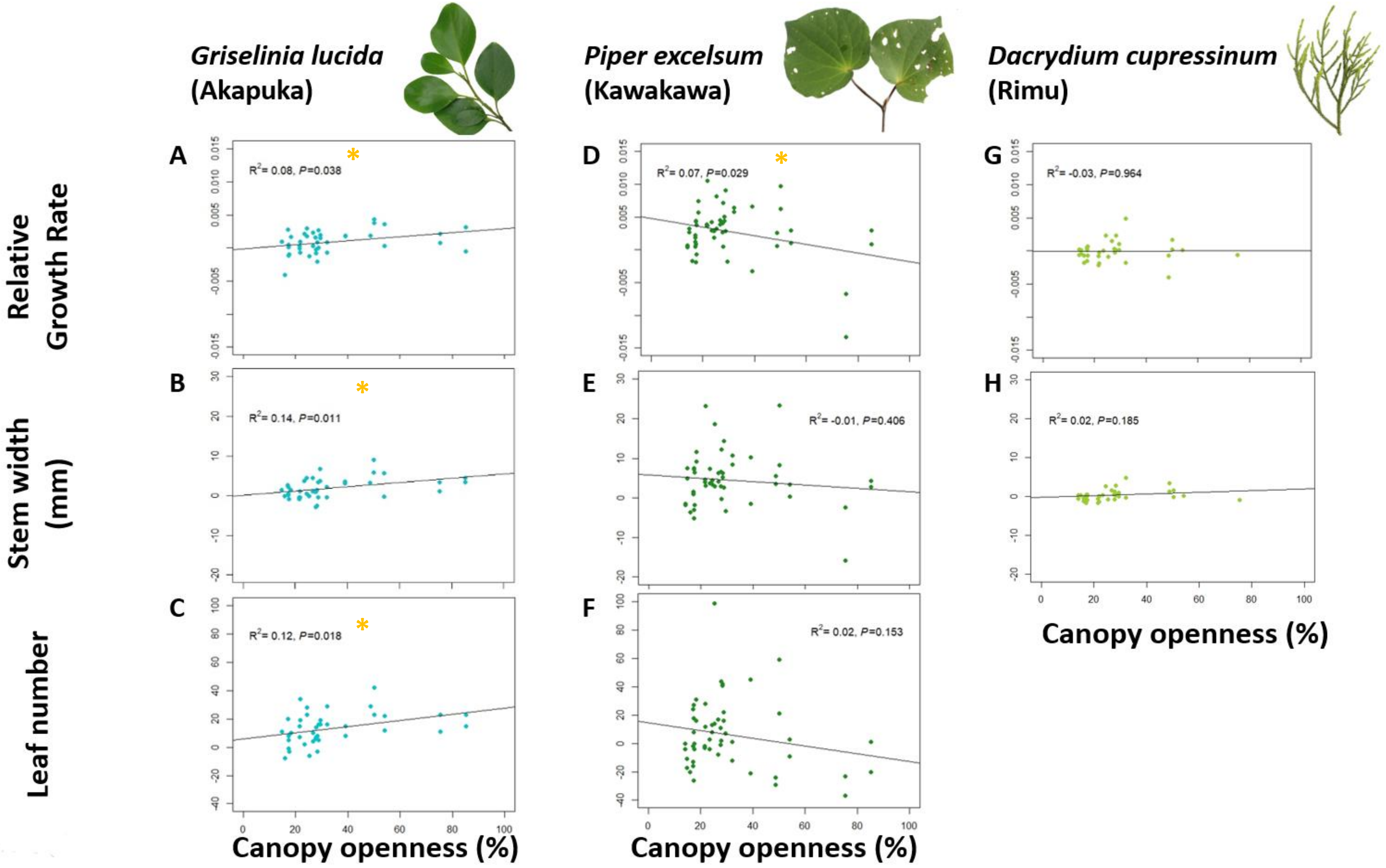


Figure 3.3: Linear regression models showing the relationship between canopy openness on the x-axis and enrichment plant growth variables (relative growth rate, stem width, leaf number) on the y-axis for each of the three species, *Griselinia lucida* (A-C, n = 53), *Piper excelsum* (D-F, n = 50) and *Dacrydium cupressinum* (G & H, n = 48) (α = 0.05). Each point represents an individual enrichment plant, excluding dead or missing individuals. *Dacrydium cupressinum* leaf number was purposely not measured, because the leaves were too small. Significance codes: '***' <0.001, '**' <0.01, '*' <0.05, '.' <0.1, ' ' >1.

3.3 Plant growth responses to environmental conditions – *Griselinia lucida*

The microclimate variables (air temperature SD, air temperature mean, and the relative humidity mean) do not have a significant relationship with *G. lucida* growth (Fig. 3.4A-I). However, there are statistically significant (or marginally significant) negative linear relationships between all *G. lucida* growth variables and size of the host tree. The larger host trees are associated with a decrease in *G. lucida* RGR (Fig. 3.4J; *P* <0.001), marginally smaller stem widths (Fig. 3.4K; *P* = 0.094) and fewer leaves (Fig. 3.4L; *P* = 0.019).

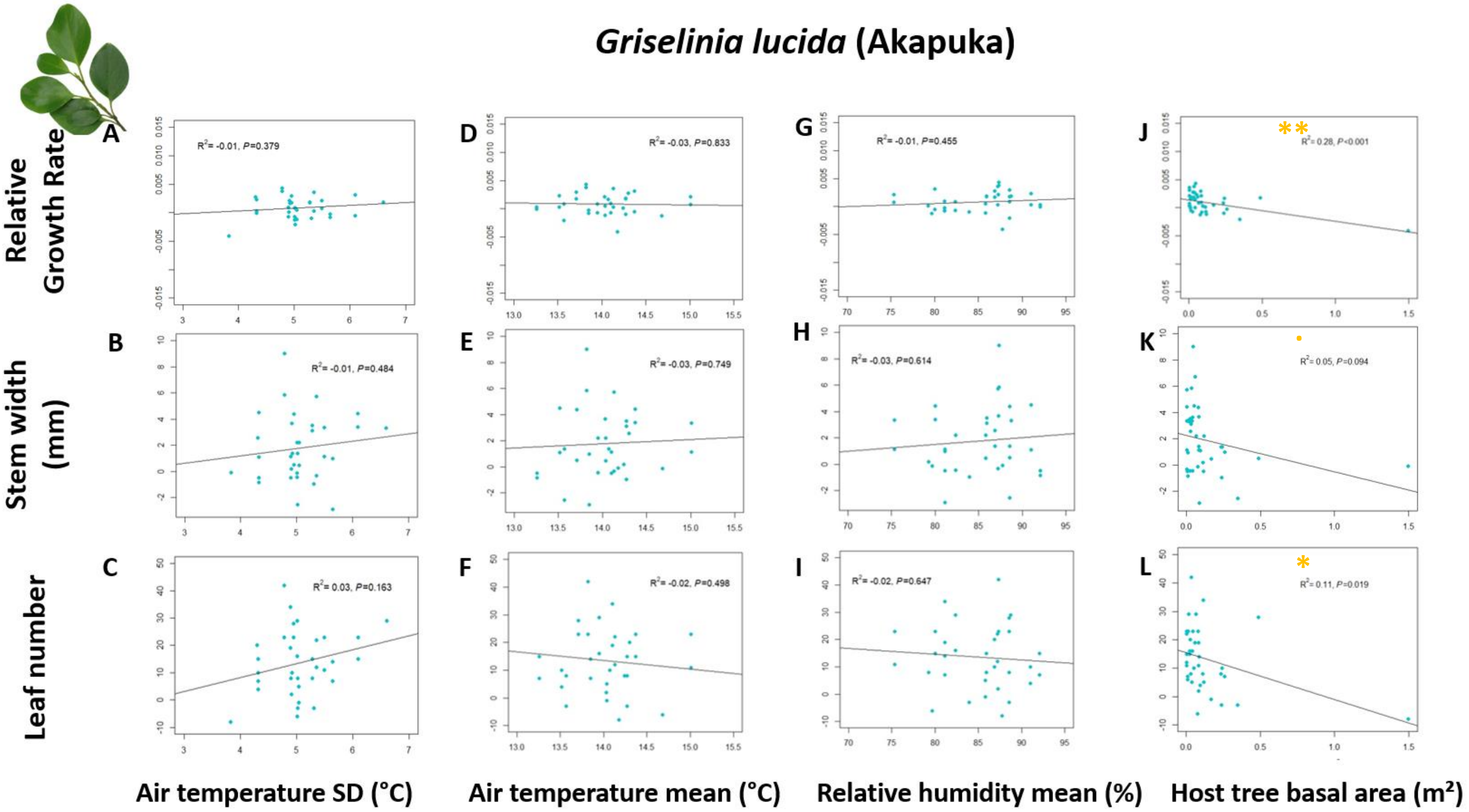


Figure 3.4: Linear regression models showing the relationships between air temperature fluctuations (standard deviation (SD)) (A-C) and means (D-F), relative humidity means (G-I) and the host tree basal area (J-L) on the x-axes and the growth properties (relative growth rate, stem width, leaf number) on the y-axes for *Griselinia lucida* (n = 53, α = 0.05). Each point represents an individual *Griselinia lucida* excluding dead or missing individuals. Significance codes: '***' <0.001, '**' <0.01, '*' <0.05, '.' <0.1, ' ' >1.

Some *G. lucida* root growth occurred for 13 out of the 53 experimental plants (24.53%). Host trees had visible roots growing along their bark, ranging from 10–869 mm in length (mean = 221.80 mm; Fig. 3.5). Ten of the 13 individual epiphytes had roots growing down the host tree, two grew right, and one grew left around the host tree trunk. Of the 13 individuals with visible root growth, 11 were on *Cordyline australis* (tī kōuka/cabbage tree) host trees.

Figure 3.5: A *Griselinia lucida* epiphyte root establishing on its *Cordyline australis* tree host's trunk. Right is an enlarged portion of the root image on the left (photo courtesy K. Wallace).

3.4 Plant growth responses to environmental conditions – *Piper excelsum*

The linear models for *P. excelsum* RGR relationships with three microclimate variables were all marginally significant: air temperature mean (Fig. 3.6D; *P* = 0.062), the relative humidity mean (Fig. 3.6G; *P* = 0.089) and the soil temperature mean (Fig. 3.6J; *P* = 0.072). Of the three, the RGR only responds positively to increased relative humidity (Fig. 3.6G; *P* = 0.089). Stem width and leaf number were not related to changes in microclimate.

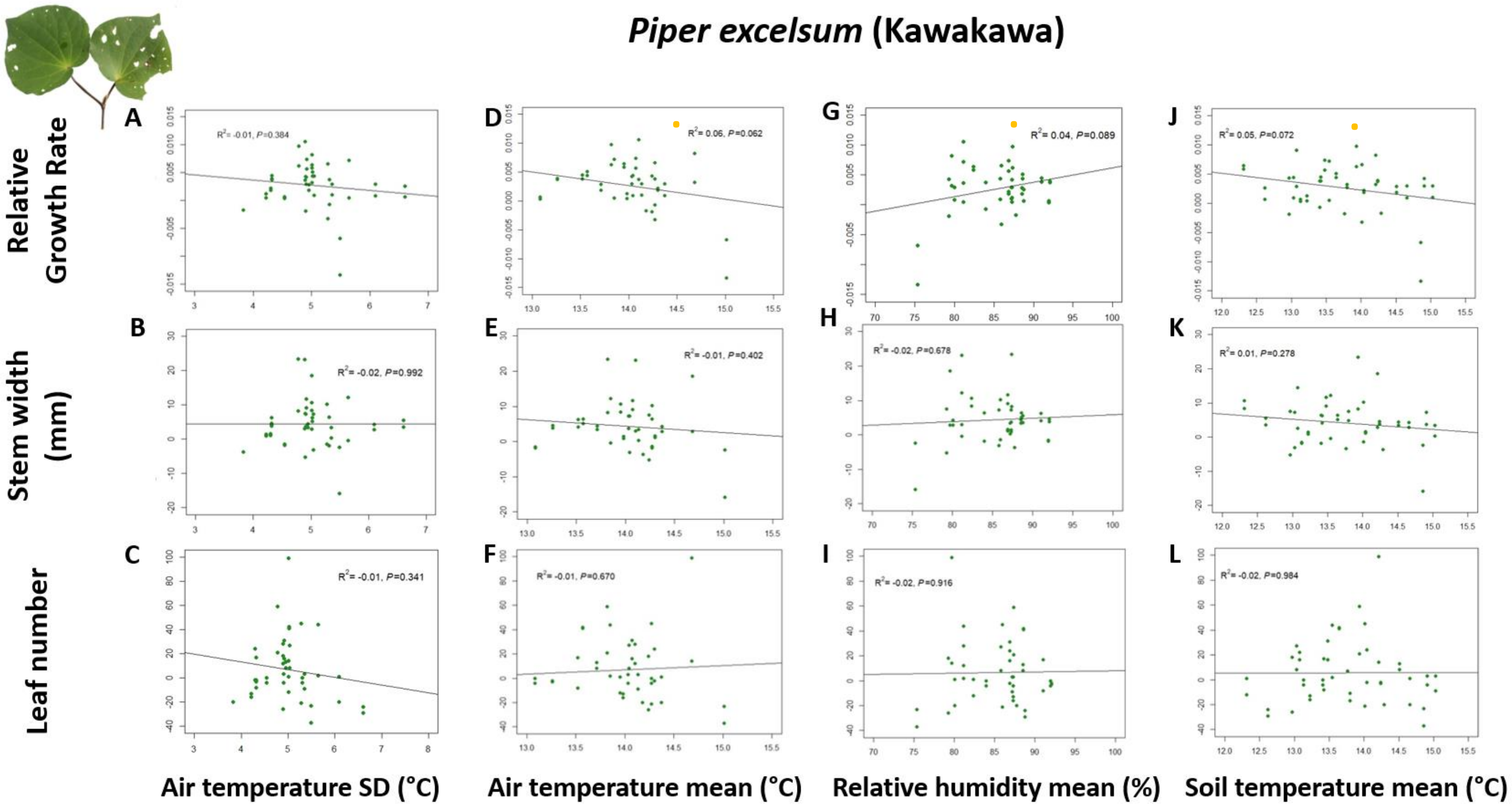


Figure 3.6: Linear models showing the relationship between air temperature fluctuations (standard deviation (SD)) (A-C) and mean (D-F), relative humidity mean (G-I) and the soil temperature mean (J-L) on the x-axes and the growth properties (relative growth rate, stem width, leaf number) on the y-axes for *Piper excelsum* (n = 50, α = 0.05). Each point represents an individual *Piper excelsum* excluding dead or missing individuals. Significance codes: '***' <0.001, '**' <0.01, '*' <0.05, '.' <0.1, ' ' >1.

A linear regression model shows there is a significant negative relationship between *P. excelsum* leaf growth rate and canopy openness, such that with increased canopy openness, the rate of leaf growth decreases (Fig. 3.7; *P* = 0.003).

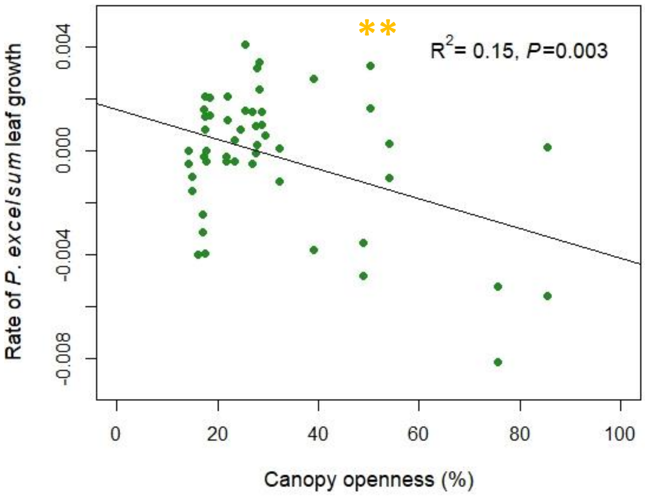


Figure 3.7: The relationship between canopy openness and the rate of *Piper excelsum* leaf growth (n = 50). Each point represents an individual plant. Significance codes: '***' <0.001, '**' <0.01, '*' <0.05, '.' <0.1, ' ' >1.

3.5 Plant growth responses to environmental conditions - *Dacrydium cupressinum*

There is a significant, positive relationship between stem width of *D. cupressinum* and both air temperature SD (Fig. 3.8B; *P* = 0.030) and herbaceous weed cover (Fig. 3.8H; *P* = 0.004) and a marginally significant relationship with air temperature mean (Fig. 3.8E; *P* = 0.091). This demonstrates that with greater swings in air temperature, the plant stem width growth increases. However, the relationship between *D. cupressinum* height and air temperature shows the opposite responses from that of stem width, where height growth decreases under larger swings in temperature and (Fig. 3.8C; *P* = 0.006) and increases under warmer mean temperatures (Fig. 3.8F; *P* = 0.017). The mean soil temperature has a marginally significant negative relationship with the stem width of *D. cupressinum* (Fig. 3.8K; *P* = 0.051). There were no relationships between *D. cupressinum* RGR and microclimate (Fig. 3.8A; *P* = 0.534, 3.8D; *P* = 0.553, 3.8J; *P* = 0.904) or non-native herbaceous weed cover (Fig. 3.8G; *P* = 0.447).

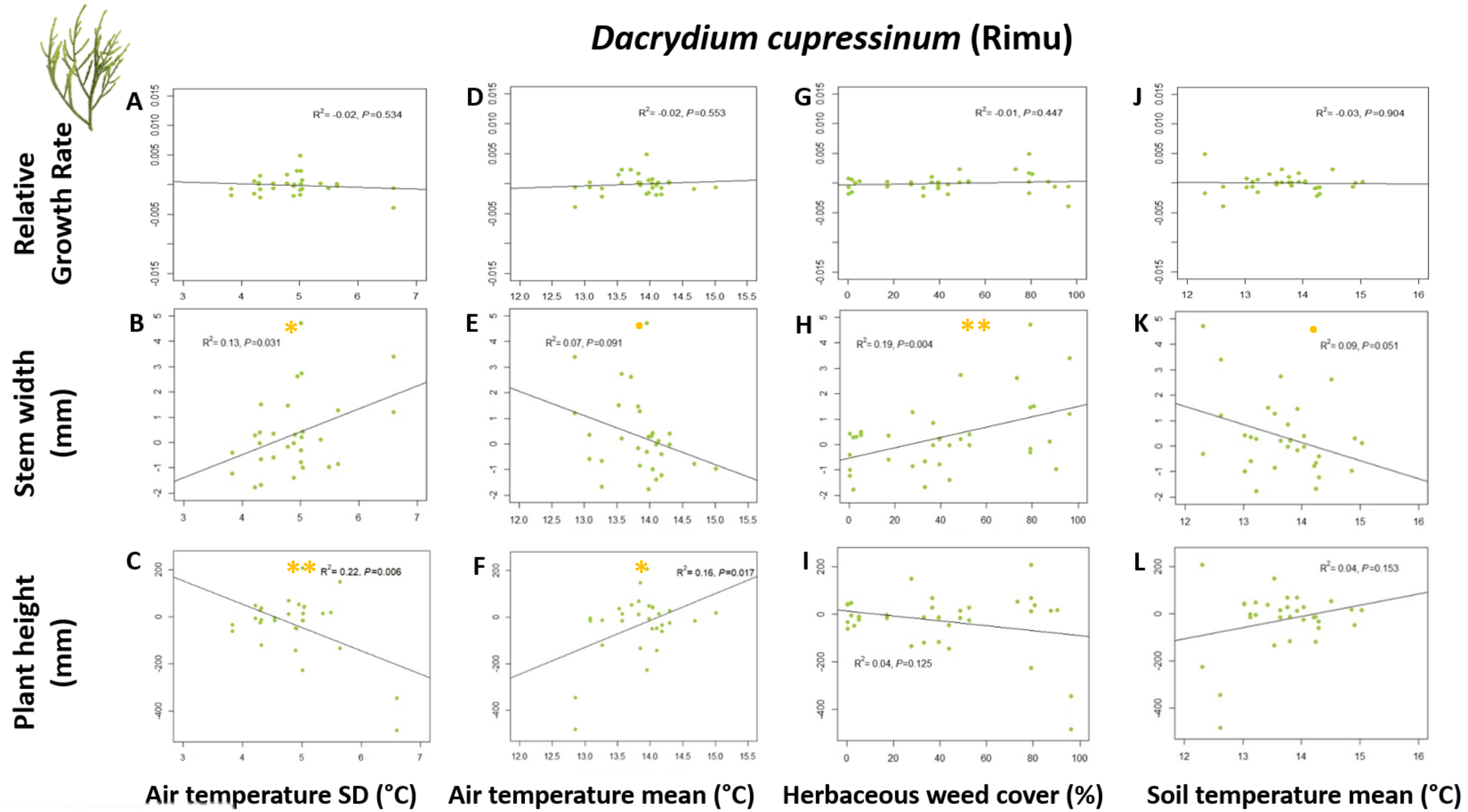


Figure 3.8: Linear regression models showing the relationship between air temperature fluctuations (standard deviation (SD)) (A-C) and mean (D-F), herbaceous weed cover (G-I) and the soil temperature mean (J-L) on the x-axes and the growth properties (relative growth rate, stem width, plant height) on the y-axes for *Dacrydium cupressinum* (n = 48, α = 0.05). Each point represents an individual *Dacrydium cupressinum* excluding dead or missing individuals. Significance codes: '***' <0.001, '**' <0.01, '*' <0.05, '.' <0.1, ' ' >1.

Canopy openness may drive different aspects of enrichment plant growth. These results indicate a possible trend towards shorter *D. cupressinum* individuals (black line) with wider stems (green line) under more open canopies (Fig. 3.9), however statistical results were not significant.

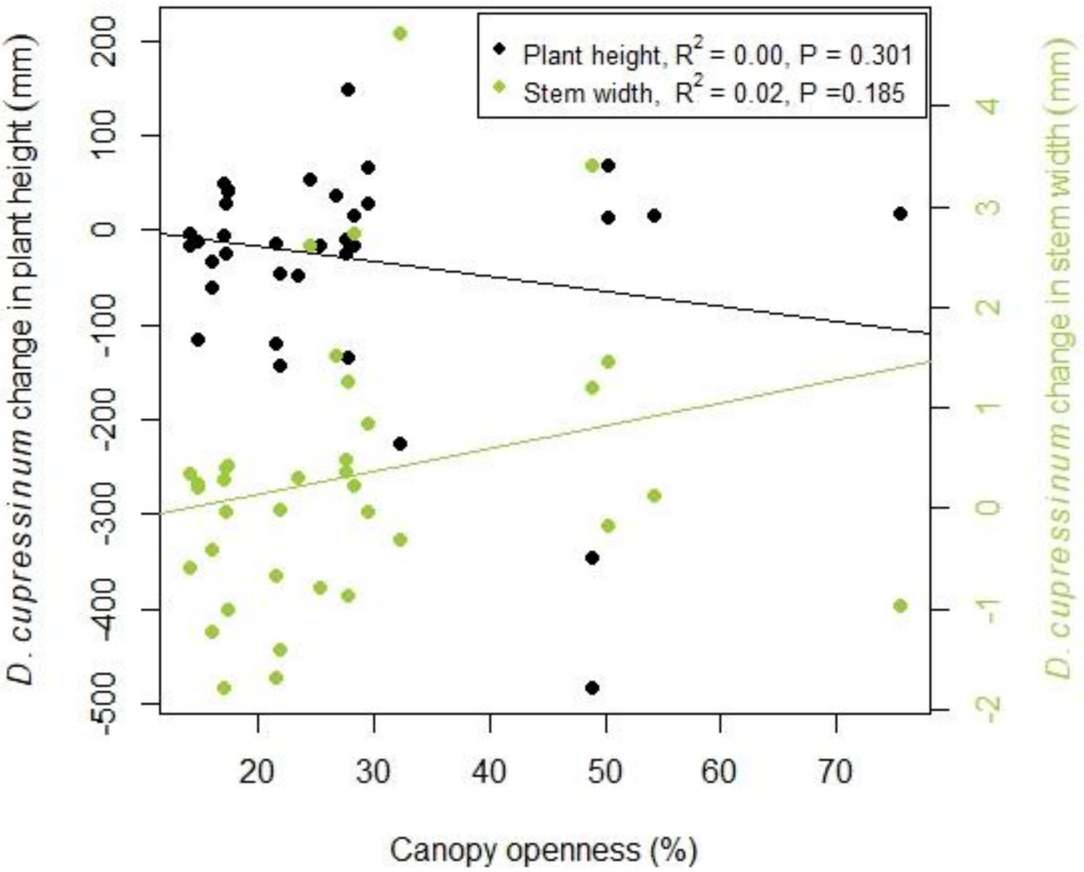


Figure 3.9: The contrasting trends (possible trade-off in resource allocation) between the changes in plant height (n = 48, *P* = 0.301) and stem width (n = 48, *P* = 0.185) of *Dacrydium cupressinum* and canopy openness. Each point represents a change in individual plant height and stem width over a year.

Upon further investigation, the *D. cupressinum* stem width growth is explained best by herbaceous weed cover (*P* = 0.053) and not air temperature SD (*P* = 0.354) when these variables are modelled together as predictors in a multiple regression (R^2 = 0.21, F = 4.91, *P* = 0.015). Taken together with the canopy openness analysis above, this indicates that light availability dictated by canopy openness may support herbaceous weed growth (and competitive ability) and therefore may be an indirect driver of *D. cupressinum* stem width growth.

CHAPTER 4

Discussion

4.1 Forest structural and environmental development after initial restoration plantings

Importance of microclimate versus macroclimate for late-successional plant juveniles

Canopy development in forests is a major driver of many understorey environmental conditions (Wallace *et al.*, 2017; Doroski *et al.*, 2018; Laughlin & Clarkson, 2018; Meijide *et al.*, 2018; Forbes *et al.*, 2020). Canopies are an integral part of forest structure because they provide a microclimate for understorey life, buffering against exposure to macroclimate extremes of environmental conditions outside of the forest (Bazzaz, 1979; Chen *et al.*, 1993; Meijide *et al.*, 2018).

Microclimate can protect late-successional plants from the negative effects of macroclimate. It is interesting to compare each city's historical macroclimate with the macroclimate during the one-year research period, and also compared with the microclimate under the most developed canopies. When doing so, the canopy's mediating role on microclimate is evident. For example, the macroclimate during the research period (2018-2019) was, on average, warmer during February for all three cities (between a 0.37-1.09°C increase depending on the city) than the average macroclimate for these cities collected during the period 1981-2010 (see chapter 1, Fig. 1.4). When comparing this same average temperature during February for the macroclimate during the research period to the microclimate of the oldest forests, the temperatures were lower in Hamilton (a 0.73°C decrease) and New Plymouth (a 1.16°C decrease) (microclimate data for Napier unavailable). For all of the cities, the amount of rainfall was less during the one-year research period (between a 6.47-13.27% decrease depending on the city) and the number of frost days was lower during the 2019-2020 research period (between a 29.60-55.00% decrease depending on the city) than the long-term macroclimate averages. These variations in the research period's macroclimate and long-term macroclimate averages illustrate the importance of canopy presence to provide microclimate buffering, effectively reducing the effect of yearly climate variation extremes on the juvenile plants. In all three cities, the microclimate in the oldest forests (with the most developed canopies) showed the maximum highest air temperatures to be 2-5°C lower than each city's macroclimate during the research period.

My results illustrate this important mediating role of the forest canopy, as each research city has a somewhat different macroclimate, but my results also showed that the macroclimatic differences did not significantly affect the growth rates of the studied late-successional plants. The microclimate and the macroclimate both affect the growth of late-successional plants, but the relative importance of the two may depend on the region and the presence of forest canopy. Instead, the growth rates of the late-successional plants were significantly affected by the microclimate within each forest, so restoration age is more important than the city where it is located. This highlights the pre-eminent importance of restored forest age and structural development stage (e.g., canopy formation) for late-successional juvenile enrichment planting success.

Canopy formation after initial restoration plantings

Planted forests' canopies form as the initially-planted trees grow in size and age (Wallace *et al.*, 2017). My results detected a threshold point in canopy closure at 10.88 years (~30% canopy openness) since forest restoration plantings first occurred. Wallace *et al*. (2017) studied restored urban forests in two cities in Aotearoa New Zealand. They demonstrated that as restored urban forest age increases, basal tree area also increases, causing canopy openness to decrease and reach a threshold point in the rate of canopy closure at 7.0 years (~22% canopy openness) and 18.1 years (~12% canopy openness) since restoration plantings first occurred (Wallace *et al.*, 2017).

Few studies have investigated whether there are thresholds in the canopy closure process in restored urban forests. Brazilian research focused on a five-year-old restored urban riparian forest and found canopy openness to be 30% (Londe *et al.*, 2017). Londe *et al*. (2017) suggest that the studied planting would undergo substantial development yet and would require active management, including enrichment using native species. In comparison to my results, five years after initial planting is very early in the development of a forest, but the canopy in Londe *et al*. (2017) is more closed than the restored urban forest canopies in this study, which were 46% closed at the same age. This is possibly explained by the study's location climate, as Londe *et al*. (2017) is in a tropical setting. Tropical rainforests receive greater amounts of rainfall and sunlight and the canopy trees produce leaves throughout a longer season than canopy trees in temperate rainforests (Lowman, 1992) which may indicate that tropical rainforest canopies will develop faster than temperate rainforest canopies. Therefore, this highlights the important role macroclimate plays in the speed of initial early-successional planting growth and forest canopy development.

Outside the urban setting, there is more information available about predictable trajectories in rural forest canopy development after disturbance events. In pristine tropical forests (generally undisturbed by humans) in Panama (Brokaw, 1985) and Mexico (Horvitz & Schemske, 1986), naturally-occurring treefall gaps increased the canopy openness, and recruitment and the remaining trees took five and ten years (respectively) to close the gap in the canopy. Forests undergoing more severe disturbances, to the similar rigour of disturbance found in the urban forests I researched, can take much longer to recover full canopies, e.g., after a fire, Ghanaian semi-deciduous forests took 10-20 years to reform a canopy, with the help of active restoration maintenance (Owusu-Afriyie, 2008).

Restored, planted forest ecosystems in rural contexts also take in the order of a decade or two to develop canopies. Studies in the Brazilian and Australian tropical rainforests found that canopy closed at ten years after initial restoration planting (Suganuma & Durigan, 2015; Shoo *et al.*, 2016). During these dynamic first decades, changes in canopy openness affect understorey plants in different ways. In humid subtropical forests in Changting, China, the shrub and grass stabilised in the extent of cover when canopy openness was at 48.5%, ten years since restoration plantings began (Cao *et al.*, 2017). Finally, the canopy openness stabilised near to full canopy closure at 20 years since restoration (Cao *et al.*, 2017), similar to my results from the restored urban forests. These three studies in planted restored forests stated that their forest restoration management plans were actively incorporating ecological succession theory (Suganuma & Durigan, 2015; Shoo *et al.*, 2016). However, one of the studies suggested that different ecosystems could follow different trajectories in development (Cao *et al.*, 2017).

Canopy and effects on understorey environmental conditions

As forests develop, canopy closure shelters the understorey from the external environment, especially macroclimate conditions (Lemenih *et al.*, 2004). This occurs, for example, by dampening fluctuations in microclimate, e.g., more stable soil temperatures, air temperatures and humidity (Chen *et al.*, 1993; Lemenih *et al.*, 2004). One study found that the temperatures and humidity fluctuations are significantly dampened under an urban forest initially planted ~17 years prior, with the canopy at ~8% canopy openness (Wallace *et al.*, 2017). My results generally aligned with these findings, however, I found that relative humidity fluctuations were reduced substantially at a slightly later stage in forest age, at 33.86 years since planting, when the canopy openness reached 17.68%. This threshold is vital to create a suitable microclimate for native seedlings to germinate. A study of restored urban forests in Auckland found that canopy openness between 2–30% allowed for any native seedlings to establish naturally (Pothercary, 2012). Therefore, this long time interval until a relatively closed canopy reaffirms the management recommendation to use fast-growing species planted close together for the initial early-successional plantings to create a closed canopy as rapidly as possible (Doroski *et al.*, 2018), paving the way for ideal conditions for germination and establishment of mid to late-successional species. The protocol to plant fast-growing species follows basic succession theories proposed by Connell and Slatyer (1977) regarding the idea of facilitation by the early-successional species for late-successional species to colonize (Bazzaz, 1979; Bazzaz & Carlson, 1982).

Not just understorey microclimate is impacted by canopy development, but light availability at the forest floor is also highly altered. Canopy openness can be considered a proxy of light availability (Rich *et al.*, 1993). As light availability decreases due to canopy closure, the shade-intolerant species, such as light-demanding introduced herbaceous weeds also decreases (Johnson & Handel, 2016; Wallace *et al.*, 2017). The photosynthetic flexibility for early-successional species such as the herbaceous weeds is high compared to the low photosynthetic flexibility of more desirable, long-lived, woody late-successional species (Bazzaz & Carlson, 1982). Therefore, the extent of canopy presence can dictate what species can persist in the understorey based on their light requirements, and rapid canopy formation can be a viable management strategy to suppress introduced weeds that may outcompete regenerating native tree seedlings.

General effects of altered understorey conditions on the three model experimental late-successional species

We know that forest canopies generally buffer the extremes in climate and therefore can promote survival of most late-successional enrichment plant species that are sensitive to microclimatic conditions (Pothercary, 2012; Wallace *et al.*, 2017; Forbes *et al.*, 2020). However, we must gain a more specific understanding of the extent of individual late-successional species' tolerances, especially within different functional guilds. This will help with informing successful establishment through restoration management actions. The species in this study are from entirely different guilds: an epiphyte, an understorey shrub and a canopy tree, and they fill different ecological roles (Simberloff & Dayan, 1991). Even though they may be present at the same point in forest succession, it is crucial to recognise that not all late-successional guilds will have the same ecological niches, and even those species within a single guild may differ further in their niches (Wilson, 1999) as a result of resource partitioning (Galia Selaya *et al.*, 2008) or competitive exclusion (Valladares *et al.*, 2016).

A buffered understorey microclimate caused by canopy closure is not always worth the trade-off in lost access to light. In my findings, for example, the epiphytic *G. lucida*'s growth rates actually increased significantly with canopy openness and the additional light it provides. This may not be the case for all epiphytes. Despite their collective habit of growing on trees, the physiological requirements for light vary hugely for epiphytic plant species (Zotz, 2016). Research suggests that *G. lucida* requires high light environments, as it is commonly found on trees growing in or on the edge of canopy gaps (Smale & Gardner, 1999). My results agree with this, indicating that a high degree of light availability is a fundamental niche requirement for *G. lucida* growth. Opposingly, *Piper excelsum*'s relative growth rates decreased under a more open canopy with higher light availability. This is not surprising, as late-successional understorey shrub species, like *P. excelsum,* are often shade-tolerant with growth increasing outside of high light environments (Valladares *et al.*, 2016). This likely comes as a trade-off to take advantage of sheltered understorey conditions, as *P. excelsum* is frost tender (de Lange, 2019). *Dacrydium cupressinum* growth rates were not affected directly by altered understorey conditions following canopy closure. Previous studies on *D. cupressinum* found no growth responses under elevated light levels when compared to responses of other late-successional tree species (Ebbett & Ogden, 1998), and it does not appear affected by temperature or humidity. Therefore, we can conclude that different guilds of late-successional species respond very differently to understorey conditions driven by forest canopy development.

4.2 Experimental plant growth responses to environmental conditions - *Griselinia lucida*

Temperature and Relative Humidity

The mean annual temperature is a major determinant of the distribution of *G. lucida* as it is somewhat sensitive to frost (Bryan *et al.*, 2011). This may not be too much of a constraint when restoring epiphytes to urban forests however, as the urban heat island effect increases the ambient temperatures of the city landscapes (Ziter *et al.,* 2019). One study compared temperatures in *G. lucida*'s natural range distribution with temperatures in the urban experimental forests, and the temperatures of urban sites were indeed, statistically significantly higher (Bryan, 2011). Another study using tropical epiphytic species found increased growth of individuals in warmer climates (Müller *et al.*, 2018). However, the warmer temperatures are possibly having an effect in concert with other variables that are difficult to isolate in a research context, such as water availability, which could also cause a negative physiological response in the epiphytes. This could be a confounding variable in my results as well, as the air temperature is elevated in urban sites due to the urban heat island effect, and therefore vapour pressure deficit is also higher there (Bryan, 2011). A higher vapour pressure deficit means drier conditions, providing a difficult environment for epiphytes to survive in due to the risk of desiccation (Zotz, 2016).

Epiphyte growth generally requires moderate humidity for water security and warm temperatures with a low range of fluctuations to minimise the chance of desiccation (Zotz, 2016). This is because epiphytes have exposed roots that are not directly in the soil, where the water source is more reliable. In epiphytic habitats on host tree branches, ’canopy soil’ forms from the accumulation of detritus and organic material which the epiphytic roots can access (Zotz, 2016). As a part of my method, I artificially introduced canopy soil by using sphagnum moss and coconut fibre, so potentially the *G. lucida* individuals did not respond to changes in humidity as much because these artificial materials provided more water security.

The presence of epiphytes can influence the forest canopy microclimate and the water economy of their host plants (Stanton *et al.*, 2014). The increase of leaf area in canopies containing epiphytes also slows air movement and decreases the boundary-layer conductance of the leaves and how rapidly gas exchange occurs and thus determines the degree of water interception (McJannet *et al.*, 2007). Epiphytes slow the water vapour loss, thus retaining it longer in the forest canopy (Veneklaas *et al.*, 1990). A study conducted in Chile found a significant decrease in the forest floor soil moisture after epiphytes were removed from a host tree (Stanton *et al.*, 2014). The presence of epiphytes can also be viewed as stabilisers of the canopy microclimate by buffering temperature fluctuations (Stanton *et al.*, 2014). This is a trait characteristic of epiphytes that they can have on their ecosystems after establishment, but they first require stable canopy microclimates and adequate light to successfully establish (Bryan *et al.*, 2011; Zotz, 2016). However, for *G. lucida* specifically to establish and affect the forest canopy microclimate, my results suggest temperature and humidity stability did not influence their establishment.

Root growth

Epiphytic root growth is often not a good indicator of successful establishment (Zotz, 2013). *Griselinia lucida* will typically establish initial vertical roots followed by lateral roots around the host tree (Dawson, 1966). These clinging roots descend the host trunk at ~1.2 m per year as a response to inadequate resources, such as lack of water and nutrients (Dawson, 1966; Bryan *et al.*, 2011). My observations found vertical root growth down the trunks of the host trees. I found the root growth occurring predominantly on *Cordyline australis* (tī kōuka/cabbage tree) host trees, perhaps due to the rough bark texture that would assist with root attachment and harbour moisture. Rapid root growth of *G. lucida* has been observed in the stringy bark of *Podocarpus totara* (Tōtara) and the fibrous trunks of tree ferns (Bryan *et al.*, 2011). The rough, corky bark of a *C. australis* host, which is also often lacking a fork in the trunk to stabilise epiphytic growth, requires *G. lucida* to invest energy into root growth for stabilisation and water security. Therefore, it may be better to choose host trees with more forked branches for introducing *G. lucida* to restoration plantings, where possible.

Light and trade-offs in Griselinia lucida requirements, as related to host tree size and location in the canopy

My results show that *G. lucida* growth increases when there is more light available due to more open canopies. Thus, light requirements appear to outweigh this species need for a stable microclimate. My methodology of attaching the epiphytic seedlings to the host tree at 1.5 m from the ground regardless of forest age and stage of canopy development meant that older forests with larger trees (and hence more closed canopies) were shading out the experimental epiphytes placed so far from the canopy and any light coming through it. Epiphytes tend to naturally establish around the middle and higher portions of the canopy (Freiberg, 1996; Rudolph *et al.*, 1998). When observing epiphytes in an individual host tree, there is typically a positive correlation between epiphyte species richness and individual host tree size, due to the size of the crown and hence available perching locations (Flores-Palacios & García-Franco, 2006). Within the host tree, the thinner, younger host tree branches growing on the periphery of the tree act as a 'net' for wind-dispersed epiphyte seeds, while also providing high light conditions for seed germination (Rudolph *et al.*, 1998). By the time the epiphytes reach adulthood, the host tree branches have also grown and can support epiphyte weight and provide arboreal detritus around them. For maximising successful establishment, planting *G. lucida* juveniles within the crown and periphery of larger host trees would be more in line with my results and other observations of naturally occurring individuals (Bryan, 2011).

Seeds of epiphytes are mostly dispersed by the wind (Rudolph *et al.*, 1998; Zotz, 2016). In contrast, natural dispersal of my model species, *G. lucida,* is by birds as the flesh of the fruit needs to be removed by them through ingestion, for eventual deposit and seed germination (Thorsen *et al.*, 2009; Bryan *et al.*, 2011). Furthermore, *G. lucida* seeds require high light conditions to germinate, such as those on the exterior of the host tree branches (Burrows, 1999). However, in urban forest ecosystems, there are very small populations of epiphytes, and therefore spread is limited by both seed availability and bird-dispersal (Overdyck & Clarkson, 2012). As a result, *G. lucida* needs enrichment planting intervention. For successful establishment they should be introduced into high light conditions, as evidenced by my findings.

Colonisation theories for epiphytes suggest that time and space are most important for their establishment and species richness (Zotz, 2016). The older the host-tree is, the longer it is available for colonisation, and the larger the host-tree crown is, the more space is offered for seeds to successfully lodge into a stable crevice (Zotz, 2016). Like all succession, epiphytic succession begins with early colonist species tolerant to drought and low-nutrient stresses in younger, exposed forests and trees, followed by the less tolerant, longer-lived species (Giordano *et al.*, 2004; Burns, 2007). *Griselinia lucida* is a late-successional epiphytic species which naturally occurs more in old-growth forests (Bryan *et al.*, 2011). Therefore, we may be able to accelerate its establishment in forests undergoing restoration, but must understand its niche requirements and limitations when doing so.

4.3 Experimental plant growth responses to environmental conditions - *Piper excelsum*

<u>Relative growth rate, air temperature and RH</u>

The relative growth rate of entire *P. excelsum* plants, as well as more specifically, their rate of leaf growth, both tended to decrease under more open canopies. This suggests that the shelter of the canopy was protecting the *P. excelsum* juveniles from extreme variation in microclimate conditions, such as the low temperatures causing frosts which *P. excelsum* is sensitive to (de Lange, 2019). Less leaf growth under a more open canopy is a typical characteristic of late-successional plant species (Galia Selaya *et al.*, 2008; Hagemeier & Leuschner, 2019), an opposite response to that of early and mid-successional understorey shrub species. For some early-successional understorey shrubs, the relative growth rate increased with more canopy openness (Chacón & Armesto, 2005). *Piper excelsum*'s response to canopy openness is in contrast to that of *G. lucida*, which requires more light despite the trade-off causing more exposed microclimate conditions. With higher air and soil temperatures, a decrease in *P. excelsum* growth may be due to the positive relationship between air temperatures and water vapour deficit, which may be causing water stress (Tibbitts, 1979).

My results showed an increase in *P. excelsum* growth rates with higher relative humidity. This aligns with the observations of the close relative of *P. excelsum*, *P. methysticum*, where under humid conditions, its growth rate increases (Dyer & Palmer, 2004). Research has found a positive relationship between relative humidity and soil moisture, where humidity explains the variation in the soil moisture (Ravi & D'Odorico, 2005). Within a restoration management context, this implies that planting *P. excelsum* in a location where the soil moisture or humidity are known to be high, may provide conditions favouring increased plant growth and survival.

Soil temperature and speculation about soil moisture

Soil conditions are likely important for *P. excelsum* growth (de Lange, 2019). For example, two *P. excelsum* individuals within one of the research plots appeared to have greater growth, far exceeding the rest of the individuals studied, and this may be caused by the greater soil moisture availability at this site. These individuals, with large increases in both leaf number and stem width, were located in a deep gully near a stream (~5 m). Plant growth is affected by soil quality, and the physical properties of different soil types affect nutrient and water availability, as well as altering the soil biology (Hawkins, 1962; Mohi, 2001; Bünemann *et al.*, 2018). Furthermore, soil type and properties differ between early, mid and late-successional forests and significantly contribute to plant growth, and thus the entire ecosystem development along with the environmental conditions (Kardol *et al.*, 2006). It appears that *P. excelsum* grows well within permanently moist soil (de Lange, 2019), hence this may be another reason that *P. excelsum* establishes better under a canopy which protects the soil from excessive drying due to sunlight. For all of the *Piper* genus, plant abundance increases in wetter regions (Dyer & Palmer, 2004). Additionally, *Piper* plant height increased more than other understorey shrub guild species when the sites were “moist” (Harrington *et al.*, 2002). This interesting observation from two individuals in my study suggests ideas for further research, for example, to include the measurement of soil moisture relative to plant growth, of which the results may have important implications for planning of restoration planting.

Effects of biomass allocation in Piper excelsum *growth response*

My results indicate that *P. excelsum* individuals did not have consistent growth responses for all parts of a plant’s anatomy. Some individuals grew wider stems in some forest sites while some grew taller in other sites. This may be due to differential biomass allocation, where, in different environments, plants will allocate energy to growth in different ways (Poorter *et al.*, 2012). Changes in plant architecture between shoots, roots, leaves or stem width may vary between species as they operate different physiologically (Poorter *et al.*, 2012). Different biomass allocations may result from each species optimising the available resources for their requirements (Bloom *et al.*, 1985). Different species have different strategies for investing in their root systems or other parts of their structure. In my research, the growth allocation of *P. excelsum* was not measured across all parts of the plant, e.g., such as the roots. However, where it was measured, more or less growth between height and stem width may not indicate unsuitable planting conditions, but instead different allocations of growth in different environments. A study looking at two understorey shrub species with intermediate shade-tolerance found canopy openness significantly affected their root and leaf allocation such that under a more open canopy, root growth increased, and when the canopy was closed, there was more leaf growth instead (Chacón & Armesto, 2005).

Unexpected reductions in Piper excelsum heights

In some of the experimental plots, *P. excelsum* was surprisingly shorter than when initially planted (n = 8, decreased heights ranged from 8-214 mm), suggesting vertebrate herbivory or other damaging forces could be causing the dramatic change in plant height. However, the possibility of browsing from introduced invasive mammalian species on *P. excelsum* affecting plant height results is unlikely. *Piper excelsum* is said to be generally unpalatable other than the larvae of one geometrid moth species (*Cleora scriptaia*) that tolerates *P. excelsum*'s otherwise insect-repellent defensive compounds (Hodge *et al*., 2000). Research on introduced invasive mammals in Aotearoa New Zealand cities has found cats, hedgehogs, rats and mice to be the most abundant within cities (Morgan *et al.*, 2009); however, these species are not herbivores (Lee, 2005). Possums affect plant growth by herbivory browse; however, their presence in cities is scarce, except for Dunedin which has higher abundances of possums and hedgehogs than the other cities (N. Fitzgerald, personal communication, November 21, 2019).

Cultural aspects of incorporating Piper excelsum *in urban forest restoration*

In Aotearoa New Zealand, the traditional herbal medicine practiced by the Indigenous Peoples (Māori) is known as Rongoā Māori. This medicinal practice uses plants for holistic healing (Ahuriri-Driscoll, 2014), and *P. excelsum* is a key focal species. Rongoā Māori is not only about physical healing, but also about restoring the spiritual connection between humans and the land, and can therefore indirectly help facilitate the restoration of the land's ecology as well (McGowan, 2009). Generally, the plants used for Rongoā are early-successional species, making them easy elements to incorporate into urban restoration planning (McGowan, 2009). Planting these species not only increases species richness but would also contribute to keeping the Mātauranga Māori (traditional Māori knowledge) associated with their use available to urban dwellers (McGowan, 2009). In Aotearoa New Zealand an increasing number of people, specifically Māori, are moving into urban centres from their rural tribal area. For example, over the 20th century, the percentage of the country's total Māori population that were living in cities increased from 15.6% to +85% (Statistics New Zealand, 2005). This rapid increase of the Māori population in cities would suggest that there is a requirement for Rongoā Māori within the urban areas, as well as the gathering and collection of materials like *P. excelsum*.

During urban forest restoration, it would be beneficial to consider Rongoā Māori conceptual frameworks as a guide to imitate the natural regeneration of the land but also to make Rongoā species more accessible to urban-dwelling Māori for cultural harvesting (Wehi & Wehi, 2010). Rongoā practitioners (Tohunga) are well acquainted with the local flora and fauna, and may also provide insight as to what originally grew in target restoration areas (Taiepa *et al.*, 1997) that are now part of urban landscapes. Urban planning and greening should work alongside the local Indigenous Peoples to identify the crucial species of cultural importance and how it is best to incorporate them into the urban ecosystem (Uprety *et al.*, 2012).

Piper excelsum has been an 'ambassador' species for Rongoā as it is easy to identify and has a widespread natural range (McGowan, 2009). Many people associate Rongoā Māori with *P. excelsum* because it is used for many ailments, such as pain relief and is thought to improve the efficiency of the heart, liver and kidney function (R. McGowan, personal communication, September 14, 2019). *Piper excelsum* could be, and already is, a gateway species for increasing understanding of Rongoā Māori. Successfully re-introducing *P. excelsum* into urban forests via enrichment planting will bring not only ecological benefits but also a reconnection with the land.

Māori understand that Rongoā Māori also heals the land, but it appears that few practitioners of urban forest restoration are considering the benefits that Rongoā provides (Busbridge, in revision). There are protocols for Rongoā harvesting that restoration practitioners should consider before planting. For example, *P. excelsum* leaves collected for Rongoā should be from leaves which receive the morning sun (R. McGowan, personal communication, September 14, 2019). This suggests that while planting *P. excelsum* during forest restoration, it would be culturally beneficial if a certain proportion are planted on the eastern side of the forest patch. Other research has investigated how forests environmental condition's affect *P. excelsum* oil production, finding oils were produced in higher quantities in the leaves which were partially shaded (Mohi, 2001) and harvested in the morning (Smith, 1999). Understanding how enrichment plants are used for Rongoā and purposefully incorporating them in restoration planning will enhance the biodiversity within urban forests, while also restoring important cultural practices.

4.4 Experimental plant growth responses to environmental conditions - *Dacrydium cupressinum*

Light and the relationship with herbaceous weeds

The growth performance of plants in response to light intensity varies depending on the age or growth stage of the individual (Kunstler *et al.*, 2009). *Dacrydium cupressinum* seedlings have been known to lack responses to light intensity, which demonstrates its shade-tolerance (June, 1982; Ebbett & Ogden, 1998). However, in contrast to this and my findings, a review of knowledge of on *D. cupressinum* found increases in one-year-old seedling heights with increasing light intensity (Norton *et al.*, 1988). My results did not show a relationship between canopy openness (a proxy for light) and the growth rate of *D. cupressinum* juveniles. This may be because the variation in growth response to light availability is often dependent on the age or growth stage of the individual plant (McEwen, 1983; Smale & Kimberley, 1986; Kunstler *et al.*, 2009). It may also be dictated by the juvenile plant's competition context (e.g., Smale and Kimberley (1986) were studying juveniles in a mature, relatively undisturbed rural forest, while my work was in weed-infested urban forest understoreys). Older, larger *D. cupressinum* saplings display a positive growth response to light intensity (Cameron, 1963; Kunstler *et al.*, 2009), likely because at that growth stage they are responding to reach the canopy. When comparing trade-off strategies between other Aotearoa New Zealand native tree seedlings, variation in growth responses are suggested to be caused by a trade-off for slow-growing but shade-tolerant seedlings, or fast-growing but shade-intolerant seedlings (Kunstler *et al.*, 2009).

My results possibly show there are opposing responses of plant height and stem width to a canopy openness gradient. This suggests the plants are possibly allocating biomass to their stem when there is readily available light (an open canopy). A study by Ebbett and Ogden (1998) also found the stem width of *D. cupressinum* increased with higher light intensity in glasshouse and forest experiments. Ebbett and Ogden (1998) did not find a trade-off with height growth, but the *D. cupressinum* plant height measurement they took had negligible growth as light intensity increased (Ebbett & Ogden, 1998).

The lack of *D. cupressinum*'s response to light could be due to the competition with introduced herbaceous weed cover for light (Wallace *et al.*, 2017; Laughlin & Clarkson, 2018). For example, an open canopy allowing more light to the forest floor promotes conditions for introduced herbaceous weeds, which are common in city forests. My multiple regression results showed that the weed cover explains changes in stem width of *D. cupressinum* more than air temperature fluctuations do. As herbaceous weed cover increases, so does the stem width of *D. cupressinum* and the plant height tends to be shorter, a biomass allocation strategy that *Quercus liaotungensis* (Liaodong oak) also displays (Yang *et al.*, 2019). There is a positive correlation between the intensity of competition and the root biomass, reducing the allocation to the height and branches (Yang *et al.*, 2019). This suggests that *D. cupressinum* that do not have to compete for space may instead be competing more intensively belowground.

This could be an important trade-off affecting growth and stability later in life, as research has found that *D. cupressinum* seedlings do generally have weak root systems, particularly under low light levels (Cameron, 1963; Norton *et al.*, 1988). A study on other conifer species found the same biomass allocation response, where low light (e.g., competition aboveground) caused aboveground biomass allocation (Kneeshaw *et al.*, 2002). This was in the context of a forest canopy gap, where the root growth response to low light increased more than the stem width and plant height did. Kneeshaw *et al.* (2002) discuss this occurrence being due to the initial functional balance requirements, where the roots grow to meet the structural needs before the tree can allocate growth into plant height. Further to structural requirements, under higher light conditions, rapid root growth will be in response to the need for water and nutrients due to the heightened threat of desiccation from evapotranspiration (Yin *et al.*, 2008).

Temperature response and biomass allocation

Higher temperatures tend to positively drive *D. cupressinum* growth (McEwen, 1983), with the optimum temperature for net photosynthesis at about 27°C (Hawkins & Sweet, 1989). My results align with this and show that higher air temperatures were associated with taller *D. cupressinum* plants with thinner stems. This increased height response to increased temperature is consistent with previous research on coniferous tree species where the stems, plant height and overall biomass of the studied conifers increased with temperature (Domisch *et al.*, 2002; Danby & Hik, 2007; Yin *et al.*, 2008; Zhao & Liu, 2008).

The natural distribution of *D. cupressinum* is Aotearoa New Zealand wide (Norton *et al.*, 1988). The findings of *D. cupressinum* growing best when the temperatures are warmer would suggest higher growth rates in the North Island than in the South Island. However, McEwen (1983) found that fewer fluctuations in the air temperature were also a driver of the distribution and successful establishment of *D. cupressinum*. This is also confirmed by my results, as the *D. cupressinum* plants grew best under stable air temperatures.

Generally, biomass allocation appears to be a very plastic trait for *D. cupressinum,* with allocation controlled in part by air temperature but influenced by other factors as well. Hawkins and Sweet (1989) found that at optimal growing temperatures, *D. cupressinum* put a significantly higher proportion of resources into root tissue than four other tree species did. However, increased root biomass allocation can also be a response to limited belowground resources (Zhao & Liu, 2008). While comparing two coniferous species, Yin *et al.,* (2008) found one species increased root biomass and the other species decreased root biomass under warmer temperatures. The response may be determined by water availability, as an increase of root biomass due to warmer temperatures would be an advantage, as water stress would increase with an increase in temperature. A decrease in root biomass (assuming a resulting increase in aboveground biomass) would maximise competition for light (Yin *et al.*, 2008).

My results showed *D. cupressinum* changed its mode of biomass allocation differently whether the driver was mean air temperature or fluctuations in air temperature. Under widely fluctuating temperatures the stem widths were wider, and the plants were shorter. Air temperatures tend to range less when buffered by the vegetation of a late-successional canopy (Bazzaz, 1979). There is little other research on how air temperature fluctuations might affect biomass allocation in plants (and specifically stem width). As a result, it is difficult to determine whether the primary driver of increasing stem width is canopy openness or air temperature fluctuations, especially due to that nature of these variables' collinear relationship (i.e., canopy openness causes temperature fluctuations). There is generally thought to be a positive correlation between canopy openness and air temperature fluctuations (Chen *et al.*, 1993; Frey *et al.*, 2016). Although not a significant relationship, my results show the stem width appears to increase as canopy openness increases. Furthermore, there is a significant positive relationship between air temperature fluctuations and the stem width of *D. cupressinum*. My work indicates that although light might not be a major driver of *D. cupressinum* stem width growth, air temperature fluctuations are.

4.5 Urban Forest Restoration Management Implications

It is important to conduct enrichment planting of late-successional species during forest development with particular regard to their environmental requirements. Awareness of different requirements of different guilds can be helpful.

For the epiphyte *Griselinia lucida,* the primary driver of growth is light. Secondarily, the stable microclimate conditions (e.g., temperature and humidity) created by canopy presence are likely to be necessary as long as the plant receives adequate light. Thus, *G. lucida* should be "planted", or attached to host trees at high positions in their crowns, hence requiring planted forest age to be fairly advanced before planting can occur, at least several decades old. This species is truly a late-successional plant. Furthermore, the importance of nest epiphyte clump associations is often overlooked; again, a function of size and age of the host tree but in particular because nest epiphyte clumps provide nutrients and water. As well, *G. lucida* is a hemi-epiphyte and without root connection to the ground will not reach its full potential.

For *Piper excelsum,* the primary driver for growth is high relative humidity. Regions of Aotearoa New Zealand with higher mean humidity levels will provide better results in *P. excelsum* growth than drier areas, but microclimate within each forest should also be considered as a humid microclimate is possible in a dry region. Planting under a closed canopy that causes humid understorey conditions could also increase leaf growth and plant survival. Additionally, when planting culturally significant species like *P. excelsum,* it is important to consider cultural implications in restoration practice. This may include creating respectful partnerships with local Indigenous People to develop better understandings of individual plants for use in urban forest restoration planning. For example, a clearer understanding of *P. excelsum* within Te Ao Māori (the Māori worldview) will enhance restoration outcomes so that more *P. excelsum* plants may be available for Rongoā Māori (traditional herbal medicine), and a respectful, balanced relationship between Indigenous and non-Indigenous people can also be developed.

For *Dacrydium cupressinum,* the primary driver of plant height growth within an urban restoration setting is higher air temperatures with less fluctuation. Thus, ideal planting conditions are in older restored forests with closed canopies. These closed canopies will also limit light reaching the forest floor, reducing the introduced herbaceous weed competition and creating a microclimate that buffers the temperature fluctuations. However, *D. cupressinum* needs managing into a canopy gap to become a tall emergent unless it is included in the mid-successional plantings with discontinuous canopies where it can grow to the canopy before it closes completely. Furthermore, areas with a warmer mean air temperature will likely cause more rapid responses in *D. cupressinum* plant height growth. To overcome competition from shade-tolerant introduced herbaceous weed weeds (e.g., *Tradescantia fluminensis,* wandering willie), it is best to plant taller enrichment juveniles (Wallace, 2017). Taller plants will also be more resilient to any harsh environmental conditions (Mangueira *et al.*, 2019).

4.6 Future research

This thesis research has demonstrated different (and sometimes opposing) optimal conditions for various aspects of the growth of the three model enrichment species. Therefore, further research should focus on other late-successional enrichment species in these three guilds to determine whether these findings are representative of these guilds more widely. Furthermore, little is known about many other late-successional plant species' ideal growing conditions in relation to forest restoration management. The knowledge gaps regarding late-successional plant growth identified throughout writing this thesis include: environmental condition requirements for other functional guilds (e.g., plant parasites like *Dactylanthus taylorii*), underground biomass allocation, effects of soil type and soil compaction, the importance of juvenile age when planted, and the socio-ecological and cultural aspects of urban forest restoration.

Late-successional plant functional guilds are rarely incorporated into forest restoration work (even more so, urban forest restoration) and therefore have had little research conducted on them. Epiphytes do not have established planting techniques available to follow because they are perched on a host tree rather than in the soil. Future research into how and where it is best to introduce epiphytes into urban forest ecosystem development would likely increase the biodiversity and dynamics of urban forests. Additional late-successional plant guilds should be researched and may also need to be used in enrichment planting of urban forests, such as vines or parasitic plants.

A great deal of research indicates that belowground biomass allocations vary as environmental conditions change. Further research focusing on how the terrestrial enrichment species studied here are allocating resources belowground to root growth will demonstrate how these particular species responds to trade-offs between growth or vulnerability to exposure.

Soil type has a considerable effect on nutrient and water availability for plants (Bünemann *et al.*, 2018). As forests ecosystems go through succession aboveground, the belowground dynamics are also changing (Kardol *et al.*, 2006). Future research should focus on the stages of belowground succession and its effects on the survival of late-successional plants adapted to those soils. Furthermore, the different soil types may be playing a part in the growth responses and survival of the terrestrial enrichment plants. Therefore, understanding the preferred soil types for each enrichment species would benefit the restored forests.

Previous research has identified the age of *D. cupressinum* seedlings when first planted varies the growth response to different environmental conditions (Kunstler *et al.*, 2009). It would be beneficial to identify the threshold to plant the youngest possible enrichment juvenile while still maximising the chance of survival.

Lastly, socio-ecological aspects of urban forest restoration management may include the input and perspectives from local indigenous knowledge holders (Wehi & Lord, 2017; Mata *et al.*, 2020). Indigenous Peoples believe they are inseparable from the environment, and their ancient knowledge about the natural world is built on a much larger timescale than that of modern-day scientific research trials. I advocate for future partnerships that expand across culture, ethnicity and race within the urban areas under restoration. Creating a space for equal power and respect between modern-day science and local indigenous knowledge would benefit the environment by refining restoration practice, but also produce social benefits of reconnection to the land for many more urban-dwellers (Uprety *et al.*, 2012; Broughton & McBreen, 2015; Mata *et al.*, 2020).

4.7 Conclusion

In summary, this thesis demonstrates the importance of understanding late-successional plant species environmental niches to conduct successful enrichment planting in urban forest restoration. Introducing late-successional plants into urban forests benefits all urban-dwellers through the manifold ecosystem services they provide. However, to be successful in the restoration of these species, careful urban forest restoration planning must include knowledge about their niche requirements to increase their chance of survival and growth. My research found that *G. lucida, P. excelsum* and *D. cupressinum* juveniles had a 75.5%, 100% and 75% chance of survival, respectively, after one year in the urban forests of three cities in Aotearoa New Zealand. I also found that the formation of a forest canopy is crucial for buffering extreme environmental conditions such as macroclimate and creating a hospitable understorey for juvenile enrichment plants. I found a threshold in canopy closure (~70%

closure) at 10.88 years since the initial cohort of tree planting, and a threshold in understorey humidity (~80% closure) at 33.86 years since that planting, after canopy closure.

I determined that as forests developed, canopy openness affected each model enrichment species differently. *Griselinia lucida* grew more when the host trees were smaller because it needed the light from the more open canopy, whereas *P. excelsum* grew more when the canopy was closed, under more humid conditions, and when the air temperatures were lower. Enrichment planting of *P. excelsum* using this knowledge will benefit local Māori who use *P. excelsum* as a medicine as it will be more accessible and grow more robustly. *Dacrydium cupressinum* is shade-tolerant, and its growth varied due to different biomass allocations and grew more when the air temperature was higher, and there were fewer competing weeds. Informed planting of late-successional species to ensure forest maturation, stability and longevity is vital in urban forest restoration to provide the flourishing and self-perpetuating forests we are aiming to re-create.

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Appendices

Table A.1: Restored urban forest patches used in this study. City, forest site name, year planted with current forest age, size of the forest patch, and coordinates are shown.

City name	Forest site name	Year planted (age in 2019)	Forest patch size (ha)	Coordinates
Hamilton	Waiwhakareke young	2012 (7)	7.95	37°46’14.83” S 175°13’15.56” E
	Avalon	2006 (13)	0.46	37°46’13.50” S 175°14’29.08” E
	Waiwhakareke old	2005 (14)	1.32	37°77’10.31” S 175°22’46.84” E
	Featherstone	2001 (18)	0.10	37°44’01.06” S 175°14’15.26” E
	Hamilton lake	1999 (20)	3.20	37°47’32.70” S 175°16’28.53” E
	Brymer	1996 (23)	1.10	37°46’55.80” S 175°13’35.80” E
	Tills	1995 (24)	0.40	37°48’09.86” S 175°13’59.04” E
	Tauhara	1988 (31)	0.83	37°44’37.97” S 175°15’49.49” E
	Minogue	1980 (39)	2.44	37°46’25.74” S 175°14’59.03” E
New Plymouth	Herekawe coastal	2014 (5)	8.90	39°04’13.49” S 174°01’18.58” E
	Pukekura park	2008 (11)	18.80	39°04’21.84” S 174°05’15.99” E
	Peringa park	2006 (13)	1.19	39°02’32.90” S 174°06’42.54” E
	Te Henui	2005 (14)	12.00	39°04’21.88” S 174°05’45.26” E
	Herekawe inland	2002 (17)	2.71	39°04’35.84” S 174°01’41.67” E
	Salaman reserve	1991 (28)	4.26	39°04’46.23” S 174°03’50.01” E
	Airport	1990 (29)	1.31	39°01’48.99” S 174°09’58.20” E
	Waipu lagoon	1988 (31)	1.49	39°01’48.75” S 174°08’13.34” E
	Huatoki restored	1972 (47)	30.00	39°05’01.01” S 174°04’34.72” E
Napier	Halliwell reserve	2012 (7)	1.37	39°31’30.51” S 176°50’35.87” E
	Harakeke reserve	2011 (8)	0.37	39°30’55.78” S 176°54’38.02” E
	Dolbel young	2010 (9)	7.20	39°32’06.53” S 176°50’05.37” E
	Westshore reserve	1999 (20)	0.60	39°28’41.65” S 176°52’30.28” E
	Karamu stream	1998 (21)	0.10	39°39’49.12” S 176°52’34.92” E
	Dolbel kauri walkway	1995 (24)	11.00	39°32’03.75” S 176°50’07.06” E
	Dolbel Colenso block	1995 (24)	0.28	39°32’16.35” S 176°50’06.39” E
	Otatara park	1993 (26)	0.65	39°32’35.40” S 176°50’11.22” E
	Friends bush	1981 (38)	0.34	39°32’14.62” S 176°51’53.99” E

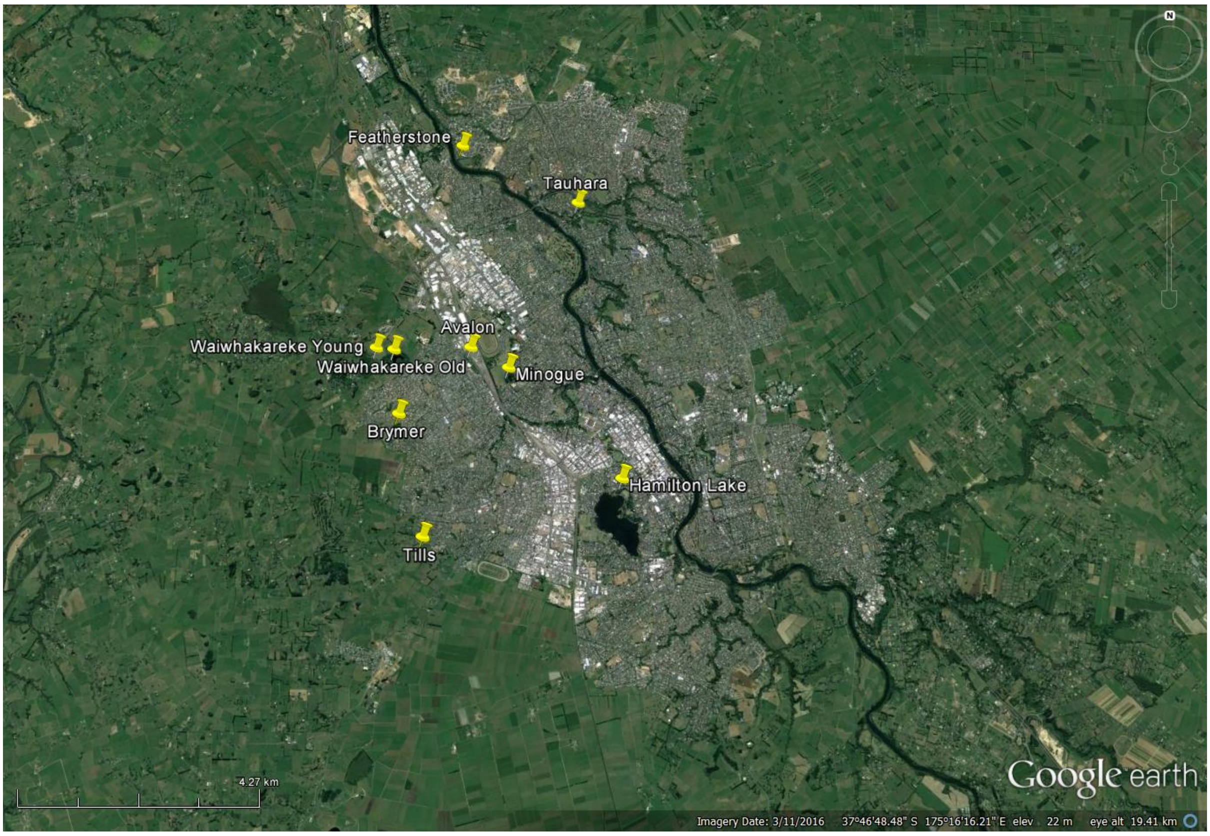

Figure A.1: Restored urban forest locations in Hamilton (Google Earth).

Figure A.2: Restored urban forest locations in New Plymouth (Google Earth).

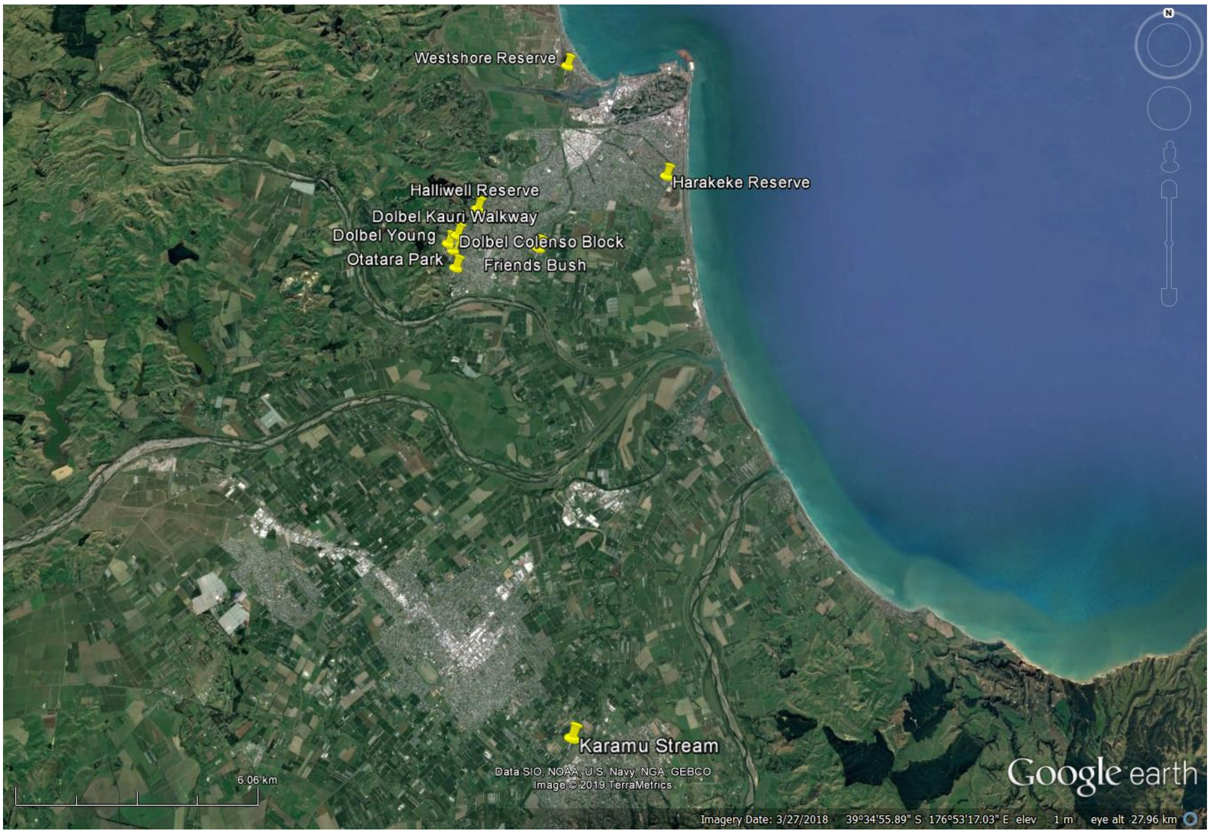

Figure A.3: Restored urban forest locations in Napier (Google Earth).