Ecology of vascular epiphytes in urban forests with special reference to the shrub epiphyte *Griselinia lucida*

A thesis submitted in partial fulfilment

of the requirements for the degree

of

Master of Science in Biological Sciences

at

The University of Waikato

by

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KO TE TANGATA

THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

2011

Abstract

This research investigated the ecology of vascular epiphytes and vines in the Waikato region of the North Island, and the water relations of the shrub hemiepiphyte *Griselinia lucida*. The main goal was to develop robust recommendations for the inclusion of epiphytic species in urban forest restoration projects. To achieve this, three broad questions were addressed:

1. How are vascular epiphytes and vines distributed throughout the nonurban and urban areas of the Waikato region, and how does this compare to other North Island areas?
2. Why are some epiphyte and vine species absent from urban Hamilton and what opportunities exist for their inclusion in restoration projects?
3. How does *Griselinia lucida* respond to desiccation stress and how does this compare to its congener *G. littoralis*?

To investigate questions one and two, an ecological survey of the epiphyte communities on host trees in Waikato (n=649) and Taranaki (n=101) was conducted, alongside canopy microclimate monitoring in five Waikato sites. Results show that epiphyte and vine populations in Hamilton City forests represent only 55.2 % of the total Waikato species pool, and have a very low average of 0.8 epiphyte species per host. In contrast, the urban forests of Taranaki support 87.9 % of the local species pool and have an average of 5.5 species per host tree. The low diversity and abundance in urban Waikato can be primarily attributed to the alteration of canopy microclimates by edge effects. Mean temperature and vapour pressure deficits in Waikato were 1.9 °C and 1.1 kPa (respectively) higher in the canopy of small urban patches than the larger, nonurban forests. These warmer and drier conditions are speculated to be interrupting species accumulation and community formation processes. This phenomenom is not as pronounced in Taranaki which has larger trees and higher rainfall. Epiphyte diversity and abundance was also found to be associated with seed dispersal distances and the size, bark type, and architecture of host trees.

To link the microclimate findings with physiological limitations of epiphytes and to address question three, a desiccation tolerance experiment was conducted on the shrub hemiepiphyte *Griselinia lucida*. Moderate and severe levels of desiccation stress were applied to seedlings of *G. lucida* and its terrestrial congener, *G. littoralis*. Both species endured over two months of drought with negligible mortality. In *G. lucida*, stomatal conductance reduced to zero, and leaf bulk elastic modulus reduced from 8.09 (±0.51) MPa in the control group to 3.66 (±0.61) MPa under severe stress. When compared to *G. littoralis*, *G. lucida* exhibited a more acute response to stress and recovered faster with rewatering. However, the overall response of each species was similar and both species can be classified as desiccation postponers.

To summarise and combine the findings of this research with existing information on *Griselinia lucida*, a contribution to the New Zealand Biological Flora Series for this species is presented.

Recommendations for the inclusion of epiphytes in restoration projects are presented. Reintroductions should use epiphyte and vine species that are appropriate for the conditions of the target forest, and focus on large host trees in relatively humid microclimates.

Acknowledgments

This Master of Science has been both the most rewarding and most challenging thing I have ever done so I would like to acknowledge the enormous contribution made by the many people who have helped me along the way.

Firstly, I would like to extend my most sincere thanks to my primary supervisor Professor Bruce Clarkson for the endless inspiration and encouragement. The many opportunities you have provided me with have played a huge part in making this experience so awesome.

A huge thank-you also goes to my secondary supervisor, Dr. Michael Clearwater for helping me to learn plant physiology from scratch and for answering my many questions; your input has changed my perspective of science and greatly improved my research, analysis and writing skills.

Enormous thanks go to the two people with whom I have shared many hours of field work, travelling, equipment design and calibration, plant measuring, writing, and stressing, but mainly laughing, mocking, and scheming. Cheers to my fantastic research comrades, Fiona Clarkson and Kieran Miller.

Thanks to Toni Cornes for providing field gear, maps, statistics advice, a welcome whiteboard, and a healthy grounding whenever we lost it. Thanks to Colin Monk for being an endless source of solutions for any and every problem. Thanks also to the friendly people in the biology office and the many other staff who have been helpful throughout the last two years.

Thanks to Stacey Foster, Emma Coleman, Rachel Thomson and Lucy Munro. You have each been very kind in giving me advice, encouragement, and your time, to process data and proofread my work.

Thanks to the people and organisations that have helped fund my studies. Your assistance has significantly reduced my stress levels and made a lot of my research possible. Accordingly, I am grateful to the University of Waikato for the Masters Scholarship and contributions from the FRST urban restoration programme (UOWX0903). Thanks to the NZ Freemasons, the Perry Foundation, the Whakatane Historical Society, Forest and Bird, the Waikato Branch of the New Zealand Federation of Graduate Women, and the Royal Society of New

Zealand for generously awarding me grants or scholarships. Thanks also to the George Mason Charitable Trust, Gary Bastin, and Puke Ariki for funding my research in Taranaki and hosting our presentations.

A lot of my motivation for this work has come from our incredible native forests. For access to these wonderful places I would like to thank the Department of Conservation, Maungatautari Ecological Island Trust, Pukemokemoke Bush Reserve Trust, Hamilton City Council, New Plymouth District Council and private land owners.

In Taranaki, my thanks go to Bill Clarkson for being an invaluable guide around your wonderful local forests and opening your home and nursery to us.

I am very grateful to my friends who have provided not only welcome distractions and enjoyable breaks, but also lots of inspiration as they pursue their own goals. Special thanks to Tess Embling for sharing with me your strength and passion, it will never be forgotten.

Much love to Mum and Dad for your unrelenting encouragement and faith in me, and of course for always being so proud. To my sister Stacey, thanks for your assistance in the lab and for being a listening ear that helped me hold onto some sanity.

Thanks to everyone who has contributed to my research that I have regrettably forgotten to mention, this has been a task achieved with many hands and I truly appreciate every one of them.

Finally, I would like to thank Hadley for being my rock and dealing with everything I have thrown at you. I simply could not have done this without you. Here’s to the future!

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Chapter One: Introduction

This research addresses the challenge of restoring indigenous ecosystems in urban environments, in particular, the guild of vascular epiphytes and vines. This first chapter provides background information on the theory and practice of ecological restoration, and the life history, distribution and restoration potential of New Zealand epiphytes and vines. Following this is an introduction to *Griselinia lucida**; the focal species chosen for this research, and the thesis objectives and outline.

1.1 Ecological Restoration

Restoration ecology is a new science that is continuously developing across the globe to support and inform the modern methods of environmental repair (Hobbs & Norton 1996; Ormerod 2003). Restoration of natural environments has been taking place for centuries, but as our society increasingly perceives environmental degradation as unacceptable, a surge in interest and numbers of active projects has occurred (Reay & Norton 1999; Palmer et al. 2004). It is important to support this activity with appropriate research that develops theoretical concepts, models, and methods. This can then assist restoration practitioners to make informed decisions and increase the scope and success of restoration achievements (Hobbs & Norton 1996; Society for Ecological Restoration International Science & Policy Working Group 2004; Zedler 2005; Cabin et al. 2010).

The motivations for ecological restoration projects are as diverse as the localities in which they occur, but a principal goal for all projects is the preservation and enhancement of biodiversity (Ormerod 2003; Menninger & Palmer 2006). According to the Convention on Biological Diversity (CBD), biodiversity is “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems” (CBD 1992). Biodiversity is important in maintaining ecosystem function, resilience, and services (Walker 1995; Chapin et al. 2000; Ormerod 2003; Menninger & Palmer 2006).

*Species nomenclature follows the New Zealand Plant Conservation Network (NZPCN 2011)

Ecosystem function can be categorised into energy and material processing (e.g. decomposition); accumulation of energy and material stocks (e.g. biomass); and the stability and resilience of these rates and stocks over time (Pacala & Kinzig 2002). Ecosystem resilience, as defined by Folke et al. (2004) is "the capacity of a system to absorb disturbance and reorganise while undergoing change so as to retain essentially the same function, structure, identity, and feedbacks." Function and resilience rely upon biodiversity because genetic, species, and population variation provide a range of functional characteristics and the capacity for response to change (Walker 1995; Folke et al. 2004; Fischer et al. 2006).

According to Daily (1997), ecosystem services are "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life." They are the components of ecosystem function which benefit humankind, for example; water cleansing, nutrient recycling and resource renewal, as well as goods that are used in everyday life such as timber and bio fuel (Daily 1997; Palmer et al. 2004).

Environmental restoration in New Zealand is rapidly growing in both practical and theoretical applications (Norton 2009). Green & Clarkson's (2005) review of the New Zealand Biodiversity Strategy estimated that the number of private or community-led projects restoring, managing, or protecting native ecosystems throughout the country was between 3,000 and 5,000. As of 2007, the Waikato Biodiversity Forum (2007) reported 170 community group restoration projects in the Waikato region. A Google scholar search for articles containing the words "ecological restoration" and "New Zealand" illustrates the significant increase in research conducted in this area, returning 64 articles published in the year 1999 and over 300 for the same search in 2009. Alongside this, most New Zealand universities now offer both study and research opportunities in restoration ecology.

There are many different ecosystems that are degraded by direct and/or indirect human disturbance, from marine estuaries (e.g. Lotze et al. 2006) to alpine herb fields (e.g. Whine & Chilcott 2003). In New Zealand, many restoration projects are directed at temperate forest ecosystems. This is because their difficult terrain has frequently protected them from landuse change and development and thus they are a predominant remaining land cover type throughout the country (Halkett 1991; Wardle 1991). Examples of restoration projects in forest ecosystems include Maungatautari Ecological Island protection and restoration, Hamilton Gullies restoration, Tiritiri Matangi Island restoration, and Karori Sanctuary protection and restoration.

On a national scale, most forest restoration occurs in nonurban settings, for example, pest control by the Department of Conservation in National Parks and Reserves, and forest acquisition and restoration by the New Zealand Native Forests Restoration trust. However, the latest frontier of ecological restoration is within towns and cities (van Andel & Aronson 2006).

Urban and suburban (collectively termed “urban” hereafter) forests often harbour many restoration opportunities; occasionally with high levels of indigenous biodiversity (McKinney 2002; Ingram 2008). Forest fragments frequently exist in public parks, gardens and reserves, adjacent to waterways and roads, in private properties, and other areas protected from development (e.g. Clarkson & McQueen, 2004; National Parks Board Singapore, 2010). Urban forests also often present unique opportunities to restore vegetation types that may be less common throughout the region, such as fertile lowlands which are developed for production in rural settings (Scott et al. 2001; Clarkson et al. 2007).

Over 50 % of people worldwide (United Nations 2007) and 86 % of people in New Zealand live in urban settings (Statistics New Zealand 2006). Miller (2005) explains that residents’ interactions with urban nature can improve not only their appreciation of biodiversity but also their motivation to protect it. Urban forests therefore present an opportunity to educate and engage the public with their local flora and fauna in a way that nonurban forests cannot. Improved public engagement can also create large workforces who are willing to assist with restoration work in their neighbourhood (McKinney 2002; Miller 2005; Ingram 2008).

The dynamic nature of urban forests means that there are many challenges to their restoration, including depleted biodiversity, incessant exotic plant invasions, pest browsing and predation, vandalism, competition for land use, air and soil pollution, altered climates, and forest isolation (McKinney 2002). Also problematic are the many ecosystem components that can and should be considered in planning and implementing restoration projects.

Both urban and nonurban forest restoration projects across the country have celebrated numerous successes, but the complexity of forest ecosystems combined with a lack of experience in this relatively new endeavour, has meant that some components of the forest systems are frequently overlooked (B.D. Clarkson, University of Waikato, pers. comm. 2009). One life form or guild that is regularly left out of research (Burns & Dawson 2005), planning, and implementation of ecological restoration is vascular epiphytes and vines. This discrepancy is reflected by a lack of literature on these plants in restoration, or inclusion of these life forms in New Zealand restoration guides (e.g. Restoring Waikato's Indigenous Biodiversity (Waikato Biodiversity Forum 2006)). Epiphytes and vines should be included in forest restoration efforts because they contribute to biodiversity, ecosystem function, resilience, and services.

This thesis aims to improve our understanding of New Zealand’s vascular epiphytes and vines, and identify the ecological and physiological processes that are important for their future inclusion in ecological restoration theory and practice. This investigation focussed on the Waikato region in the central North Island, New Zealand with an extension to the Taranaki region in the western North Island.

1.2 Epiphytes and vines

Vascular epiphytes and vines are non-parasitic plants that depend on other plants for structural support (Schnitzer & Bongers 2002; Laube & Zotz 2006). The first important differentiation of this guild is between obligate species that primarily occur as epiphytes, and facultative species that grow on all forms of media, or accidental species that only occasionally occur epiphytically (Benzing 2004). The present study focuses on obligate species (Figure 1.1).

Based on life cycles, there are two principal categories of vascular obligate epiphytes; holo- and hemi-epiphytes (Lowman & Rinker 2004). Holoepiphytes are plants that spend their entire life cycle in the canopy (Nieder et al. 2001), while hemiepiphytes spend some stage of their life rooted in terrestrial soil; either starting in the canopy and sending roots to the ground (primary hemiepiphytes), or starting on the ground, growing to the canopy and losing their terrestrial connections (secondary hemiepiphytes) (Putz & Holbrook 1986; Holbrook & Putz 1996a; 1996b; Nieder et al. 2001; Lowman & Rinker 2004; Benzing 2004) (Figure 1.1). There are no native species of secondary hemiepiphyte in New Zealand. Strangler hemiepiphytes are a class of primary hemiepiphyte that continue growing until they are freestanding trees (Putz & Holbrook 1986; Shaw 2004).

Vines are plants that root in terrestrial soil but cannot stand upright without structural support from other plants (Putz & Mooney 1991). They occur as herbaceous or woody forms. Herbaceous vines are predominantly ferns that climb using roots and grow within subcanopies, disturbed areas, or forest edges (Figure 1.2E). Woody vines climb using roots, stems, petioles, tendrils or hooks, and are commonly referred to as lianes or lianas (Dawson 1986; Gentry 1991; Putz & Mooney 1991); the latter term is used in this thesis (Figure 1.1). Lianas grow quickly towards higher light levels and often occupy the upper reaches of forest canopies of mature forests (Gentry 1991; Schnitzer & Bongers 2002).

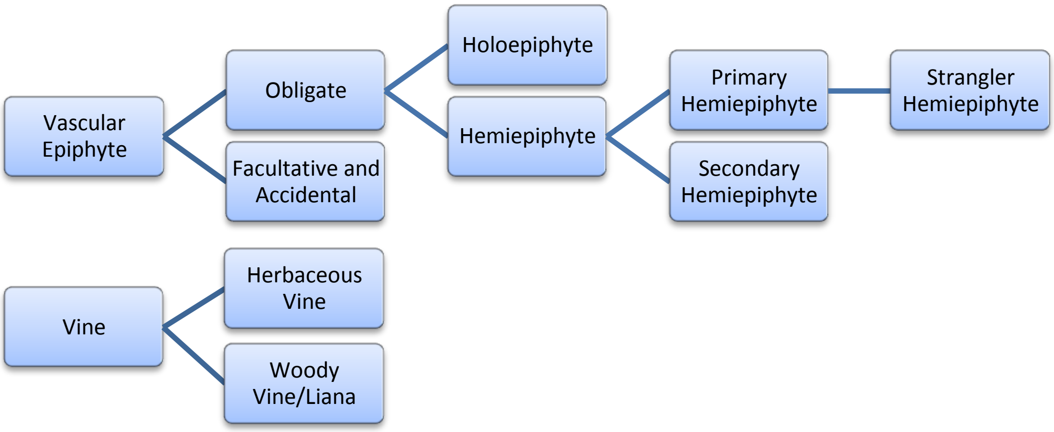

Figure 1.1: Life form classification of vascular epiphytes and vines used in the present study. Compiled from information in Dawson (1986); Gentry (1991); Putz & Mooney (1991); Nieder et al. (2001); Benzing (2004); Lowman & Rinker (2004); Shaw (2004).

Epiphytes constitute ten percent of the world’s vascular plant species and are thus an important component of global plant diversity (Nieder et al. 2001). These plants have evolved in many unrelated taxa around the world (Gentry & Dodson 1987) and are particularly well recognised members of tropical forest ecosystems, where they can represent from 15 to 50 % of total species (Benzing 1990; Dickinson et al. 1993; Zotz 2005; Laube & Zotz 2006). However, New Zealand’s temperate forests have also been shown to host a significant population of diverse epiphyte and vine species (Dickinson et al. 1993; Hofstede et al. 2001; Zotz 2005) (examples provided in Figure 1.2). From five North Island vegetation surveys (Campbell 1984; Clarkson 1985; Clayton-Greene & Wilson 1985; Dawson & Sneddon 1969; Wilcox 1999) the mean number of vascular epiphytes and vines was 45, which represented an average of 19 % of the total species count.

Epiphytes and vines contribute to species richness and play a substantial role in the processes and interactions that make a forest function (Cummings et al. 2006). They constitute a large proportion of photosynthetically active material (Hofstede et al. 2001), and contribute to abiotic processes such as water fluxes and nutrient cycling (Gentry 1991; Holscher et al. 2004), while providing habitat, nectar, water, fruits and nesting materials for invertebrates and birds (Nadkarni & Matelson 1989; Benzing 1990; Gentry 1991; Nadkarni 1992; Affeld 2008; Alvarenga et al. 2009). Therefore, to ensure that restored forests are fully-functioning, it is important that epiphytes are considered in the research, planning, and implementation of ecological restoration (Cummings et al. 2006).

One particularly distinctive element of the New Zealand epiphyte and vine flora is the shrub epiphytes, of which there are four species (Dawson 1986). The present research includes a case study on the obligate shrub epiphyte *Griselinia lucida*.

Figure 1.2: Examples of New Zealand native vascular epiphytes and vines. A: *Drymoanthus adversus*, B: *Hymenophyllum dilatatum*, C: *Metrosideros fulgens*, D: *Collospermum hastatum*, E: *Blechnum filiforme*, F: *Brachyglottis kirkii*, G: *Pyrrosia eleagnifolia*, H: *Earina mucronata.*

1.3 *Griselinia lucida*

Griselinia lucida (Griseliniaceae), or puka, was described by Dawson (1966) as "the most conspicuous shrub epiphyte in the New Zealand rain forest". It is a primary hemiepiphyte with large glossy green leaves and thick fluted roots that often descend the host trunk to access terrestrial soil (Dawson 1966) (Figure 1.3). *G. lucida* is the only indigenous species that commonly makes a connection between a host canopy and the forest floor without losing reliance on the host tree for structural support.

Figure 1.3: Examples of the hemiepiphyte *Griselinia lucida.* A: a juvenile growing in the fork of a large pine tree. B: grooved roots of a mature plant growing on a tawa.

Griselinia lucida generally germinates in the fork of a large host, and often within the canopy soil of existing epiphytic communities. It is most abundant in the humid canopies of old growth forests where it can grow to be a very significant component of the upper forest strata; this author has observed mature *G. lucida* with spans of more than ten metres.

Griselinia lucida primarily grows as an epiphyte but also occupies terrestrial habitats in rocky and coastal environments. In occurs throughout the North Island, in a limited area of the South Island, and on volcanic offshore rocky islands (Wardle 1964; Dawson 1966; Dawson 1986; Julian 1992; Burrows 1999).

1.4 Research Objectives and Questions

The objectives of this research are to enhance the understanding of 1) vascular epiphyte and vine ecology in both nonurban and urban settings, and 2) the physiology of desiccation stress in *Griselinia lucida*. The following broad research questions address these objectives:

1. How are vascular epiphytes and vines distributed throughout the nonurban and urban areas of the Waikato region, and how does this compare to other North Island areas?
2. Why are some epiphyte and vine species absent from urban Hamilton and what opportunities exist for their inclusion in restoration projects?
3. How does *Griselinia lucida* respond to desiccation stress and how does this compare to its congener *G. littoralis*?

1.5 Thesis Outline

The results of research into each of the above questions are presented in four chapters:

Chapter One: Introduction

This chapter provides relevant background information and sets the context for considering epiphytes in urban ecological restoration. It then outlines the research objectives and summarises the thesis content.

Chapter Two: Epiphyte and vine species diversity and abundance in Waikato and Taranaki regions

This chapter presents a literature review on the effects of human activity on indigenous forest. It then utilises an ecological survey of epiphyte populations in Waikato and Taranaki regions to determine which epiphyte and vine species are absent in urban Waikato and identify the key reasons why. This information is used in Chapter Five to develop recommendations for the inclusion of epiphytes in urban restoration.

Chapter Three: Water relations of *Griselinia lucida* and *G. littoralis* under desiccation stress

This chapter surveys the literature on physiological plant stress strategies and presents the results of a drought experiment on the water relations of *Griselinia lucida* under three levels of desiccation stress with a comparison to its congener *G. littoralis*. It then discusses the characteristics of these plants under stress and identifies the predominate stress strategy with which they align.

Chapter Four: Biological Flora of New Zealand. *Griselinia lucida,* puka, akapuka, akakōpuka, shining broadleaf

This chapter is a summary of the findings from this research, alongside a comprehensive review of current literature available on *Griselinia lucida*. It has been prepared in the format of the New Zealand Biological Flora Series (e.g. Wardle 1966; Wehi & Clarkson 2007) and will be submitted to the New Zealand Journal of Botany for publication.

Chapter Five: Synthesis

This chapter summarises the findings of this thesis research and presents the developed recommendations for inclusion of epiphytes and vines in ecological restoration.

Chapter Two: Epiphyte and vine species diversity and abundance in Waikato and Taranaki regions

2.1 Introduction

Deforestation associated with land use change is an ongoing, international phenomenon that creates landscapes of spatially discrete forest fragments (Young & Mitchell 1994) that are surrounded by varying degrees of anthropogenic disturbance and activity (Laurance 2004; Bruna & Kress 2005). This destruction may cause irreversible ecosystem changes that affect all forest life forms and species; including epiphytes and vines (Belinchon et al. 2009).

As forest extent is reduced, the ratio of perimeter to area is enlarged, increasing the area of forest that abruptly meets the distinctly different ecosystems of deforested land. This sharp transition creates an ‘edge effect’ that alters the microclimate, vegetation composition and population structure up to fifty metres in from the forest boundary (Young & Mitchell 1994; Murcia 1995; Denyer et al. 2006). The overall degree of disturbance caused by fragmentation is dependent on the time since isolation, the distance between forest patches, the connectivity between patches, the size and shape of the remnant, and the surrounding landuses (Saunders et al. 1991).

In the canopy, the climate of epiphyte and vine habitat is generally drier and warmer than the understory. Freiberg (1997) found the canopy of a premontane tropical rainforest tree in Costa Rica to be 2-5 °C warmer and 15 % less humid than the ground below it. Forest canopies are also exposed to higher wind speeds and insolation, and more extreme fluctuations in water supply (Madison 1977; Matelson et al. 1993; Holbrook & Putz 1996a). Each of these conditions are intensified by edge effects (Laurance 2004; Werner & Gradstein 2008). Fragmentation also reduces epiphyte substrate through the removal of host trees; even when selective logging is undertaken, there is commonly high post-harvesting mortality of the intended retention trees (Lohmus & Lohmus 2010). Another important consequence of forest fragmentation is the increased dispersal distances for pollen and seed as patch connectivity is reduced and isolation increased (Maschinski 2006; Alvarenga et al. 2009).

As a result of intense human modification and deforestation, forest fragmentation is a dominant feature in the Waikato region of the central North Island. Arrival by Māori around 1300 AD led to initial forest clearances and some exotic plant introductions, but it was in the early 1900's that widespread deforestation by European settlers occurred. This anthropogenic disturbance has been ongoing and, in many places, has resulted in the complete replacement of native flora with introduced agricultural cultivars; especially in lowland and coastal zones (Wardle 1991; Nicholls 2002). The region is now comprised of scattered forest patches representing 25.3 % of the vegetation cover that was present in the 1840's (Leathwick et al. 1995).

The Waikato region includes the Raglan, Kawhia, Hamilton, and Maungatautari Ecological Districts (Figure 2.1) and covers 508,973 ha. Overall, only 15.2 % of indigenous forest still remains in these four districts (separately: 15 %, 36 %, 1.6 % and 9.5 % respectively (Leathwick et al. 1995)). The degree of vegetation fragmentation also varies with a marked gradient of increasing urbanisation from the outer Raglan, Kawhia and Maungatautari districts into the central Hamilton district (Figure 2.1). As seen worldwide, this urbanisation gradient has an increasing human population toward its city which is associated with increasing populations of invasive, exotic plant species and decreasing abundance and diversity of indigenous species (McDonnell & Pickett 1990; McKinney 2002).

Ecological restoration is imperative in these disturbed and highly modified landscapes in order to preserve and enhance the remaining biodiversity along urbanisation gradients. In the Waikato, forest patches are predominantly located on hills; with a smaller proportion in gullies and adjacent to waterways (Clarkson et al. 2002). Many of these forests, especially in gully sites, are the focus of ecological restoration projects run predominantly by community groups and non-profit organisations (for examples see www.waikatobiodiversity.org.nz).

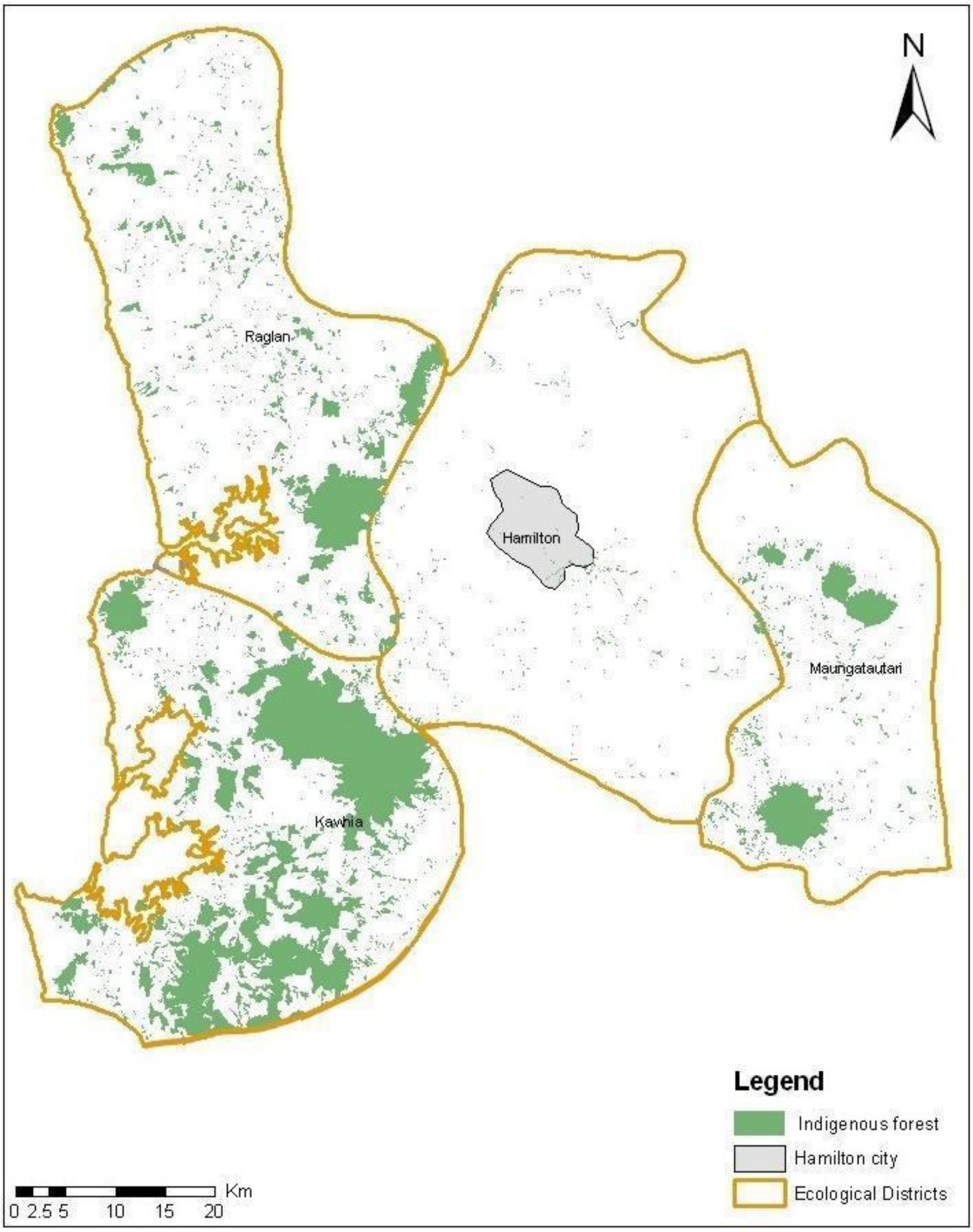

Figure 2.1: The ecological districts of the Waikato region, North Island, New Zealand, that contain study sites. The extent of desforestation throughout the region is show with decreasing vegetation cover and patch size towards Hamilton City. Figure courtesy of T. Cornes.

Urban forest patches of Hamilton City gullies have been the focus of public and private restoration efforts since 2001, or even earlier. Restoration has been encouraged through local council work, public seminars, practical workshops, native plant giveaways and funding programmes (Clarkson & McQueen 2004).

As mentioned in chapter one, restoration programmes regularly overlook epiphyte and vine species that are indigenous to the Waikato region. Information on propagation of suitable species is limited and the plants are not widely available from nurseries. Instead, restoration planners and practitioners primarily focus on canopy and understory species. A valuable opportunity can be found in the current activity and enthusiasm of existing restoration groups, to include epiphyte and vine species in both urban and nonurban forest restoration so that the scope of biodiversity preservation is enhanced.

Differences in vegetation diversity, abundance and assemblages between fragmented forest patches and more intact, old growth forests are often attributed to ecological and environmental variation between these sites (e.g. Saunders et al. 1991; Young & Mitchell 1994; Giordano et al. 2004; Laurance 2004). This holds true for epiphyte and vine species, with factors such as canopy microclimates, host tree characteristics, dispersal distances and successional processes having been identified as important for explaining species absence (e.g. Matelson et al. 1993; Zotz et al. 1999; Wolf 2005; Laube & Zotz 2006). This chapter reports the results of the first investigation into epiphyte and vine populations of the Waikato. It considers which factors best explain local differences between populations in large nonurban forest patches and small urban patches, with the aim of providing informed recommendations for the inclusion of epiphytes and vines in ecological restoration.

On a national scale, the Waikato region, and in particular Hamilton City has relatively depauperate biodiversity and vegetation cover. To provide a wider scope, this chapter also compares Waikato epiphyte and vine populations with the results of a smaller scale study around New Plymouth city in the Taranaki region; an area recognised for relatively high indigenous biodiversity (Clarkson et al. 2007).

2.2 Research objectives and questions

The present study undertakes a quantitative ecological survey of epiphyte and vine populations, to determine species diversity and abundance, and the most influential ecological factors. Temperature and relative humidity measurements are also analysed to determine the potential influence of climatic variables on epiphyte populations, in both urban and nonurban forests of the Waikato region.

This chapter addresses the following broad research questions:

- How are vascular epiphytes and vines distributed throughout the nonurban and urban areas of the Waikato region, and how does this compare to other North Island areas?
- Why are some epiphyte and vine species absent from urban Hamilton and what opportunities exist for their inclusion in restoration projects?

2.3 Methods

2.3.1 Study regions

The Waikato and Taranaki regions are both in the central North Island of New Zealand. Hamilton is the largest city of the Waikato region (population 129,249 (Statistics New Zealand 2006)) and New Plymouth is the largest city of the Taranaki region (population 40,446 (Statistics New Zealand 2006)); both of these urban centres are close the west coast of the North Island which borders the Tasman Sea.

All of the Waikato study sites are in and around the Hamilton basin. The soils of hillslopes and well drained areas are mainly derived from volcanic tephra, while peat predominates in areas where wetlands currently or previously existed. The area experiences moderate rainfall (Table 2.1), warm humid summers, heavy winter frosts, and negligible wind (McEwen 1987).

The Taranaki sites are located on the ring plain of Mount Taranaki which has recent volcanic soils from ashes and lahar deposits. The area experiences prevailing south-westerly winds, humid summers, mild winters, and has relatively high rainfall year round (Table 2.1).

Forests of the Waikato region are more fragmented than those of Taranaki. Waikato has 8,207 separate forest patches with an average size of 196 ha; however the majority (95 %) of these are less than 25 ha. In contrast, Taranaki has 2,850 forest patches with an average size of 121 ha. Therefore, Taranaki provides fewer and generally larger patches than the Waikato, and thus better connectivity between forests (Innes 2010).

Table 2.1: Macroclimate measurements for the cities of each studied region (New Zealand Meteorological Service 1983; Leathwick et al. 2003). (VPD=Vapour pressure deficit).

	Hamilton	New Plymouth
Mean rainfall (mm per annum)	1201	1649
Mean annual air temp. (°C)	13.3	13.5
Mean winter minimum temp. (°C)	5.1	4.4
Mean annual solar radiation (MJ/m^2/day)	14.9	14.7
Mean winter solar radiation (MJ/m^2/day)	5.9	5.0
Mean October (spring) VPD (kPa)	0.37	0.32

2.3.2 Study sites

Study forests were first allocated to three main categories for both the Waikato (Table 2.2) and Taranaki regions (Table 2.3). These cateogires are: mature nonurban forest, mature urban forest, and immature urban forest. The last category was further differentiated into three age classes (5-15, 15-25, and 25-100 years since establishment). These ages were based on available literature and tree coring but were not included in analysis because differences between groups were not significant. The location of study sites in each region is shown in Figure 2.2 and Figure 2.3.

Table 2.2: Waikato forest study sites surveyed for epiphyte and vine populations, categorised by land class, maturity, and age. “Plots” is the number of plots surveyed at each forests (e.g. 5x10= five plots of ten trees); see sampling methods for more detail.

Land class	Maturity	Age class	Forest name/location	Plots
Nonurban	Mature	100+	Maungakawa Scenic Reserve	5x10
			Hakarimata Scenic Reserve	5x10
			Pukemokemoke Bush Reserve	4x10
			Waingaro Forest Reserve	5x10
			Maungatautari Ecological Island	5x10
			Pirongia Forest Park	5x10
Urban	Mature	100+	Claudelands Bush	5x10
			Hammond Bush	5x5
			Berkley Bush	3x5
			Hillcrest Park	5x5
			Mooney Park	3x5
Urban	Immature	25-100	Braithwaite Park	3x5
			Chelmsford Park	3x5
			Pukete Eastern Riverbank	3x5
			Seeley’s Gully	3x5
			River Rd. (Tauhara Gully)	3x5
	Immature	15-25	Howell St. (Hudson Gully)	3x5
			Morrinsville Rd. (Mangaonua Gully)	3x5
			Ranfurly Park	3x5
			St. Andrews Riverbank	3x5
			Rimu St. (Waitawhiriwhiri Gully)	3x5
	Immature	5-15	Ashmore Ct. (Onukutara Gully)	3x5
			Sandford Park (Mangakotukutuku Gully)	3x5
			Pickering Crs. (Onukutara Gully)	3x5
			Porritt Stadium	3x5
			Clements Crs. (Tauhara Gully)	3x5

Table 2.3: Taranaki forest study sites surveyed for epiphyte and vine populations, categorised by land class, maturity and age. “Plots” is the number of plots surveyed at each forests (e.g. 5x10= five plots of ten trees); see sampling methods for more detail.

Land class	Maturity	Age class	Forests	Plots
Nonurban	Mature	100+	Ratapihipihi Scenic Reserve	5x10
Urban	Mature	50-100+	Huatoki Scenic Reserve	4x5
	Mature	25-100+	Sheppards Bush	3x5
	Immature	15-100	Te Henui Walkway Forest	3x5

Figure 2.2: The twenty urban epiphyte and vine survey sites in Hamilton City, Waikato. Figure courtesy of T. Cornes.

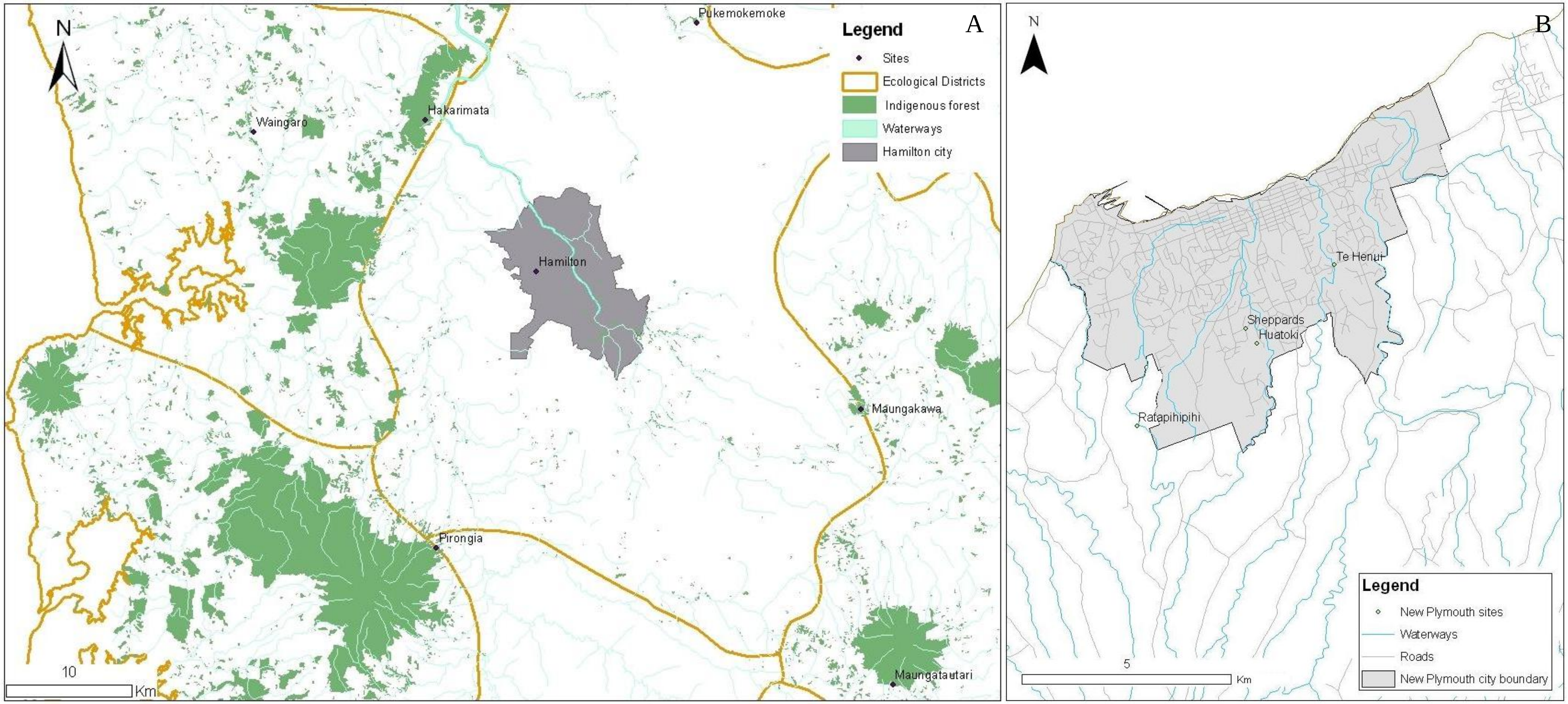

Figure 2.3: A: The six nonurban epiphyte and vine survey sites of the Waikato region in relation to Hamilton city. B: The three urban and one nonurban (Ratapihipihi) epiphyte and vine survey sites in the Taranaki region. Figures courtesy of T. Cornes.

Forest vegetation classification

For each site, a concise forest description is provided, based on published literature, the New Zealand Forest Service mapping series six (Forest Research Institute 1979; 1990), and personal observations. Major vegetation classes represented at each site are incorporated in to the headings and a summarised explanation of each is given below.

Tawa: This class is former rimu-tawa (*Dacrydium cupressinum-Beilschmiedia tawa*) forest in which the softwoods, and sometimes rata (*Metrosideros robusta*), have been felled or destroyed by fires. The main canopy is generally intact and dominated by tawa.

Rimu-tawa: Rimu is scattered but conspicuous; towering above a canopy of hardwoods in which tawa is common throughout.

Kauri-softwoods-hardwoods-beeches: Kauri (*Agathis australis*) stands with sub-dominant hard beech (*Nothofagus truncata*) over regenerating softwoods and hardwoods that have commonly been affected by burning and partial clearing.

Waikato nonurban site descriptions

Maungakawa Scenic Reserve (51 ha): **tawa and rimu-tawa**. Also known as Sanitorium hill (382 m a.s.l), this reserve is situated in central Waikato, includes a 38 ha forest patch, and is the site of the Gudex memorial park (Department of Conservation 2011). The forest was milled after purchase from Māori in 1868 and has a long history of grazing by wandering stock (Gudex 1959; Department of Conservation 2011). The forest is now protected and has native regeneration around both planted and self-establishing exotic species (Department of Conservation 2011). Local community groups and land owners are undertaking ecological restoration and pest control (Cambridge Tree Trust 2010).

Hakarimata Scenic Reserve (1850 ha): rimu-tawa, tawa & kauri-softwoods-hardwoods-beeches. This reserve is within the 2246 ha Hakarimata ranges (374 m above sea level (a.s.l.)) that lie south of Huntly and west of Ngaruawahia. It is approximately 10 km long and has a disturbance history that includes fires, pest browsing and light logging. It has been included in the restoration work of the Hakarimata Restoration Trust since 2001 (Department of Conservation 2011).

Pukemokemoke Bush Reserve (38 ha): kauri-softwoods-hardwoods-beeches & tawa. This forest patch is within 109.5 ha of vegetation that includes pine forest and an unprotected native fragment that borders an active quarry. The site is 20 km northeast of Hamilton on Pukemokemoke hill (166 m a.s.l). In the past the forest has been disturbed by milling and clearance for agriculture but is now under the care of the Friends of Pukemokemoke Bush Reserve (Department of Conservation 2011).

Waingaro Forest Reserve (8 ha): tawa. This forest patch reaches 120 m a.s.l. and is located 25 km northwest of Hamilton and 15 km from the west coast of the North Island. It is on the edge of privately owned pine forests and council-owned native forest that cover a total of 467 ha. The area has a long history of agricultural land use which only ceased with fencing in 1995. Since then, the forest has naturally regenerated with the aid of regular pest control and a small amount of planting (B.D. Clarkson 2004, University of Waikato, unpublished report).

Maungatautari Ecological Island (3363 ha): **rimu-tawa and tawa.** This reserve on Mount Maungatautari **(**797 m a.s.l) is surrounded by a pest-proof fence. It also contains two individually fenced enclosures; the 65 ha southern enclosure, located 35 km from Hamilton, was chosen for epiphyte surveying. In the past, agriculture conversion and pest browsing, particularly by possums, have caused extensive damage to the forest. Intensive protection and restoration through the Maungatautari Ecological Island Trust has been successful in restoring a range of flora and fauna to the reserve (Maungatautari Ecological Island Trust 2002).

Pirongia Forest Park: rimu-tawa & tawa. This western Waikato reserve includes both Mount Pirongia (959 m a.s.l.) and Mount Karioi (756 m a.s.l.). Surveying was only undertaken in 17,225 ha Mount Pirongia forest patch which is approximately 25 km from both Hamilton city and the west coast. Disturbance has included milling, burning and extensive browsing by pests (Department of Conservation 2011). The mountain was given Forest Park status in 1971 and is now the largest unbroken remnant in the Waikato (Pirongia te Aroaro o Kahu Restoration Society 2010). Ecological restoration in the area is being undertaken by the Pirongia te Aroaro o Kahu Restoration Society.

Waikato urban site descriptions

100+ years

Claudelands Bush (5.5 ha), or Jublilee Park, is the largest remnant kahikatea stand in Hamilton City. The canopy is 20-25 m and is dominated by kahikatea (*Dacrycarpus dacrydioides*) and tawa. The main disturbance pressures have been from logging in 1864, grazing until 1927, and ongoing weed invasion. Anthropogenic disturbance has altered the succession trajectory of this forest, resulting in low kahikatea seedling recruitment and a likely shift from wet-tolerant, shade-intolerant species to shade-tolerant, dry land species such as tawa and mahoe (Downs et al. 2000). A raised boardwalk has been installed to prevent damage from foot traffic, a cloth windbreak has been erected around the perimeter, and enrichment planting has been undertaken throughout. Also, a community group meet regularly to remove *Tradescantia fluminensis* (Weedbusters 2010).

Hammond Bush (1.8 ha) is located along the Waikato River in southern Hamilton and within a 14.8 ha gully system. The predominant forest type varies with drainage and relief but includes pukatea (*Laurelia novae-zelandiae*), swamp maire (*Syzygium maire*), tawa, titoki (*Alectryon excelsus*), alder (*Alnus glutinosa*), grey willow (*Salix cinerea*), mahoe (*Melicytus ramiflorus*), and kanuka (*Kunzea ericoides*). Damage to roots and seedlings has been minimised with the construction of paths and raised boardwalks. Exotic invasions present a threat to the high native diversity at this site but restoration by the council and private land owners is ongoing (Downs et al. 2000).

Berkley Bush is a privately owned 0.4 ha kahikatea stand in a 26.6 ha section of the Mangaonua Gully in southern Hamilton. It is one of the best remnant gully forests in the city with a relatively dense kahikatea canopy reaching 25-30 m in height. The understory is a combination of tree ferns (*Cyathea* and *Dicksonia* species), mahoe, *Psuedopanax* species, mapou (*Myrsine australis*), *Coprosma* species, and some exotics such as *Fatsia japonica*. This site was grazed 25 years ago, but today the main threat is from weed invasion (Downs et al. 2000). Numerous exotic species populate the outer areas of the section and several exotic seedlings can be found amongst the leaf litter. The level of weed control and restoration has varied with different owners and will be a key factor in preserving the current biodiversity.

Hillcrest Park is a recreational area in eastern Hamilton with a 1.4 ha stand of kahikatea that reaches 20-25 m. The forest understory and boundaries have been extensively planted with natives such as mapou, mahoe, *Coprosma*, *Pseudopanax*, and *Pittosporum* species. The park is well used by local residents and a scouts club; anthropogenic impact has been reduced with fencing and a boardwalk (Downs et al. 2000). Exotic species, including privet, *Prunus,* and *Solanum* species are present, but not dominant.

Mooney Park is a recreational area in western Hamilton with a 0.5 ha kahikatea and titoki forest reaching 20 m in height (Downs et al. 2000). It has a relatively depauperate understory with some mahoe, mapou, *Pseudopanax* species, titoki, and the exotic Chinese privet (*Ligustrum sinense*). Native plantings adjacent to the boundary help to buffer the forest and would be beneficial if extended into the forest understory. Neighbouring farmland indicates that the forest is likely to have been grazed in the past.

25-100 years

Braithwaite Park has a 0.5 ha area of kanuka forest on steep banks of the Waikato River in northern Hamilton, which is part of approximately 4.3 ha of mixed vegetation cover in the area. The kanuka canopy reaches 15-18 m with a native understory including mahoe and tree ferns (Downs et al. 2000). The groundcover is predominantly *Tradescantia fluminensis* which is up to 30 cm thick in some places and likely to be preventing native regeneration.

Pukete Eastern Riverbank (1.2 ha) is part of 4 ha of vegetation on the bank of the Waikato River opposite Braithwaite Park in northern Hamilton. The canopy is 10 m high and dominated by mature mahoe, tree ferns and grey willow with an understory of mahoe, tree ferns, pate (*Schefflera digitata*), and karamu (*Coprosma robusta*). *Tradescantia fluminensis* has invaded the understory along with

Selaginella kraussiana and Chinese privet. These exotic invasions, together with disposal of household and garden waste, present a significant threat to the forest (Downs et al. 2000).

River Road (Tauhara Gully) (3.7 ha) is at the northern end of the Tauhara gully, near River Road and has been highly altered from activity in the surrounding residential area. Forest type varies along the length of the Tauhara stream with mahoe dominating at 10-15 m. Threats to this site are predominantly weeds, including *Tradescantia fluminensis,* with some weed clearance and restoration planting evident in the most northern section.

Seeley's Gully (2.2 ha) in central Hamilton is part of the 6.1 ha Gibbon's gully. The canopy reaches 15-20 m and includes kahikatea, rimu, kauri, titoki, totara (*Podocarpus totara*), and kanuka; most of which were planted by the previous owner over the past 60 years. The understory is also largely planted but has some naturally regenerating species. Invasive species include *Tradescantia fluminensis,* Chinese privet and *Selaginella kraussiana* (Downs et al. 2000), and local vandals also pose a threat to the forest.

Chelmsford Park is a recreational area with 0.7 ha vegetation that is part of a 15.1 ha gully forest remnant. The canopy reaches 10-20 m and is comprised of exotic species such as *Salix*, *Pinus*, and *Eucalyptus* species, while the understory is predominantly native, including tree ferns, *Astelia grandis*, *Cordyline australis*, and karamu; many of which have been planted. Forest type is strongly controlled by topography and drainage with some areas being very poorly drained and bare of any vegetation. There are numerous exotic species including *Tradescantia fluminensis,* Chinese privet, blackberry (*Rubus fruticosus agg.*), *Allium triquetrum*, and ivy (*Hedera helix*) which pose the main threat to this forest (Downs et al. 2000).

15-25 years

Howell Street (Hudson Gully) (0.2 ha) is a privately owned site at the northern end of the 1.6 ha Hudson Gully forest. The section is open in the centre with a culverted stream. The canopy around the edge reaches 10-15 m and includes nikau, karaka, totara, Japanese walnut (*Juglans ailantifolia*), and *Cordyline australis*.

The understory is predominantly exotic with species such as *Camelia sp.*, *Hedychium sp.*, *Fatsia japonica*, *Tradescantia fluminensis*, and Chinese privet; which all threaten native regeneration.

Ranfurly Park is a recreational area in central Hamilton with 0.3 ha of forest where two gullies, totalling 9.8 ha, meet. Vegetation type varies with topography; a kanuka forest reaching 10-15 m runs along a ridge while the lower areas are dominated by 5-10 m high tree ferns (Downs et al. 2000), lacebark (*Hoheria sexstylosa*), *Pittosporum* species, and exotics. Threats include *Allium triquetrum*, *Tradescantia fluminensis*, and *Hedera helix*, but it is evident that some areas have been weeded and planted in the past.

Morrinsville Road (0.4 ha) is a privately owned forest in a 26 ha section of the Mangaonua gully in eastern Hamilton. This site is dominated by a 15-20 m canopy of willow and has undergone significant weeding and planting by the land owner; especially with native fern species. The understory has a range of species including karamu, pate, *Pseudopanax* species, mahoe, nikau (*Rhopalostylis sapida*), and *Fatsia japonica.* There are many exotic species in neighbouring properties but current control methods are evidently excluding them.

Rimu Street (0.6 ha) is a highly disturbed forest within the 30 ha Waitawhiriwhiri gully in central Hamilton. The canopy is made up of predominantly exotic trees, reaching 20 m in places, alongside a few native trees up to 15 m in height. Exotic weeds such as *Convolvulus* species, blackberry, *Tradescantia fluminensis*, *Lonicera japonica*, and Chinese privet are a large threat in this area; some planted natives were discovered underneath thick blankets of these weeds. The gully has also received a large amount of rubbish from the surrounding residential zone.

St. Andrews Riverbank (2.2 ha) is part of a 10 ha forest that is located between recreational/residential areas and the Waikato River in northern Hamilton. A popular path runs the length of the forest. The canopy ranges from 5-15 m in height with a mix of native plantings such as mahoe, totara, miro (*Prumnopitys ferruginea*), and tree ferns, and exotics such as *Salix* species and alder. Thick mats of *Tradescantia fluminensis* are common, as well populations of other exotic species that have “escaped” from bordering gardens. In some places the weeds have been cleared and replaced with native species.

5-15 years

Ashmore Court (3.1 ha) is within a 26.4 ha section of the Onukutara gully in northern Hamilton. This site has a 10-20 m canopy of *Alnus* and *Salix* species and an understory of planted natives including lacebark, karamu, and kanuka. The gully has open areas where weeds have been cleared and replaced with new plantings but others sections are threatened by abundant *Tradescantia fluminensis* and ivy.

Pickering Crescent (0.5 ha) is within a seven ha section of the Onukutara gully. It has a few kahikatea emerging above a 10-15 m canopy of willow. The understory includes *Salix* species, karamu, kanuka, kahikatea, Chinese privet, and mahoe. The local primary school is undertaking restoration in the area bordering their property and vegetation is protected from pedestrians by boardwalks and concrete paths.

Clements Crescent (3.1 ha) is within a 7.3 ha section of the Tauhara gully in northern Hamilton. It has a 10-15 m canopy of both native and exotic species, including *Pittosporum* species, totara, *Cordyline australis*, *Pinus* species, and Japanese walnut. The understory includes *Pittosporum* species, karamu, *Solanum pseudocapsicum*, and lacebark. The forest borders a recreational park and a road.

Porritt Stadium (Kirikiriroa Gully) (6.3 ha) is next to a sports field and recreational park in eastern Hamilton. On the hill slopes, the canopy is predominantly 15-20 m tall exotics such as *Pinus* and *Acacia* species with areas of younger *Cordyline australis*, mahoe, and tree ferns in the gully bottom. The understory includes karamu, Chinese privet, *Cordyline australis*, mahoe, and woolly nightshade. Exotic species include *Tradescantia fluminensis*, blackberry, and *Convolvulus* species.

Sandford Park (8.3 ha) is within the 60.4 ha Mangakotukutuku gully system in southern Hamilton. It has a canopy of lemonwood (*Pittosporum eugenioides*), kanuka, and wineberry (*Aristotelia serrata*) reaching 10-15 m. The understory is dominated by lacebark, lemonwood, and Chinese privet. *Tradescantia fluminensis* is present in dense patches as well as ivy and *Convolvulus* species. A community group regularly works to restore the area around the Mangakotukutuku stream.

Taranaki site descriptions

Ratapihipihi Scenic Reserve: tawa (23 ha). This nonurban semi-coastal forest is within 54.7 ha of mixed vegetation and located five km from the west coast of the North Island on the outskirts of New Plymouth city. The reserve is situated in a large gully and is surrounded by agricultural land. The majority of large trees were removed during logging in the late 1850’s. The southern section was added to the reserve around 1980 after retirement from cattle grazing (Clarkson & Boase 1982).

Huatoki Scenic Reserve (16 ha) is within 32.6 ha of forest in southern New Plymouth; approximately four km from the west coast. It is a high quality semi-coastal urban patch dominated by tawa, pukatea, and rewarewa (*Knightia excelsa*) up to 20 m in height. King fern (*Marrattia salicina*), hangehange (*Geniostoma ligustrifolium var. ligustrifolium*), kawakawa (*Macropiper excelsum*), and nikau are common in the understory as well as regenerating titoki, kohekohe (*Dysoxylum spectabile*), pukatea, rewarewa, and tawa (Clarkson & Boase 1982).

Te Henui (14 ha) is within a strip of vegetation, approximately 34.5 ha in size, that runs adjacent to the Te Henui stream and walkway. Tawa and pukatea are the most abundant canopy species reaching 15-20 metres, with kamahi (*Weinmannia racemosa*), rewarewa, and swamp maire occurring less commonly.

Sheppards Bush is part of a 3.4 ha recreational reserve and 5.6 ha of mixed vegetation in southern New Plymouth. The forest is composed of a pukatea dominated wetland on the western side and a drier tawa-rewarewa forest on the southern side. The canopy is 20-25 m high and also includes swamp maire, titoki, and puriri (*Vitex lucens*). The understory has abundant king ferns and nikau.

2.3.3 Sampling methods

Between December 2009 and May 2010 the epiphytic communities on 750 trees were surveyed; 649 in the Waikato region and 101 in the Taranaki region. All plots were located below 450 m a.s.l. in lowland forest (Smale & Burns 2002); the Waikato survey was undertaken between 10 and 350 m a.s.l.; the Taranaki sites were between 50 and 80 m a.s.l.

Modified variable area plots (Batcheler & Craib 1985) were used to estimate the species abundance and diversity of epiphyte communities. Each plot was centred on a randomly-located mature tree (defined for this study as a tree with a diameter at breast height (dbh) of at least 40 cm).

In the nonurban sites, the centre tree and the nine closest trees that measured over 20 cm dbh were surveyed; ensuring that at least five over 40 cm were included. In the mature urban sites the number of trees per plot varied according to the size of the forest patch. In small fragments (0.1-5 ha) three plots of five mature trees were surveyed. In larger fragments (>5 ha) five plots of ten mature trees were surveyed. In the immature urban sites (<100 years), three plots of five mature trees were surveyed per site.

The epiphytes on each tree were identified from the ground using binoculars. The location (trunk, inner branch, outer branch, all), vertical zone (in five metre sections), and an approximate percent coverage (following Braun-Blanquet (1932)), were recorded for each vascular epiphyte and vine species. For each host tree, the species, height, dbh, bark type, moss and lichen cover, and GPS coordinates were recorded.

2.3.4 Edge:area ratios

To indicate the extent of edge effects, edge:area ratios were calculated for each forest patch by dividing the area (ha) by the perimeter (metres). Because edge effects can influence forest function up to fifty metres in from the boundary (Young & Mitchell 1994; Denyer et al. 2006), approximate measurements of forest width were made to assess the degree of influence from edge effects. Area, perimeter and width measurements were made using aerial photographs and ERSI™ ArcGIS™.

2.3.5 Microclimate monitoring

Micro data loggers (Maxim hygrochron iButtons®, DS1923) were deployed to quantify temperature and relative humidity variation in the canopies of two nonurban and three urban Waikato forests from April until December, 2010 (inclusive). The loggers recorded measurements hourly with resolution of 0.0625 °C for temperature and 0.04 % for relative humidity. At each site, two data loggers were positioned in the canopy of the forest using a rope pulley system (Figure 2.5) and one data logger was installed outside the forest, no more than 500 metres from the boundary. These exterior loggers were located in open, usually pastoral, areas to provide a reference for local climatic conditions and compare forest and non-forest conditions. The interior data loggers were moved to new canopy locations every two months to account for within-forest variation. The nonurban loggers were installed between 14 and 24 m high in the canopy (Figure 2.5) and the urban loggers were between five and 14 m high.

Prior to deployment, the loggers were calibrated for relative humidity (RH) by rotating them through four desiccation chambers of known RH, generated using saturated NaCl, KCl, MgCl and $Mg(NO_2)_3$ solutions. During RH calibration the chambers were stored at a constant temperature. To calibrate for temperature, the loggers were moved between an oven at 36 °C and a refrigerator at four °C. One logger was chosen as a standard for temperature and RH. The results of each logger were plotted against the results from the standard and fitted with a trend line. The slope and intercept of the line were used to correct all subsequent results.

In the field, each data logger was housed in Gill radiation shields to protect the sensor from being heated by direct or reflected solar rays and to shelter it from severe weather. The loggers deployed in forest interiors were housed in custom made shields constructed from six plastic plates stacked approximately one centimetre apart to allow natural ventilation (Figure 2.4). All custom shield components were plastic to minimise heat absorption. The loggers deployed outside forests were housed in commercially-produced shields (HortPlus, New

Zealand). These shields were of a similar design to the interior shields (Figure 2.4) and tests confirm that shield design had no significant effect on results. Mean annual temperatures and vapour pressure deficits were calculated from hourly averages. Mean seasonal measurements were calculated from daily averages.

Figure 2.4: Hortplus radiation shield (left) and custom-made radiation shield (right) used to shelter iButtons® data loggers in forest canopies, see below.

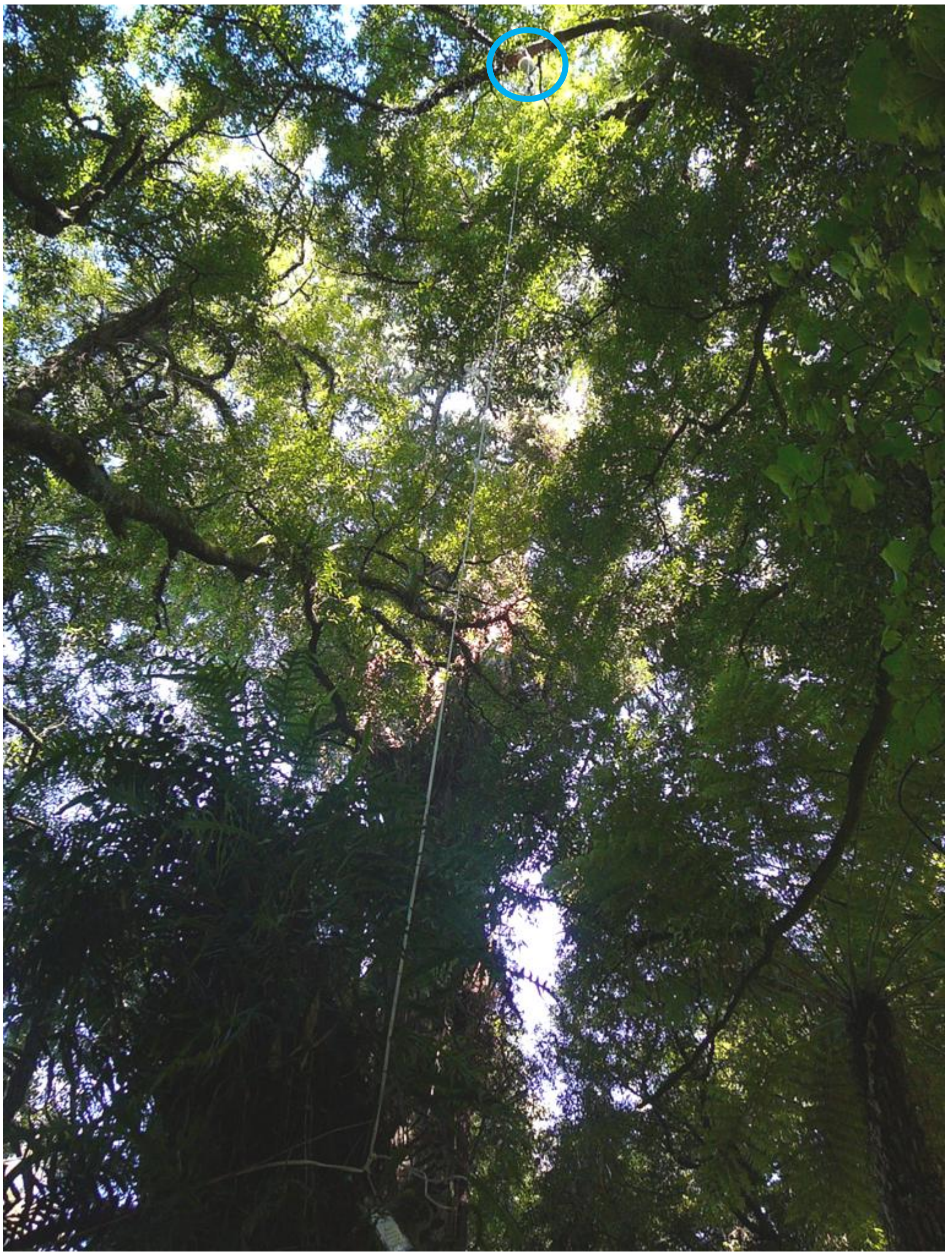

Figure 2.5: Shielded data logger (circled) in position in the canopy of tawa forest.

2.3.6 Dispersal distances

The distance between nonurban and urban sites was measured because large distances may limit the arrival and/or maintenance of epiphyte and vine populations. Mean dispersal distances were calculated from measurements of distance between the edges of forest patches. Distances were measured using aerial photographs and ERSI™ ArcGIS™. Dispersal modes for each species were established from New Zealand Plant Conservation Network (NZPCN 2011) and B.D. Clarkson, University of Waikato, pers. comm. (2011).

2.3.7 Successional profiling

Epiphytes and vines can be broadly classed into successional categories (e.g. Nadkarni 2000 & Giordano et al. 2004). Based on the work of Oliver (1930); Dawson (1986); Burns (2007), and B.D. Clarkson, University of Waikato, pers. comm. (2010), classifications were delineated and applied to epiphyte and vine species recorded in Waikato and Taranaki regions. Early successional species are those that colonise the high stress environments of bare branches in developing forests; mid successional species arrive after the colonisers have established branch substrate; and late successional species are typical of diverse communities in developed forest with large, old growth host trees (Nadkarni 2000; Burns 2007). Although some species may match more than one category, and others may be intermediary; the allocated groups represent the best ecological fit in the studied regions. Accidental or facultative species are excluded because their low abundance makes classification difficult.

The epiphyte and vine species presence and absence on the 399 host trees that were surveyed in Taranaki and nonurban Waikato forests were analysed in relation to host diameter. This allowed the assessment of successional classifications. The proportion of trees in each diameter class that hosted each epiphyte was graphed to show abundance with host size. Larger trees were assumed to represent later successional communities. Because trees under 20 cm in diameter were not surveyed, the species abundance of early successional epiphytes and vines was not entirely captured. This analysis was only applied to species that were relatively abundant.

2.3.8 Statistical analysis

Ecological data were analysed using Analysis of Variance (ANOVA) and post-hoc Fisher LSD tests. The assumption of homogeneity of variance was assessed using the Levene’s test and the condition of normal distribution was verified using the Sharpiro-Wilk test. Assumptions were ignored when sample sizes were over 30, as per the central limit theorem. Small data sets that did not meet assumptions were analysed using non-parametric Kruskal-Wallis ANOVA. Correlation between variables was investigated using linear regression and Pearson correlation coefficients. The null hypothesis was rejected and statistically significant results reported when the p-value was less than 0.05; p values are reported with each result. Temperature and relative humidity data was converted to daily averages before being analysed in an attempt to avoid autocorrelation and false relationships.

2.4 Results

2.4.1 Epiphyte and vine presence and absence

Waikato region

In the Waikato region, a total of 1460 individual vascular epiphyte and vine species from 34 genera and 28 families were recorded on 649 host trees. Nonurban forests were host to 80.8 % of total species while 19.2 % were in urban forest sites.

A total of 44 epiphyte and vine species were recorded in the Waikato region. Of those, 36 occurred in nonurban areas and 30 were recorded in urban areas. When species that occurred less than three times are excluded, the total is 29 species with 27 in nonurban forests and 16 in urban forests (Figure 2.6).

Using the life form classification given in chapter one, 54 % of all records were holoepiphytes; 1.2 % primary hemiepiphytes; 19.7 % herbaceous vines; 24.2 % lianas; and 1 % accidental epiphytes; see Figure 2.7 for a breakdown of nonurban and urban records. The most abundant holoepiphyte species was *Pyrrosia eleagnifolia*, the most abundant liana and herbaceous vine were *Metrosideros fulgens* and *Microsorum pustulatum*, respectively. *Griselinia lucida* was the only hemiepiphyte recorded. *Leucopogon fasciculatus* was the most frequent accidental epiphyte. Appendix one provides details of family, genera, and species abundance, and the life and growth forms of all recorded Waikato species.

Orchidaceae was the most abundant family, with representation by five species, followed by Asteliaceae and Myrtaceae; each with four species. *Metrosideros* and *Asplenium* were the most abundant genera with four and three species respectively. The most common species were *Pyrrosia eleagnifolia* with 244 records, *Asplenium flaccidum* with 116 records, and *Microsorum pustulatum* with 112 records (Figure 2.8).

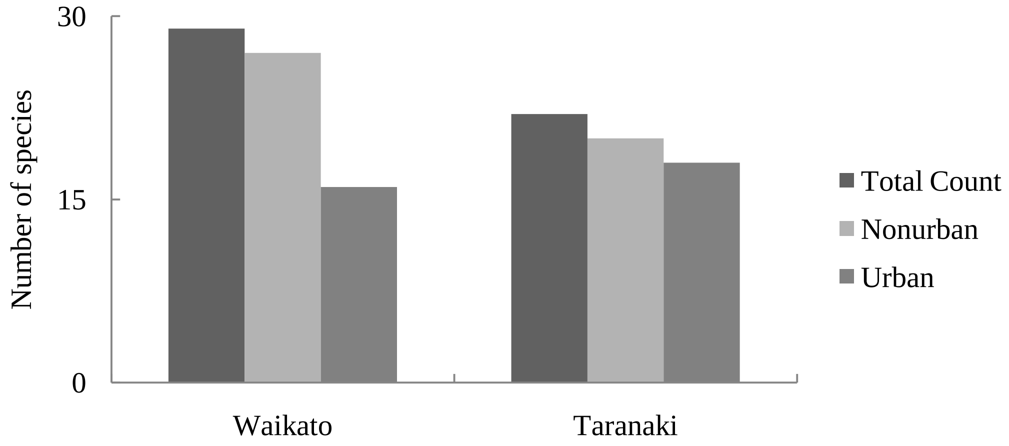

Figure 2.6: Total, nonurban, and urban epiphyte and vine species count for the Waikato and Taranaki regions

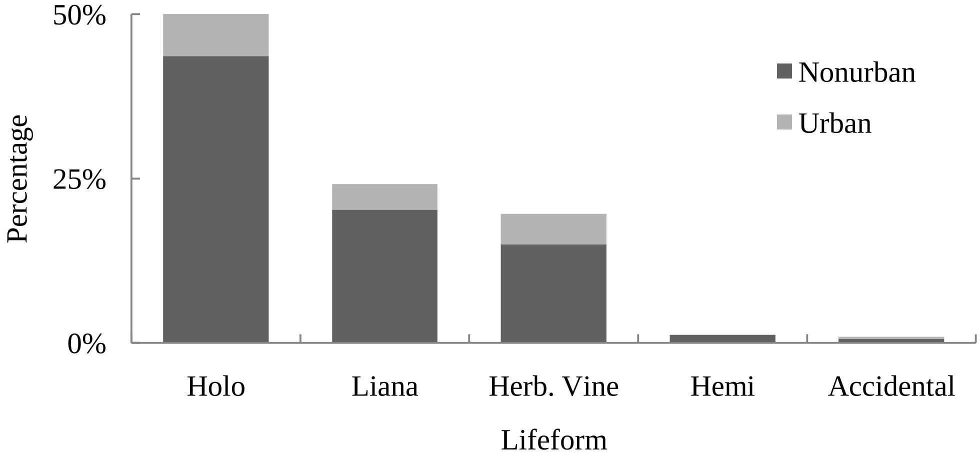

Figure 2.7: Type of epiphyte or vine species recorded in Waikato nonurban and urban forests. (Holo: Holoepiphyte, Herb. Vine: Herbaceous vine, Hemi: Hemiepiphyte).

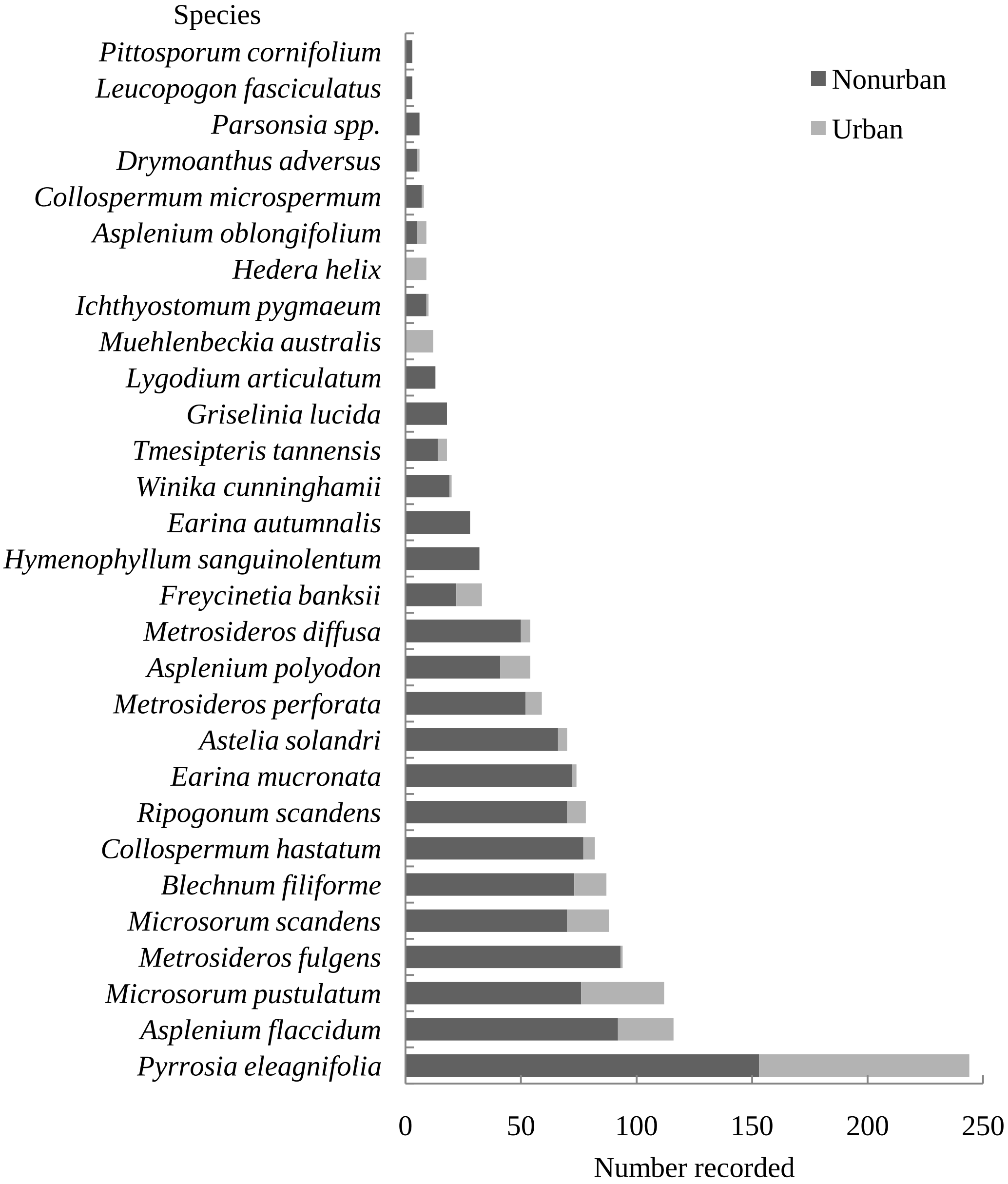

Figure 2.8: Number of each epiphyte and vine species from Waikato nonurban and urban forest (excluding species with fewer than three records).

Taranaki region

In the Taranaki region, 550 individual epiphytes and vine species were recorded from 25 genera and 21 families, on 101 host trees. The one nonurban site was host to 45.1 % of total species while 54.9 % were recorded in urban sites.

The total number of epiphytes and vine species in the Taranaki region was 33 with 26 in nonurban forest and 29 in urban forest. When species with less than three records are excluded, the total species count is 22, with 20 occurring in nonurban forest and 18 occurring in urban forest (Figure 2.6).

Using the life form classification given in chapter one, holoepiphytes represented 48.9 % of plants surveyed, while 3.1 % were primary hemiepiphytes, 21.1 % were herbaceous vines, 16.4 % lianas and 10.5 % accidental epiphytes. The proportion of these life forms in urban and nonurban forests is shown in Figure 2.9. The most abundant holoepiphyte species was *Pyrrosia eleagnifolia*; the most abundant lianas were *Metrosideros fulgens* and *Metrosideros perforata*, equally. *Microsorum scandens* was the most abundant herbaceous vine and *Griselinia lucida* was the only hemiepiphyte recorded. *Geniostoma ligustrifolium* var. *ligustrifolium* was the most abundant accidental epiphyte. Appendix two provides details of family, genera, and species abundance, and the life and growth forms of all recorded Taranaki species.

Orchidaceae and Asteliaceae were the most abundant families with four species each, followed by Aspleniaceae and Myrtaceae; each with three species. *Metrosideros* and *Asplenium* were the most abundant genera with three species each. The most common species were *Collospermum hastatum* with 59 records, *Microsorum scandens* with 54 records, and *Pyrrosia eleagnifolia* with 49 records (Figure 2.10).

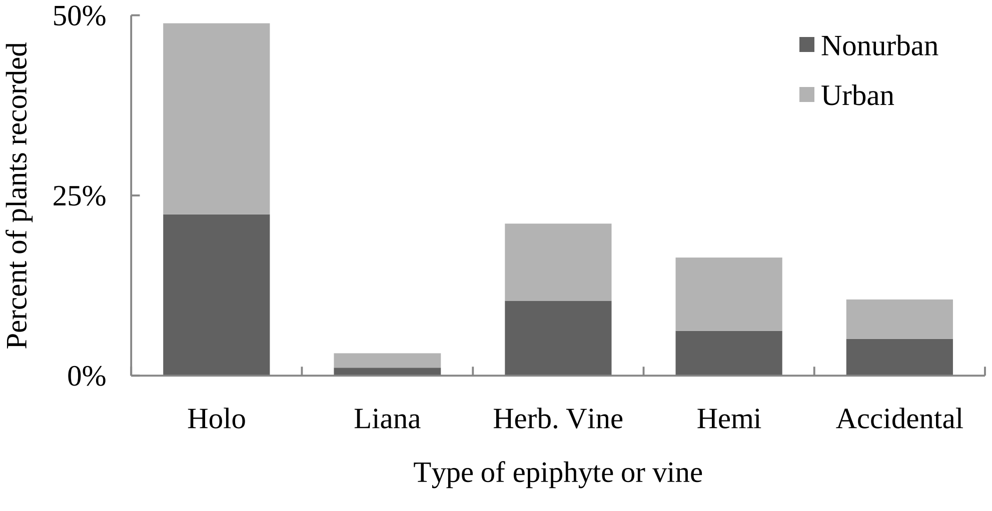

Figure 2.9: Type of epiphyte or vine species recorded in Taranaki nonurban and urban forests. (Holo: Holoepiphyte, Herb. Vine: Herbaceous vine, Hemi: Hemiepiphyte).

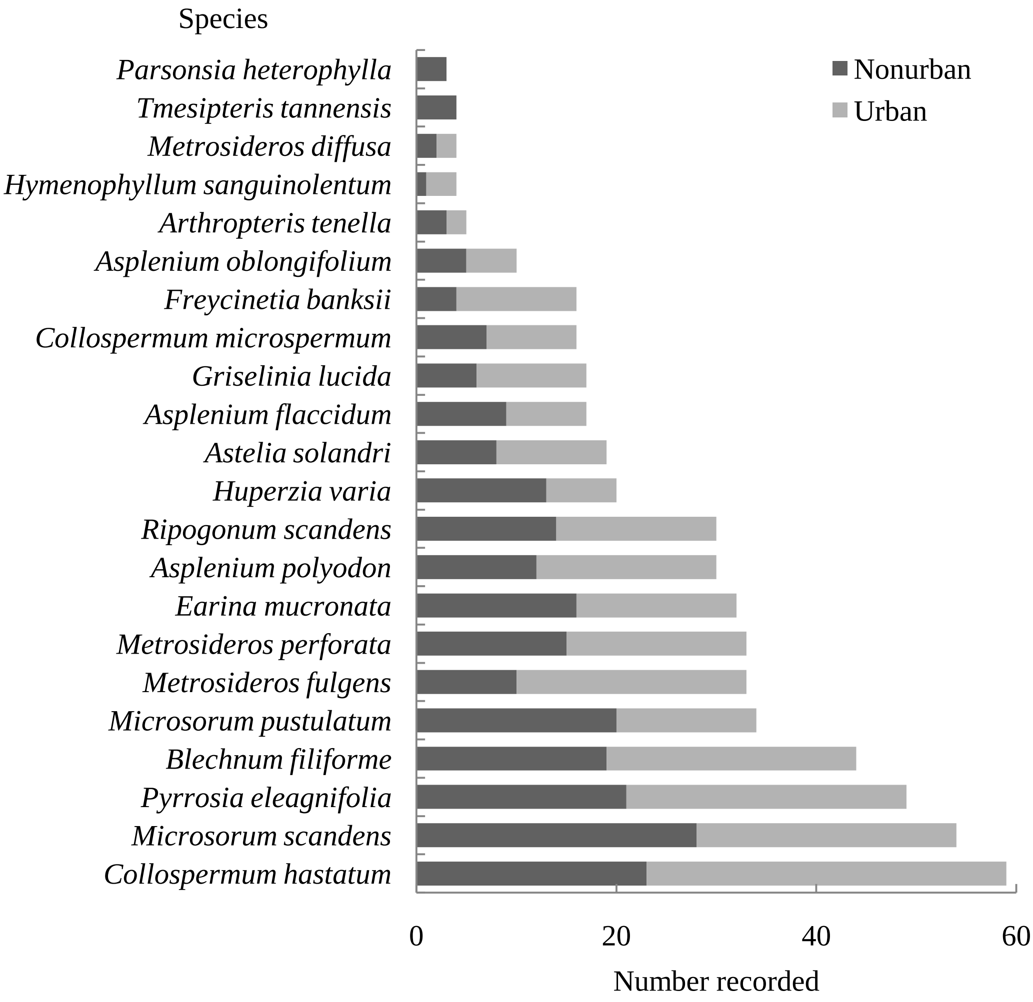

Figure 2.10: Number of each epiphyte and vine species from Taranaki nonurban and urban forest (excluding species with fewer than three records).

2.4.2 Epiphytes and vines per host tree

The forests of nonurban Waikato, urban Waikato, and Taranaki had considerably different assemblages of host tree species which in turn, supported different sized populations of epiphytes. These populations were measured in number of epiphyte and vine species per host and total percent cover of the host surface area by epiphytes and vines (Figure 2.11, Figure 2.12, and Figure 2.13)

The mean number of epiphytes and vines across all host trees in Waikato forests were lower than Taranaki forests in every class (Table 2.4). Significant differences exist between Waikato nonurban forests and Waikato urban forests ($p<0.001$), and between Taranaki forests (nonurban and urban combined) and Waikato urban forests ($p<0.001$). The difference between Waikato nonurban forests and Taranaki forests was close to statistical significance ($p=0.0501$).

Table 2.4: Mean number of epiphytes per host tree in different forest classes in the Waikato and Taranaki regions. Standard errors are presented in brackets. Waikato n=27 forests, Taranaki n=4 forests.

Region	Total	Nonurban	Urban
Waikato	2.31 (0.11)	4.00 (0.17)	0.87 (0.08)
Taranaki	5.45 (0.32)	4.84 (0.47)	6.06 (0.43)

Kohekohe supported the highest species richness and abundance in nonurban Waikato forests and with a significantly different mean number of species than rimu, kahikatea, kanuka, pukatea, mahoe, tanekaha, and totara ($p<0.05$) (Figure 2.11).

Pukatea had the greatest richness and abundance of epiphytes and vines in urban Waikato forests with a significant difference ($p<0.05$) over every other host species (Figure 2.12). The host trees in Taranaki forests supported a relatively high species richness and surface area cover per tree with the top three host species having larger epiphyte and vine populations that any of the Waikato hosts (Figure 2.13). In Taranaki, the mean number of species on mahoe was significantly different to that of rewarewa, pukatea, matai, and swamp maire.

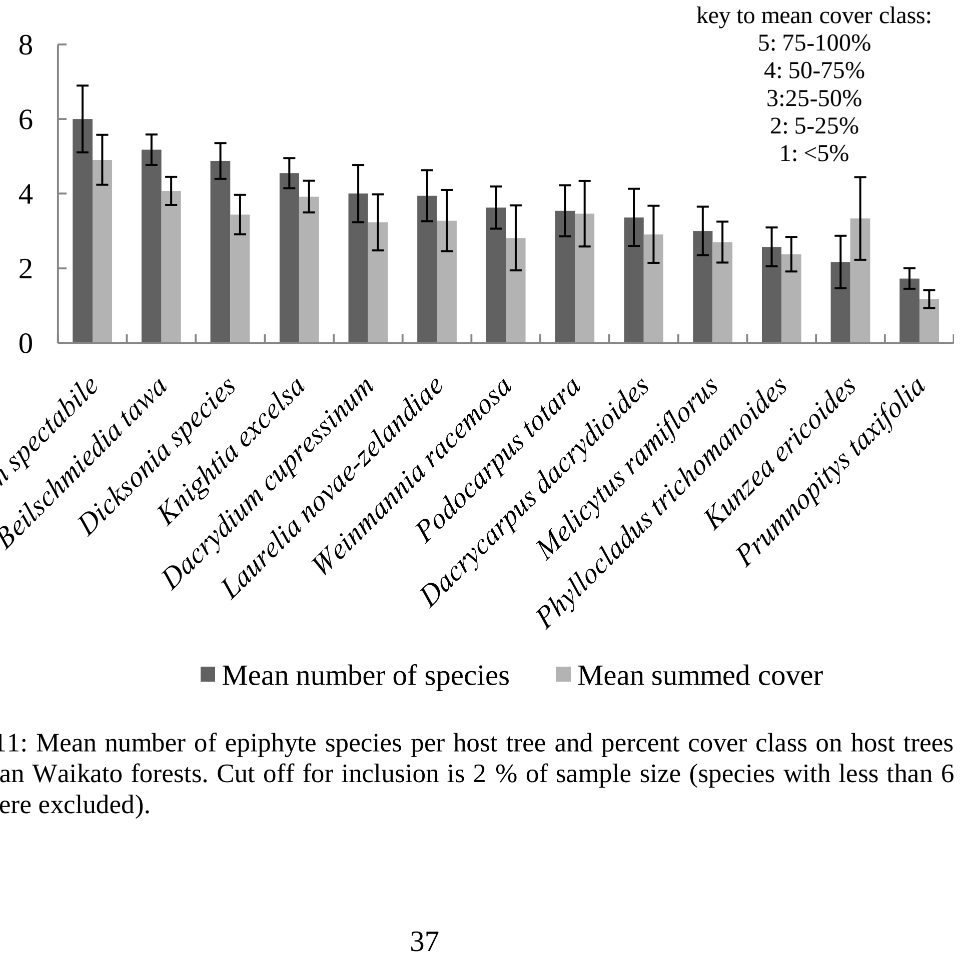

Figure 2.11: Mean number of epiphyte species per host tree and percent cover class on host trees in nonurban Waikato forests. Cut off for inclusion is 2 % of sample size (species with less than 6 records were excluded).

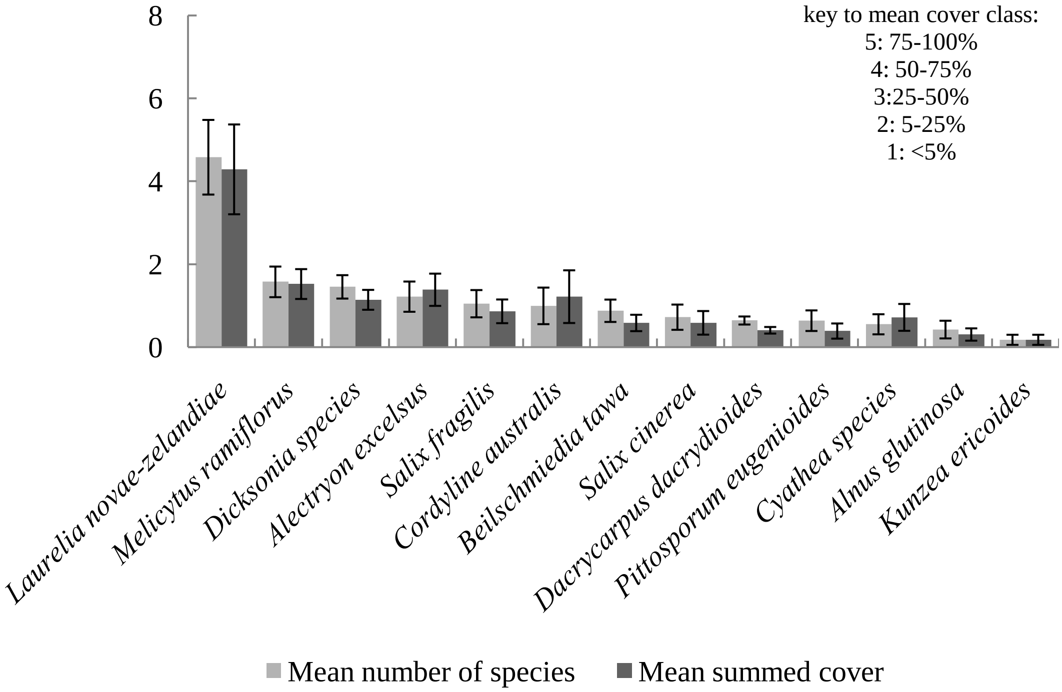

Figure 2.12: Mean number of epiphyte species per host tree and percent cover class on host trees in urban Waikato forests. Cut off for inclusion is 2 % of sample size (species with less than 7 records were excluded).

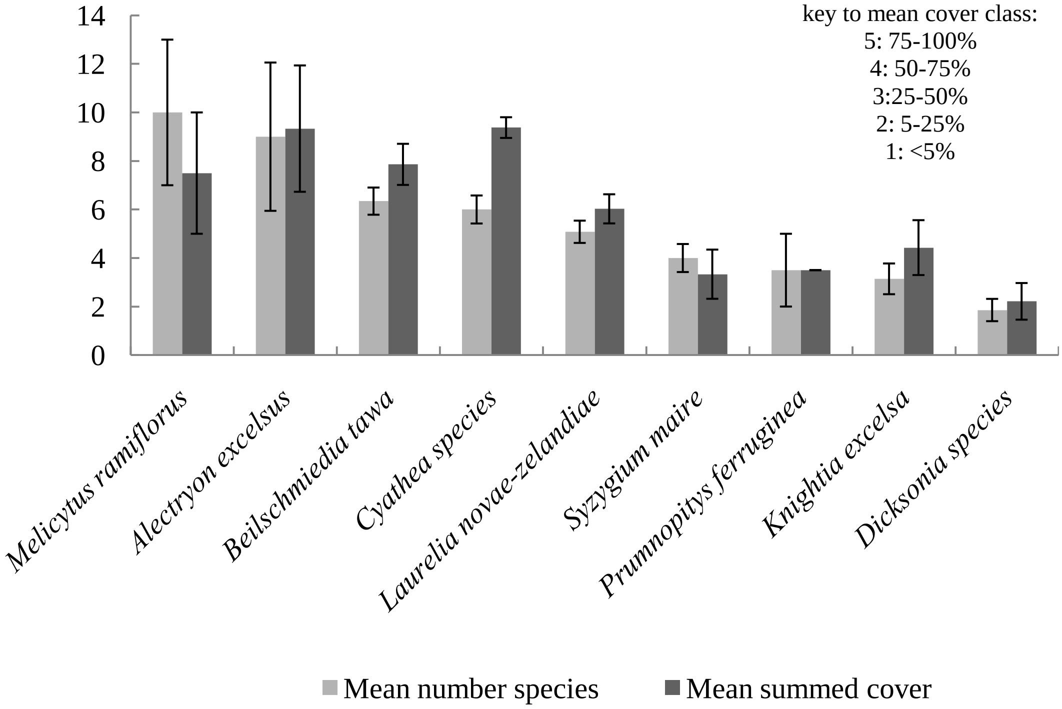

Figure 2.13: Mean number of epiphyte species per host tree and percent cover class on host trees across all Taranaki forests (urban and nonurban combined), note the different y axis scale. Cut off for inclusion is 2 % of sample size (species with less than 2 records were excluded).

Across the three forest classes, some host trees showed significant differences in the mean number of epiphyte and vine species they supported (Table 2.5).

Table 2.5: Host tree species with statistically significant differences in the mean number of epiphytes supported (*Tree ferns*: Cyathea and Dicksonia species).

Difference between: Waikato nonurban & Waikato urban	Difference between: Waikato urban & Taranaki	Difference between: Waikato nonurban & Taranaki
Beilschmiedia tawa	*Beilschmiedia tawa*	*Melicytus ramiflorus*
Tree fern spp.	*Melicytus ramiflorus*	*Dysoxylum spectabile*
Alectryon excelsus	Tree fern spp.	
Dacrydium cupressinum	*Alectryon excelsus*	
Kunzea ericoides		
Podocarpus totara		
Dacrycarpus dacrydioides		
Dysoxylum spectabile		

Pukatea and rewarewa showed no significant differences in number of epiphytes between different forest classes. Other host species such as wineberry, *Salix* species, and karaka (*Corynocarpus laevigatus*) could not be tested because they only occurred in single forest classes.

To establish which host species provide the best support for epiphytes and vines, the host tree records from the least disturbed forests (Waikato nonurban and Taranaki) were combined and compared without forests classes. Figure 2.14 shows the ranking of host species for number of epiphytes and vines per host tree supported and percent of surface area covered.

Titoki (*Alectryon excelsus*) had the highest mean number of epiphyte and vine species and percent cover. It was significantly different in number of species hosted from all other hosts shown in Figure 2.14, except tawa and *Dicksonia* species.

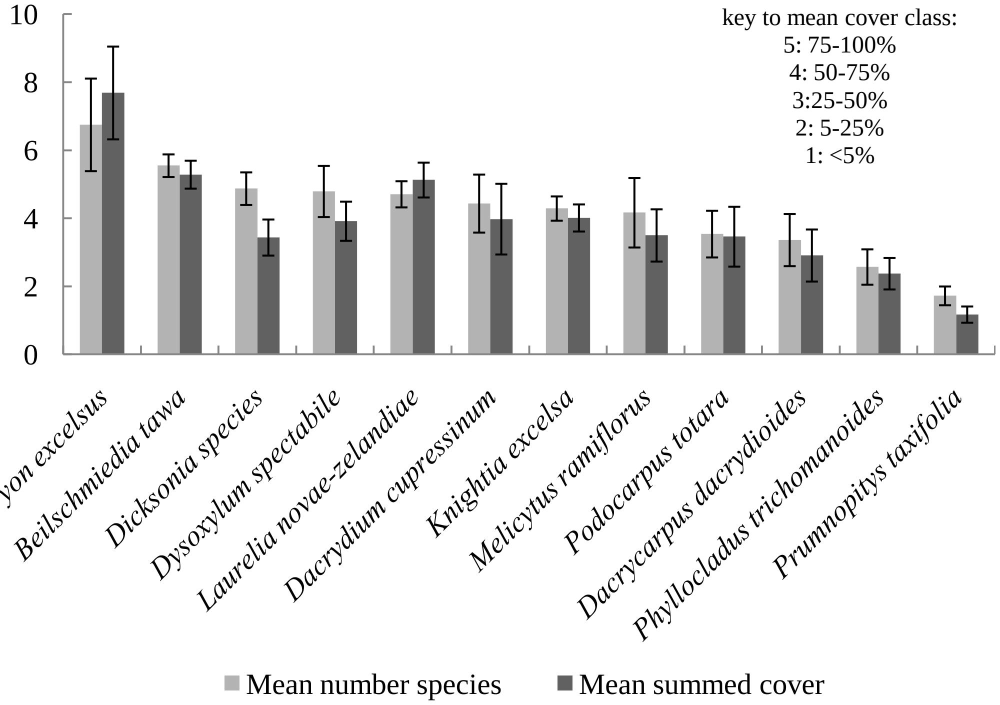

Figure 2.14: Mean number of epiphyte and vine species on hosts from Waikato nonurban and Taranaki forests; without forest classes. Cut off for inclusion is 2 % of sample size (species with less than 13 records were excluded).

2.4.3 Variables potentially affecting number of epiphyte and vine species per host tree

Host tree assemblages and characteristics

The four most abundant host trees recorded in Waikato nonurban forests were tawa (68), rewarewa (31), matai (*Prumnopitys taxifolia*) (29), and tanekaha (*Phyllocladus trichomanoides*) (28) (Table 2.6). The most common hosts in Waikato urban forests were kahikatea (85), alder (21), mahoe (19), and crack willow (*Salix fragilis*) (19) (Table 2.7). In Taranaki forests, the leading dominants were pukatea (19 nonurban, 18 urban) and tawa (14 nonurban, 18 urban) (Table 2.6).

Overall, host trees in Taranaki are taller than those of Waikato forests. Both Taranaki and nonurban Waikato host trees were significantly taller than urban Waikato trees ($p<0.001$) (Table 2.7). Host tree diameters were similar in nonurban and urban Waikato forests. Taranaki host trees had larger diameters than those in the Waikato; urban Taranaki trees were significantly larger than each other class ($p<0.03$) (Table 2.7).

Table 2.6: Frequency of host tree species in four forest classes. Species with an asterisk are exotic.

Host tree species	Waikato nonurban	Waikato urban	Taranaki nonurban	Taranaki urban
*Acer palmatum**	-	5	-	-
Agathis australis	4	-	-	-
Alectryon excelsus	5	9	1	2
*Alnus glutinosa**	-	21	-	-
Aristotelia serrata	-	10	-	-
Beilschmiedia tawa	68	17	15	18
Coprosma arborea	1	-	-	-
Coprosma robusta	-	1	-	-
Cordyline australis	1	9	-	-
Corynocarpus laevigatus	-	3	-	1
Cyathea spp.	-	9	4	-
Dacrycarpus dacrydioides	11	85	-	-
Dacrydium cupressinum	22	4	1	-
Dead- unknown species	-	1	-	-
Dicksonia spp.	8	24	-	-
Dysoxylum spectabile	17	-	4	2
Elaeocarpus dentatus	1	-	-	-
Eucalyptus sp.*	-	1	-	-
*Exotic angiosperm**	-	11	-	-
*Exotic gymnosperm**	-	16	-	-
*Ginkgo biloba**	-	1	-	-
Hedycarya arborea	4	-	-	-
Hoheria sexstylosa	-	9	-	-
*Juglans ailantifolia**	-	6	-	-
Knightia excelsa	31	1	3	4
Kunzea ericoides	6	11	-	-
Laurelia novae-zelandiae	18	12	19	18
Litsea calicaris	3	-	-	-
Melicytus ramiflorus	10	19	2	-
Myrsine australis	2	-	-	-
Nestegis spp.	2	-	-	-
Olearia rani var. rani	3	-	-	-
Phyllocladus trichomanoides	28	-	-	-
Pinus species*	1	8	-	-
Pittosporum eugenioides	1	14	-	-
Podocarpus hallii	-	1	-	-
Podocarpus totara	13	4	-	-
Prumnopitys ferruginea	1	1	1	1
Prumnopitys taxifolia	29	-	-	-
Prunus sp.*		1	-	-
Pseudopanax spp.	-	2	-	-
Quercus sp.*	-	1	-	-
*Salix cinerea**	-	11	-	-
*Salix fragilis**	-	19	-	-
Schefflera digitata	-	2	-	-
Syzygium maire	-	2	-	3
Vitex lucens	-	-	1	-
Weinmannia racemosa	8	-	-	1
TOTAL	298	351	51	50

Table 2.7: Mean height and diameter of host trees in each region and forest class.

	Waikato		Taranaki	
	nonurban	urban	nonurban	urban
Mean height (m)	18.2 (0.3)	15.8 (0.4)	19.1 (0.7)	19.4 (0.4)
Mean diameter (cm)	48.7 (1.5)	48.5 (1.5)	56.4 (3.9)	69.0 (4.9)

The number of epiphytes supported by host trees was plotted against different characteristics of those hosts. Host size (measured as dbh) and host bark type were the only characteristics that exhibited a statistically significant ($p<0.01$) relationship with number of epiphytes supported; tree height, moss coverage, and lichen coverage did not exhibit significant associations.

Host size

Linear regression of host tree size against number of epiphytes was performed using the records from nonurban Waikato and Taranaki records; urban Waikato was excluded to remove the effects of heavy disturbance. The results indicate a significant relationship between the host size and the number of epiphyte and vine species it supports with an *r* value of 0.551 ($p<0.01$) (Figure 2.15). When urban Waikato forests were included the relationship was weaker ($r = 0.3896$, $p<0.01$).

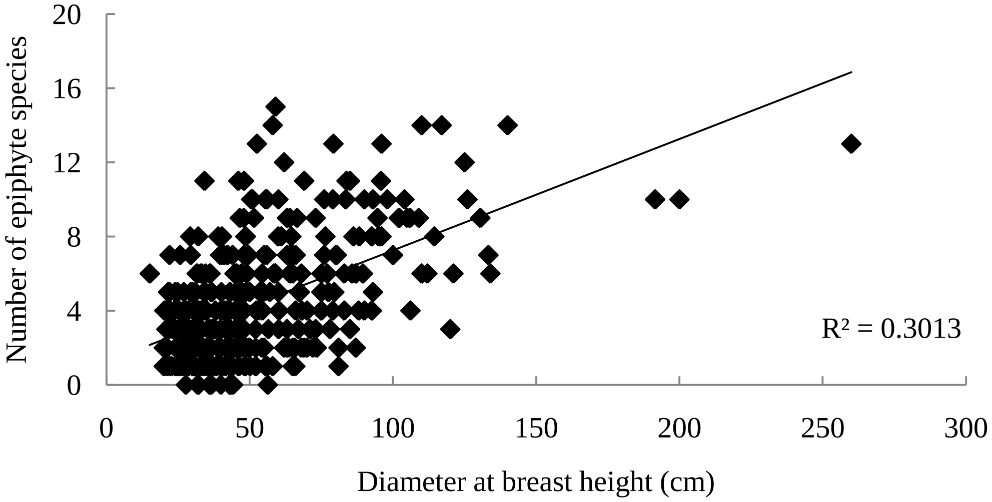

Figure 2.15: Linear regression of host tree diameter at breast height and number of epiphyte species per host using records from nonurban Waikato and Taranaki forests ($p<0.01$).

Bark type

Different bark types are associated with different abundances of epiphytes and vines. Figure 2.16 shows the bark types that occurred more than twice and the mean number of species they supported. Both fibrous and smooth bark types were significantly different from peeling and scaly types (p<0.007).

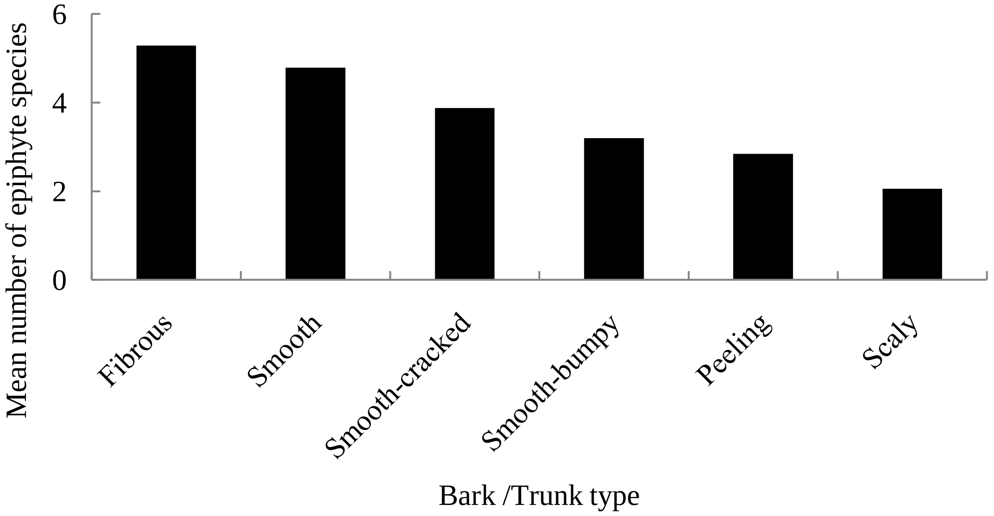

Figure 2.16: Mean number of epiphyte species per host by bark type.

Dispersal modes and distances

The mean distance between Waikato urban and nonurban sites was 20.1 km while the mean distance between Taranaki urban sites and Ratapihipihi (nonurban) was 4.4 km. Of the 37 epiphyte and vine species recorded in both regions, 54 % of species dispersed seed via wind, 30 % by bird, and 16 % via gravity, capsule, or vegetative fragments.

Edge:area ratios

Waikato nonurban forests had the lowest mean edge:area ratio which was significantly less than Waikato urban immature forests patches (p<0.001) but not significantly lower than Waikato urban mature forests (p=0.068). The Taranaki forest class includes all surveyed sites in this region which have a mean edge:area ratio that is intermediary between Waikato nonurban and Waikato urban classes.

Table 2.8: Mean edge:area ratios (E/A) for each forest class.

Forest class	Mean E/A (m/ha)
Waikato nonurban mature	23.7
Waikato urban mature	315
Waikato urban immature	365.4
Taranaki	179

Nonurban Waikato forests were between 100 and 9200 m in width while all Waikato urban forests were less than 250 m in width and most spanned only 50 to 100 m. Taranaki forest widths ranged from 140 to 500 m in width. The survey plots in both regions were located between 30 and 240 m from the forest boundary and thus encompassed a range of edge effects.

Microclimates

The canopy data logger records show that the nonurban forests (Maungatautari and Waingaro) had lower mean temperatures and vapour pressure deficits than urban sites (Berkley, Chelmsford, and Howell). This trend is consistent and significant ($p<0.001$) across all seasons. Temperature records are significantly different between the two nonurban sites and between each nonurban and urban sites ($p<0.003$). Vapour pressure deficit records are significantly different between all sites except the two nonurban sites and two of the urban sites (Howell & Berkley) (Table 2.9 & Table 2.10, Figure 2.17 & Figure 2.18).

Table 2.9: The mean and range of daily average temperatures (°C) over the nine month monitoring period for interior (Int.) and exterior (Ext.) data loggers from each forest. Standard error for all means = 0.2.

	Maungatautari		Waingaro		Berkley		Chelmsford		Howell	
	Int.	Ext.	Int.	Ext.	Int.	Ext.	Int.	Ext.	Int.	Ext.
Mean	10.5	10.8	11.4	11.7	12.2	11.7	11.8	12.7	12.3	12.0
Range	15.1	15.1	17.0	17.7	16.0	17.5	17.6	17.3	17.0	17.7

Table 2.10: The mean and range of daily average vapour pressure deficits (kPa) over the nine month monitoring period for interior (Int.) and exterior (Ext.) data loggers from each forest. Standard error for all means = 0.1.

	Maungatautari		Waingaro		Berkley		Chelmsford		Howell	
	Int.	Ext.	Int.	Ext.	Int.	Ext.	Int.	Ext.	Int.	Ext.
Mean	0.12	0.13	0.11	0.16	0.23	0.15	0.19	0.31	0.20	0.17
Range	0.71	0.76	0.67	0.70	0.75	0.85	0.68	0.97	0.92	0.84

Comparisons between the temperature and vapour pressure deficit records from loggers in the canopy of forest interiors and loggers outside the forests showed that nonurban forest interiors were buffered (had lower ranges). Waingaro and Maungatautari canopy temperatures had consistently higher minimums and lower maximums than outside the forest boundary; Figure 2.19 shows the winter data set as an example and other seasons are provided in appendix three. Buffering was also apparent in vapour pressure deficit records for nonurban sites with consistently lower maximums inside the forest compared to outside; Figure 2.20 shows the winter data set as an example and other seasons are provided in appendix three. Vapour pressure deficits below zero are the results of relative humidity measurements over 100 % which are within the error range of the data loggers.

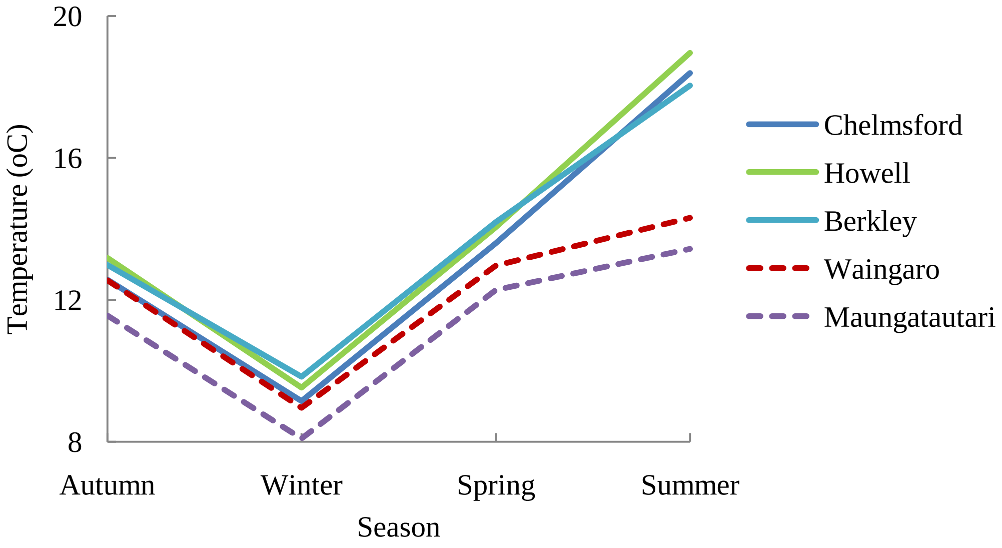

Figure 2.17: Mean temperature (^{o}C) of each season across surveyed forests. Solid lines represent urban forests, dashed lines represent nonurban forests. (Autumn: March, April, May; winter: June, July, August; spring: September, October, November; summer: December (summer records are incomplete)). Means calculated from daily averages.

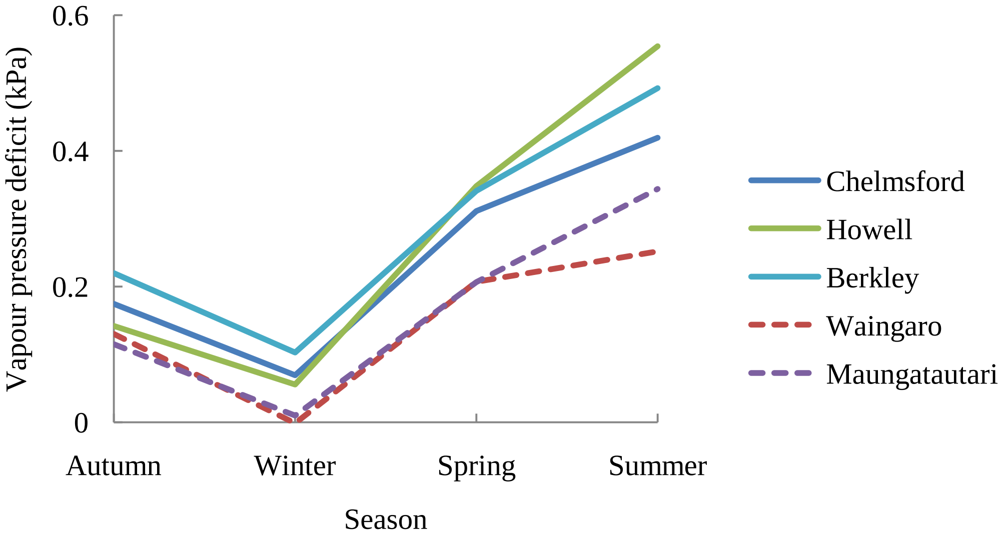

Figure 2.18: Mean vapour pressure deficits (kPa) of each season across surveyed forests. Solid lines represent urban forests, dashed lines represent nonurban forests. (Autumn: March, April, May; winter: June, July, August; spring: September, October, November; summer: December (summer records are incomplete)). Means calculated from daily averages.

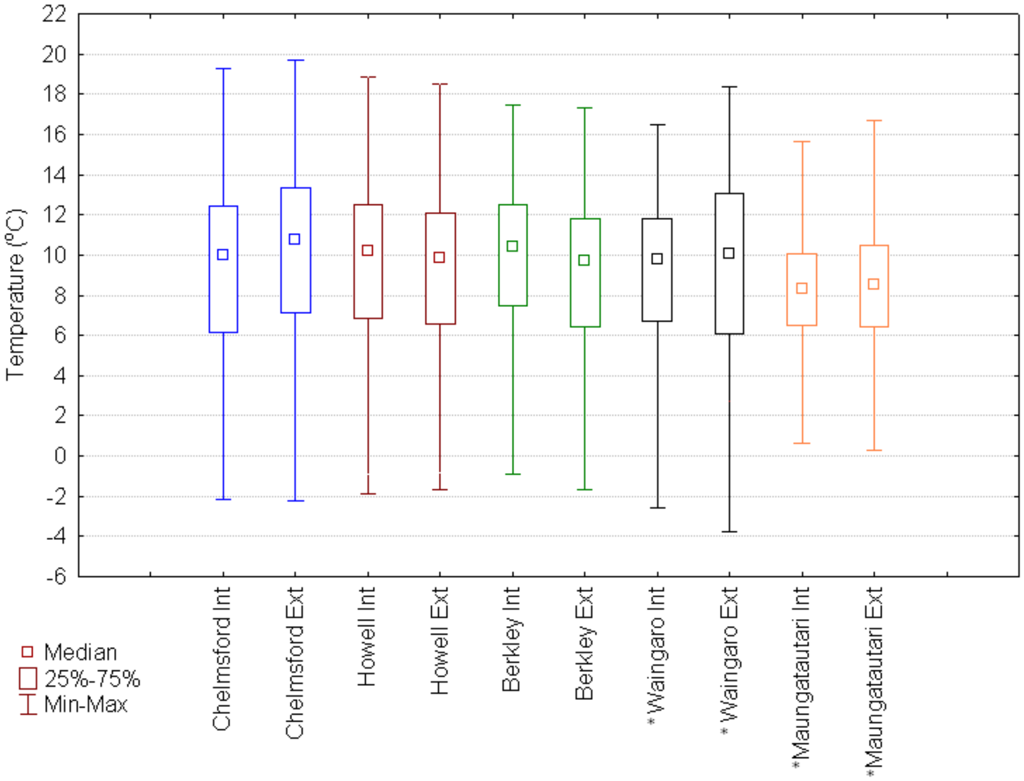

Figure 2.20: Temperature (^{o}C) data from hourly averages recorded by interior (Int) and exterior (Ext) loggers at each site over winter. The nonurban sites with greater buffering are indicated by asterisks.

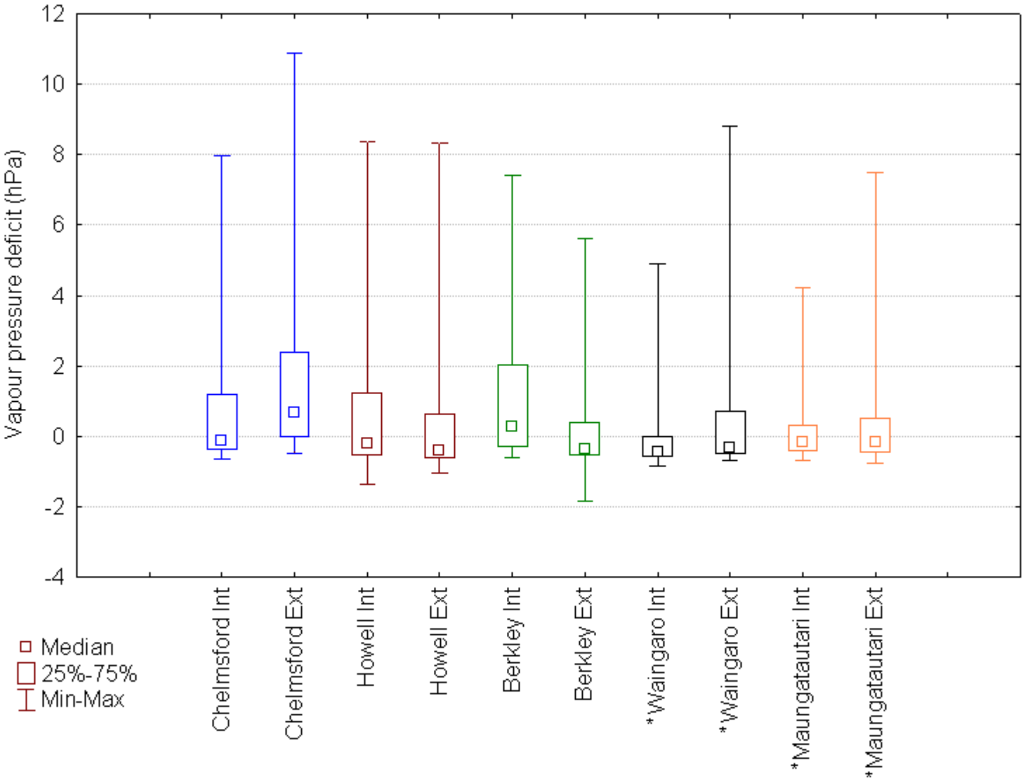

Figure 2.19: Vapour pressure deficit (kPa) data from hourly averages recorded by interior (Int) and exterior (Ext) loggers at each site over winter. The nonurban sites with greater buffering are indicated by asterisks.

Species associations

The communities that had both nest species (*Collospermum hastatum* and *Astelia solandri*) had the highest mean total number of epiphytes and vines, while those with one or the other have larger populations than those that have neither (Figure 2.21). All differences were statistically significant (p<0.01) with the

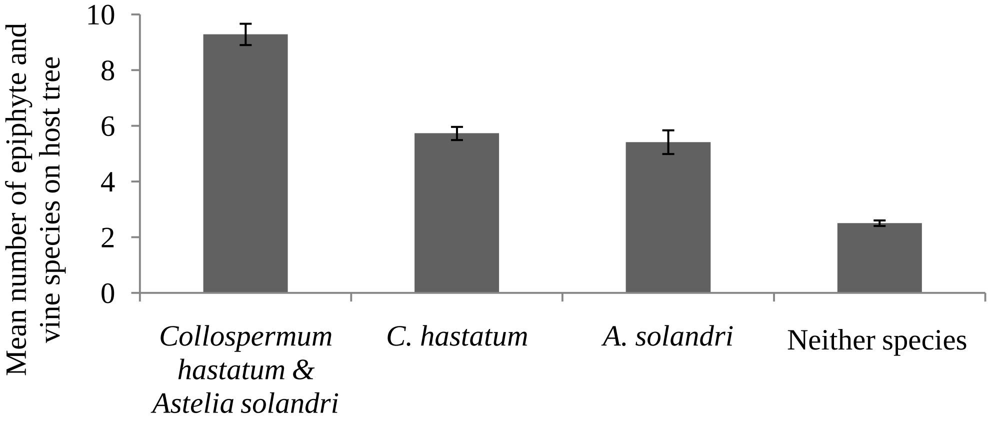

Figure 2.21: Mean number of epiphyte and vine species associated with the presence and absence of *Collospermum hastatum* and *Astelia solandri.* Note: Species counts in each assemblage exclude *C. hastatum* and *A. solandri*.

Successional profiling

Each recorded epiphyte or vine species was classed into early, mid or late successional categories. The majority of species were mid successional while early and late classes had similar counts (Table 2.11).

Table 2.11: Successional classification of epiphyte and vines species recorded in Waikato and Taranaki regions. Listings marked with an asterisk are exotic species. Accidental and facultative species are excluded from the classification.

Early Successional	Mid Successional	Late Successional
Blechnum filiforme	*Arthropteris tenella*	*Brachyglottis kirkii*
Convolvulus spp.*	*Asplenium flaccidum*	*Freycinetia banksii*
Earina mucronata	*Asplenium oblongifolium*	*Griselinia lucida*
*Hedera helix**	*Asplenium polyodon*	*Huperzia varia*
*Jasminum polyanthum**	*Astelia solandri*	*Metrosideros fulgens*
Microsorum pustulatum	*Clematis paniculata*	*Passiflora tetrandra*
Microsorum scandens	*Collospermum hastatum*	*Pittosporum cornifolium*
Pyrrosia eleagnifolia	*Collospermum microspermum*	*Ripogonum scandens*
*Rubus fruticosus**	*Drymoanthus adversus*	*Winika cunninghamii*
*Tradescantia fluminensis**	*Earina autumnalis*	

	Hymenophyllum sanguinolentum
	Ichthyostomum pygmaeum
	Lygodium articulatum
	Metrosideros diffusa
	Metrosideros perforata
	Muehlenbeckia australis *Parsonsia* spp.
	Tmesipteris elongata

The populations of each successional class in different forests were investigated to identify any patterns that could contribute to the varying species richness and abundance across forest classes (Figure 2.22 and Figure 2.23). Throughout the four forest classes, early successional species-counts were relatively constant while mid and late successional species increased with age in the Waikato forests, reaching a maximum of 16 species in Waikato nonurban mature forests. Taranaki had 15 mid successional species and the highest number of late species with eight (Figure 2.2).

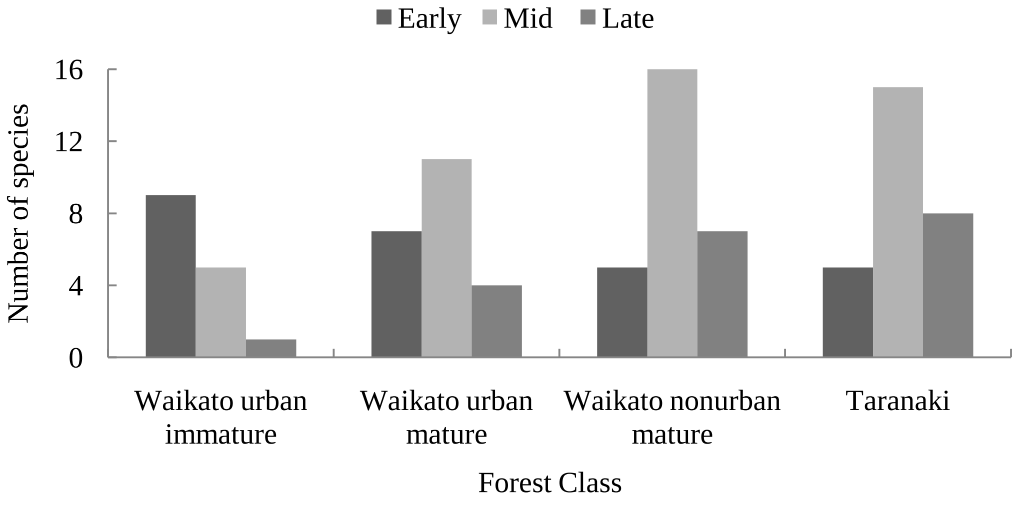

Figure 2.22: Number of epiphyte and vine species in each successional class for Taranaki forests and the three forest types surveyed in the Waikato.

In terms of numbers of individuals, Waikato urban immature forests (under 100 years old) were dominated by early successional species alongside a small population of mid successional species and only 1.5 % from the late class (Figure 2.23). Waikato urban mature forests (over 100 years old) had a slightly smaller proportion of early plants and a higher representation from the late successional group. Waikato nonurban mature and Taranaki classes and had the lowest percentages of early successional plants and the highest mid and late fractions (Figure 2.23).

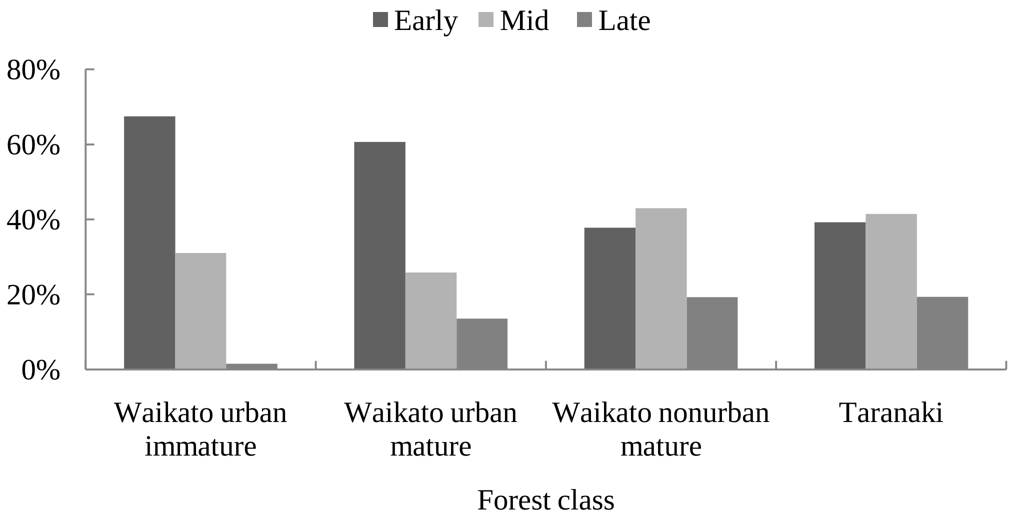

Figure 2.23: Percentage of individual epiphyte and vine species in each successional class for the three forest types surveyed in the Waikato and Taranaki regions.

Moss and lichen were recorded on 71.2 % and 66.2 % of all host trees, respectively (data for Maungatautari and Claudelands not recorded). Lichen commonly occurred on the outer limbs in open sites with high sunlight. Mosses were more common on shaded areas near the trunk and on branch undersides. Moss communities were often associated with early successional epiphytes and vines. The moss and lichen coverage on host trees throughout all forests was predominantly classed as light or moderate moss and lichen coverage, with only a small proportion having dense cover (Figure 2.24).

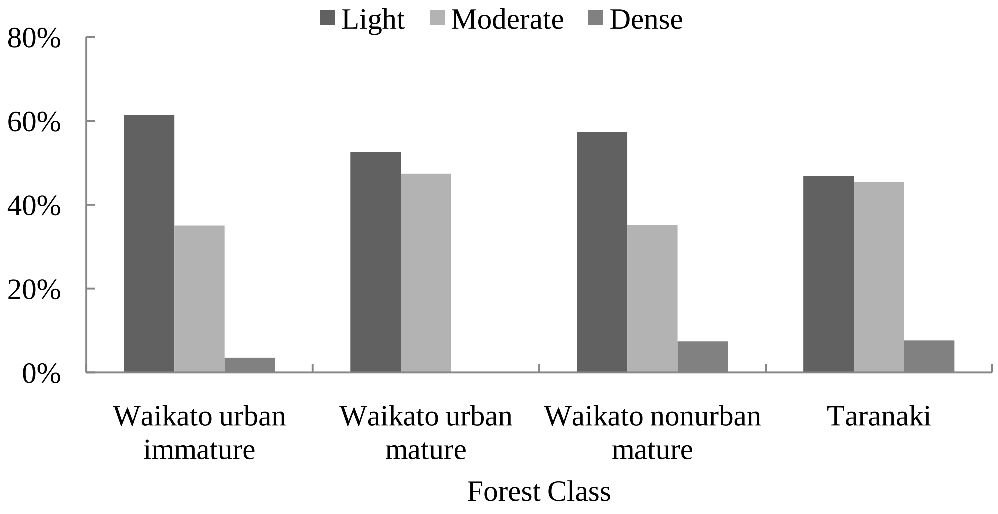

Figure 2.24: Percentage moss and lichen coverage in Waikato and Taranaki forests from semi-quantitative percent cover assessments.

The two main patterns of species abundance and host diameter are shown in Figure 2.25: (1) early arrival and persistence (*Metrosideros fulgens*) and (2) increasing abundance with increasing host diameter (*Astelia solandri*). Fourteen epiphyte and vine species were abundant enough to allow construction of these graphs and although the patterns were similar to the examples below (Figure 2.26), every one showed a slightly different relationship with host size (appendix four). It is evident from the 14 graphs that the epiphyte and vines studied either persisted with increasing host size or increased in abundance; there were no species that were absent from all large host trees (appendix four).

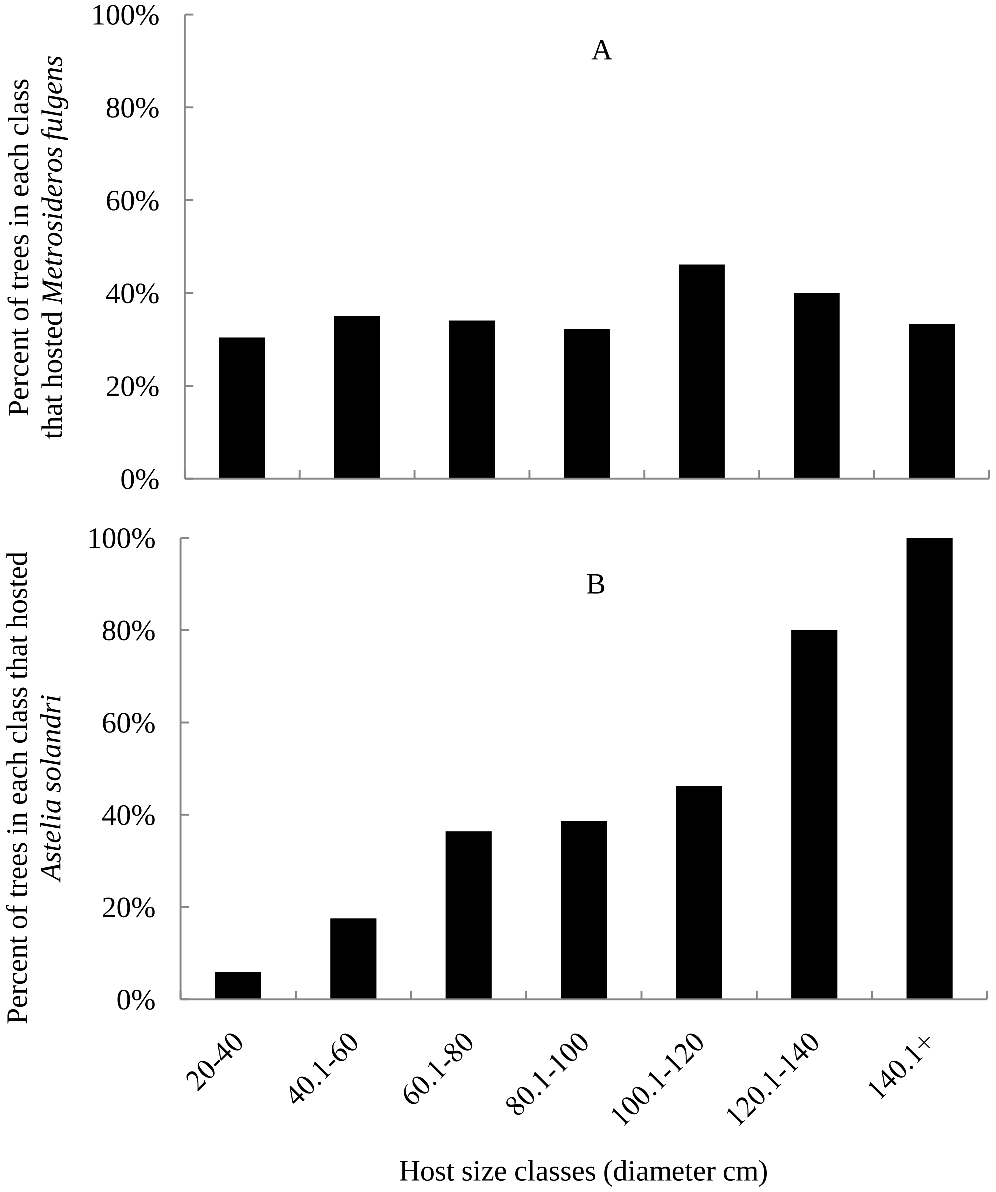

Figure 2.25: Example graphs for A: *Metrosideros fulgens* and B: *Astelia solandri*. Bars show the percent of trees that host each species.

2.5 Discussion and conclusions

Waikato epiphyte population

This first specific assessment of epiphyte and vine populations in lowland (<450 m a.s.l.) forests of the Waikato region has revealed a guild of 29 species. This total is comparable to North Island lowland species counts from Campbell (1984) and Clarkson (1985) who recorded altitudinal information in their reports (Table 2.12). Other reported epiphyte counts are higher because they include montane or submontane forests which inherently have greater species richness and abundance (Table 2.12).

Table 2.12: Total species count and lowland species count of vascular epiphyte and vine species found in forest surveys in the North Island, New Zealand surveys.

Total species count	Lowland species count	Location	Author(s)
45	25	Orongorongo Valley, Wellington	Campbell (1984)
52	31	Kaitake Range, Taranaki	Clarkson (1985)
50	N/A	Mount Karioi, Waikato	Clayton-Greene & Wilson (1985)
35	N/A	Maungataniwha Range, Northland	Dawson & Sneddon (1969)
44	N/A	Pureora Forest Park, Waikato	Wilcox (1999)

The high proportion of holoepiphytes and obligate epiphytes (definition provided in chapter one) found in both Waikato and Taranaki forests is consistent with the relative proportions of these life forms throughout all New Zealand epiphytic species (Oliver 1930; Burns 2008; 2010). The high fraction of accidental species in Taranaki is likely to be related to the dominance of nest epiphytes in these forests which provide a good source of substrate (Burns & Dawson 2005), as well as the higher annual rainfall in this region (Table 2.1).

Waikato urban forests had the lowest epiphyte and vine species diversity and abundance of all forests with only 55.2 % of the local species pool present in forest patches of Hamilton city, and a relatively low average of 0.8 epiphyte species per host. This result is similar to the reduction in species richness and cover of epiphytic bryophytes with increased human disturbance reported by

Giordano et al. (2004) in a comparison of urban and extra-urban sites in Campania, southern Italy.

The total species count for Waikato forests was greater than for the Taranaki region but this is likely to have been affected by the significantly smaller Taranaki sample size. The urban forests of Taranaki, with 81.8 % of the Taranaki species pool represented, and a mean of 6.06 (±0.43) species per host tree, had much higher epiphyte and vine diversity and abundance than urban Waikato. The nonurban number of species per host tree was also higher in Taranaki than Waikato.

Previous studies have found that assemblages of epiphytes in a forest represent neither random nor uniform selections from the local species pool; suggesting that multiple factors are affecting species distributions (Nieder et al. 2000; Laube & Zotz 2006). The following discussion considers in more detail the factors that are indicated to be important in the results.

Influencing factors

Host tree assemblages and characteristics

The host tree species assemblages in urban Waikato forests were different from the other surveyed forest types. This can be attributed to three key factors; firstly, the surveyed forest patches in urban Waikato have a high abundance of introduced species such as alder, crack willow, and grey willow. Secondly, the highly modified nature of these urban forests has resulted in communities of indigenous species that have been planted (such as lemonwood), are colonising species (such as mahoe), or are remnant from original forest types (such as kahikatea); resulting in species assemblages that vary from that of the more mature and undisturbed nonurban forests. Thirdly, the terrain of urban Waikato is predominantly gullies which, although somewhat similar to the surveyed Taranaki landscapes, differ considerably to the hillslopes of nonurban Waikato, which present inherently different forest types.

These variable host populations influence the diversity and abundance of epiphytes and vines in each forest because different tree species have a range of associated biotic and abiotic features that affect the germination and survival of an epiphyte or vine. These features include host architecture, bark type, microclimate, fruiting, and flowering (Todzia 1986; Zotz et al. 1999; Laube & Zotz 2006). Each host species offers a unique combination of characteristics that result in a host-specific epiphytic spectrum from the local species pool (Zotz et al. 1999). These characteristics influence the numbers of epiphytes per host tree; for example, the high species richness on titoki will be related to the smooth bark, large branches, spreading architecture and attractive fruit for seed dispersers, along with other factors. Thus, each forest has a unique and diffusely-related species composition and relative abundance of epiphytes and vines (Nieder et al. 2000; Zotz & Vollrath 2003; Laube & Zotz 2006).

Host size

The weak relationship between host tree size (diameter) and number of epiphyte and vine species (r=0.511) indicates that there is an association between large host trees and diverse epiphytic communities. Similar correlations have been found by many authors (e.g. Catling & Lefkovitch 1989; Knightbridge & Ogden 1998; Nieder et al. 2000; Muñoz et al. 2003; Laube & Zotz 2006; Flores-Palacios & Garcia-Franco 2006; Burns 2008). This relationship is related to the greater number of habitats provided by large trees than small trees (Flores-Palacios & Garcia-Franco 2006); the lifespan of larger trees providing more time for humus to accumulate and epiphytes to establish (Knightbridge & Ogden 1998; Hofstede et al. 2001; Laube & Zotz 2006); and large trees intercepting more light and water than small trees (Benzing 2004; Cummings et al. 2006). The greater diameter and height of host trees in Taranaki is likely to be related to the relatively high average number of species per host tree in this region.

It has also been observed that the bark texture of some host tree species, such as kahikatea and rimu, changed with size and often exhibited increased fissuring which is likely to favour epiphyte establishment.

Bark type

This study found a dissimilar mean number of epiphytes species on different bark types, which indicates that host bark contributes to the epiphytic species spectrum in each forest. The characteristics that influence how well a bark type supports epiphytes include texture, the degree of peeling, water-storage capacity, and the presence or absence of alleochemicals (Catling & Lefkovitch 1989; Callaway et al. 2002; López-Villalobos et al. 2008). The significant differences found between surveyed host bark types were related to texture and the degree of peeling however, bark water-storage and alleopathy were not tested for. The significantly higher number of epiphytes per host tree for titoki and tawa reflects the suitability of the smooth bark of these species.

The influence of bark type on epiphyte establishment and survival in the survey sites of the present study should be relatively direct because moss and lichen coverage is generally not thick enough to homogenise the substrate; as has been observed in tropical environments (Hofstede et al. 2001; Zotz & Vollrath 2003).

Architecture

The shape and form of a host tree influences the epiphyte and vine populations it supports (Laube & Zotz 2006; Blick & Burns 2009; Burns & Zotz 2010). Although this was not directly measured in the present study, architecture is clearly an important characteristic of different host tree species for both species richness and abundance. For example, titoki has many large branches that spread laterally out from the trunk and also had the highest mean number of epiphytes per host tree in both nonurban Waikato and Taranaki forests.

It is apparent from the above that different host tree assemblages in each study site would likely result in an inherently different assemblage and relative abundance of epiphyte and vine species. However, the low species per tree in urban Waikato forests is unlikely to be solely related to host tree differences but also due to other disparities between the studied forest types; as detailed below.

Dispersal modes and distances

The establishment of epiphyte and vine species requires a seed source within dispersal distance but there is limited information on distances for this guild of plants (Benzing 1990). Similar to findings from other localities, the majority of epiphytes and vines in the present study are wind dispersed, and it is assumed that this facilitates relatively large dispersal ranges (Gentry & Dodson 1987; Nieder et al. 2000). However, other authors have found dispersal distances to be quite limited (e.g. Wolf (2005) suggested that distances greater than 10 km are rare). For the studied species, it is speculated that those not dispersed by wind will be limited by the relatively large dispersal distances into urban Waikato (Hamilton City) (mean: 20.1 km) forests, while all dispersal mechanisms should be effective in the Taranaki region (mean: 4.4 km).

Edge:area ratios and microclimates

A high proportion of urban forests in both Waikato and Taranaki exist in gully systems. The branched nature of these gullies and the small size of urban patches is reflected in relatively large edge:area ratios and low forest width for both Taranaki and urban Waikato forests. These narrow strips of forest will have microclimates, vegetation compositions and population structures that vary from the larger nonurban forests because of strong edge effects (Denyer et al. 2006; Young & Mitchell 1994). Microclimate monitoring in five Waikato forests allowed quantification of these edge effects on the canopy temperature and vapour pressure deficits.

The nine month monitoring period showed that urban forests have temperatures that are on average 1.9 °C higher and vapour pressure deficits that are on average 1.1 kPa higher than nonurban forests. A similar result was reported by McDonnell et al. (1993) who found that temperature monitoring across an urbanisation gradient over a six year period showed urban forests to be consistently around two degrees warmer than nonurban sites. Botkin & Beveridge (1997) also reported urban temperatures from midlatitude areas of America to be 1–2 °C higher in the winter and 0.5–1.0 °C higher in summer than nonurban areas. In a relevant study Kessler (2001) found a correlation between epiphytic pteridophyte species richness with both rainfall and bryophyte cover. He explained that rainfall and bryophyte cover are a proxy for air humidity, reflecting the requirement of high humidity for early epiphyte colonisation and further epiphyte succession. Kessler (2001) also found a negative correlation between species richness and human impact but noted that this was not independent from humidity because human activity was focussed in more arid areas.

It is likely that the warmer, drier microclimates of urban Waikato are the result of small patch areas and strong edge effects that reduce or prevent microclimate buffering. It is therefore speculated that these conditions are limiting substrate availability and increasing desiccation stress for epiphytes and vines which consequently inhibits successional processes and limits species diversity and abundance (Nieder et al. 2000; Wolf 2005).

Microclimate differences are likely to contribute to the significantly different epiphyte and vine diversity on the same host species across different forests. Similarly, the different species abundance and diversity between Waikato and Taranaki regions is likely to be related higher rainfall (Figure 2.1) and humidity.

Facilitation and species associations

Analysis of species presence and absence in relation to host tree diameter provided a method of testing the allocated successional classifications. The unique relationship that each species had with varying host tree size reflects the complexity of ecological interactions.

From the persistent nature of all species across host tree sizes, it is apparent that the species studied do not exhibit true succession. It suggests that each “successional” group of species is not replaced by the next, but instead, the community of epiphytes and vines is gradually enriched with more species as the environmental conditions are altered and the suitability of habitats are improved. Therefore, each category described above may be better labelled as *facilitative* rather than *successional* because each group modifies canopy habitats in a way that facilitates the arrival of later groups.

Most of the species-host diameter patterns (appendix four) support the allocated “early/mid/late” categories described above, with the exception of *Metrosideros fulgens* (Figure 2.26) and *Ripogonum scandens* (appendix four) which were relatively more abundant on smaller trees than expected. It should be noted that this analysis is biased because the data used excluded any immature forests and therefore, more accurate results could be achieved by sampling a wider range of forest ages.

Facilitation processes are important for understanding the species richness and abundance of epiphytes and vines across different forest classes as the underlying species trajectory of a forest is the result of interactions between many other factors; some of which have been discussed above.

Lichens and mosses are generally the first epiphytes to colonise the high stress environments of bare host branches. This initial layer of organisms ameliorates the environmental conditions by providing the substrate, moisture, and nutrients that initiates succession of vascular species, often with the establishment of small colonising ferns such as *Pyrrosia eleagnifolia* and *Microsorum pustulatum* (Dawson 1986; Benzing 1990; Nadkarni 2000; Nieder et al. 2000; Burns 2007). As an interwoven mat forms from moss, lichen, humus and the roots of colonisers, more water and nutrients can be stored and more early species arrive (Matelson et al. 1993). In the present study these species include the orchid *Earina mucronata*, and the climbing ferns *Microsorum scandens*, and *Blechnum filiforme*.

The community continues to slowly build with increasing species diversity and abundance as more moisture and substrate becomes available (Nadkarni 2000; Zotz & Vollrath 2003). Once an area is colonised, mid-arrival orchids (e.g. *Ichthyostomum pygmaeum, Drymoanthus adversus, Earina autumnalis*), lianas (e.g. *Metrosideros* vines), nest epiphytes (e.g. *Collospermum hastatum*, *Astelia solandri*), and ferns (e.g. *Asplenium* species) become established and continue to develop the habitat for the next group of species. Nest epiphytes in particular can create very sizeable community clumps with long, narrow leaves that impound water, nutrients, and detritus, which develops into large quantities of humic soil over time (Cockayne 1910; Burns & Dawson 2005). The substrate and resources provided in these nests enhances their own microhabitat and facilitates the establishment and growth of later species such as *Pittosporum cornifolium* and *Huperzia varia.* A positive relationship is thought to exist between host tree size, the mass of nest epiphytes and broad patterns of species diversity (Dickinson et al. 1993; Burns & Dawson 2005). In the present study, the presence of nest epiphytes had a significant correlation with the number of other epiphytes on the same tree.

The establishment and survival of late arrival species requires the continuously high atmospheric humidity that mature forest and epiphyte communities provide. If this is not available, the ecosystem trajectory of epiphyte and vine populations can be suspended in a state of early-mid development (Nieder et al. 2000; Hofstede et al. 2001; Giordano et al. 2004). The combination of survey and microclimate results in the present study indicates that this suspension has occurred in urban Waikato forests, and that a healthy population of late arrival species is unlikely to exist until microclimate humidity is increased.

The high proportion of late arrival species and the relatively high epiphyte and vine diversity and abundance in Taranaki forests indicates that this region has more suitable microclimates than urban Waikato. This study has also highlighted that the forests of Taranaki have larger host trees, smaller seed dispersal distances, and higher rainfall than those of the Waikato, as well as reasonably high edge:area ratios. These conditions are all likely to result in a greater abundance of suitable habitats for epiphytes and vines.

To conclude, epiphyte and vine species richness and abundance is low in Waikato urban forests with current populations dominated by early and mid arrival species. Investigations into a range of related factors indicate that this is likely to be the result of large edge:area ratios and associated edge effects increasing the canopy temperature and vapour pressure deficits, and decreasing the availability of substrate and moisture; thus preventing progression from early and mid arrival species. This study has also indicated that the characteristics of the variable host tree assemblages, and the large distances between urban forests and abundant seed sources may also be limiting epiphyte and vine species richness and abundance. Chapter five presents recommendations for restoration ecology that have been developed from these results.

Chapter Three: Water relations of *Griselinia lucida* and *G. littoralis* under desiccation stress

3.1 Introduction

Epiphytes of New Zealand's temperate rainforests have comparable biomass and diversity to the famed canopy flora of many tropical forests (Dickinson et al. 1993; Hofstede et al. 2001; Zotz 2005), and like all canopy-dwellers, their growth and survival is strongly limited by the scarcity of water (Zotz & Tyree 1996; Martin 2004; Benzing 1990). To overcome this common constraint, epiphytes are frequently xerophytic (Benzing 1990) with physiological features and responses that facilitate the maintenance of turgor and numerous associated metabolic functions (Richter & Kikuta 1989; Ludlow 1989). Different combinations of features and responses can be broadly classed into three strategies (Ludlow 1989) that apply to both epiphytes and terrestrial plants; (1) desiccation escape, (2) desiccation postponement, and (3) desiccation tolerance. Each strategy requires a trade-off between the ability to tolerate stress and potential growth; for example, while desiccation escapers are susceptible to drought stress, they have the advantage of fast growth to rapidly reach maturity while conditions suit (Bader et al. 2009). Features and physiological responses are not exclusive to one class, and plants often exhibit strategies that fit along a continuum between categories (Ludlow 1989). Stress tolerance is also related to the stage of plant development (Levitt 1980; Zotz et al. 2001; Bader et al. 2009) with seeds and mature forms generally exhibiting the most tolerance (Ludlow 1989).

3.1.1 Stress strategies

Desiccation escape

Plants that can escape desiccation have high degrees of developmental plasticity which allow them to maximise resource use and complete their life cycle while water is available (Ludlow 1989; Chaves et al. 2003). Members of this group are very sensitive to substrate moisture levels and respond rapidly to available water with expeditious germination and growth to avoid conditions that may cause turgor loss (Ludlow 1989; Meyre et al. 2001). The escape strategy is important for plants growing in seasonally arid climates such as deserts because their existence during dry conditions as a dormant seed allows maximal drought tolerance (Ludlow 1989). This is not often reported as a strategy in epiphytic life forms; most likely because the limited substrate would not support dormant seeds. An example of desiccation escape comes from Tevis (1958) who followed the life cycle of the wildflower *Plantago insularis* on Californian sand flats. This species rapidly responds to the first seasonal rainfall so as to complete its life cycle while conditions are favourable; in 1957 it reached maturity after receiving only 51 mm of rainfall between January and April (Tevis 1958). Morphological features of this group vary, with some species exhibiting stress-tolerating features such as high root to shoot ratios while others are very intolerant of any desiccation (Ludlow 1989).

Desiccation postponement

Desiccation postponers have traditionally been labelled "drought avoiders" (e.g. Ludlow 1989), but because drought is a climatic phenomenon that all plants in the exposed area must endure, only those in the first group, the desiccation escapers are true "avoiders" (Taiz & Zeiger 2002). Postponers maintain their turgor and tissue water potential under drought stress for as long as possible because their tissues are sensitive to dehydration. This strategy requires the (2a) minimisation of water loss and/or (2b) maximisation of water uptake (Ludlow 1989), which can be achieved through a range of features and responses, including sensitive stomatal control (Bannister & Kissel 1986; Zhang et al. 2009), crassulacean acid metabolism (CAM), extensive root networks, small leaves, leaf shedding, reduction of leaf angle of incidence (Ludlow 1989), low cuticular conductance, high root to shoot ratios (Smith & Griffiths 1993), and water storing tissues (Cavelier & Goldstein 1989). The characteristics of desiccation postponement are often reported for epiphytes; an example is *Tillandsia urticulata*, a bromeliad epiphyte that utilises water storage, highly elastic cell walls, and CAM to maintain high water potential and turgor under water stress (Stiles & Martin 1996).

Desiccation tolerance

Desiccation tolerators are the least sensitive to desiccation and can withstand severe tissue dehydration (Ludlow 1989). This group includes the exceptional poikilohydric or "resurrection" species, which can tolerate extreme water loss and in some cases, survive in a state of quiescence for many years (Scott 2000). However, the majority of desiccation tolerators cannot survive such extreme limitations and Kozlowski and Pallardy (2002) differentiated these non-resurrecting members into those that survive by either (3a) maintaining high relative water content or (3b) enduring both low relative water content and low water potential (Figure 3.1). Desiccation-tolerators minimise the effect of drought stress through physiological adjustments over time (Ludlow 1989; Smith & Griffiths 1993). To maintain turgor, plants can adjust leaf osmotic potential or cell elasticity (Richter and Kikuta 1989). When plant water potential decreases, osmotic adjustment assists in turgor maintenance by increasing the net accumulation of solutes in a cell; thus lowering the osmotic potential and attracting water into the cell. Similarly, increases in cell wall elasticity (measured by a reduction in bulk elastic modulus (ε)) improve water storage capacity of the cells and reduce sensitivity to drought stress by means of prolonged turgor maintenance (Kirkham 2005; Lambers et al. 2008). Lambers et al. (2008) explain that elastic and osmotic adjustments do not occur simultaneously because lowered osmotic potential along with elastic walls would cause cell swelling and be ineffective at maintaining turgor. Therefore, plants that maintain high relative water content (3a) reduce water loss through osmotic adjustment, while plants that endure low water content (3b) can do so because elastic cells facilitate higher relative water loss.

An example of desiccation tolerance is reported by Drivas and Everett (1988) who found that *Artemisia arbuscula*, a shrub growing on dry stony clay loams in western Nevada, can endure water potentials as low as -5.5 MPa while still actively transpiring and losing water. The ability of epiphytes to survive canopy climates is often described as desiccation tolerance (e.g. Hietz & Briones 1998; Zotz et al. 1999; Bader et al. 2009).

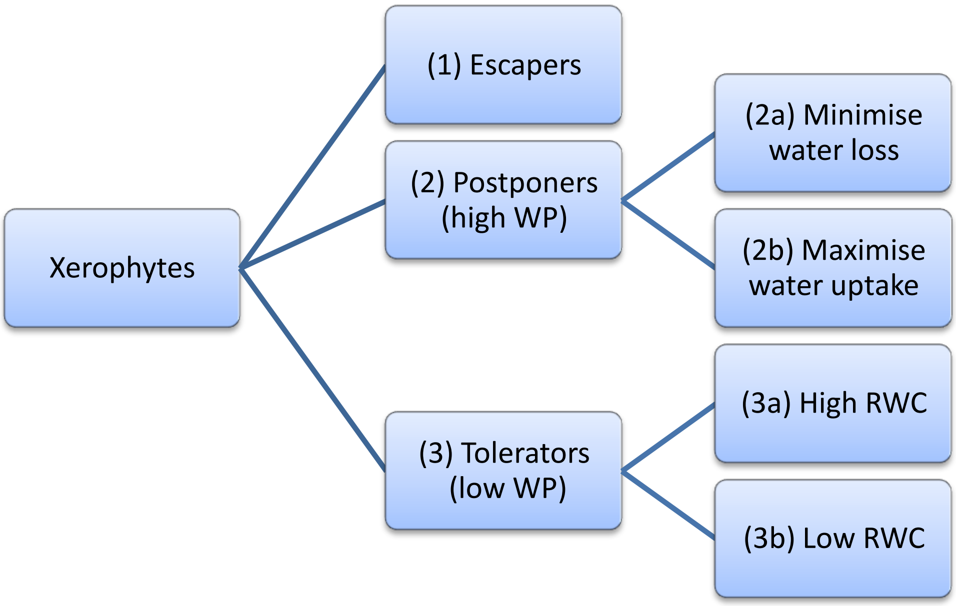

Figure 3.1: Strategies of xerophytic plants. The three main classes are escapers, postponers and tolerators but plant characteristics may fit along a continuum between these groups. Adapted from Kozlowski & Pallardy (2002).

3.1.2 Water relations of *Griselinia lucida* and *G. littoralis*

Research into the water relations and physiology of New Zealand epiphytes is predominantly restricted to morphological and anecdotal observations by Oliver (1930), along with general descriptions of a few particular genera (e.g. Holloway 1923; Dawson 1966). New Zealand is likely to have epiphytic species belonging to each of the above stress classes, as well as those that exhibit features of more than one group. The investigations into epiphyte water stress strategies in the present study were focussed on the hemi-epiphyte, *Griselinia lucida*. This species is one of only four shrub epiphytes in New Zealand and one of two indigenous members of Griseliniaceae. It was chosen for this study because very little is known about its water relations and how it responds to the aridity of canopy climates. The terrestrial congener of *Griselinia lucida, G. littoralis,* was included in to compare characteristics of a different lifestyle.

Griselinia lucida is clearly set apart from other native epiphytes by its large size (up to ten metres in spread) and distinctive grooved roots that regularly extend down the host trunk to access soil moisture and nutrients. It also has large, thick, glossy green leaves that have been suggested to store water (Oliver 1930; Dawson 1966). In contrast, *Griselinia littoralis* has a predominantly terrestrial lifestyle with the exception of occasional canopy-dwelling above the altitudinal range that

G. lucida occupies; where it has also been reported to occasionally establish terrestrial roots (Cockayne 1967; B.D. Clarkson, University of Waikato, pers. comm. 2011).

The academic literature on Griseliniaceae is limited. Available research focuses on descriptive morphology (e.g. Oliver 1930; Dawson 1966), ecology (e.g. Wardle 1964; Zotz 2005), and taxonomy (e.g. Dillon & Muñoz-Schick 1993; Philipson 1967), with only a small number of physiology-based articles (e.g. White & Lovell 1984; Burrows 1995).

Griselinia lucida is commonly considered to be able to withstand water stress (e.g. Ogden 1976) while *G. littoralis* has been reported to be relatively sensitive (Bannister 1986). The leaves of *G. lucida* are much larger than those of *G. littoralis*, as well as most other indigenous epiphytes. Although it often roots in nest epiphytes or terrestrial soil (Oliver 1930), this large shrub epiphyte will experience regular water stress. In order to minimise the water loss from the large leaf area, it is hypothesised that *G. lucida* is a desiccation postponer which, under water stress, "shuts-down" and delays turgor loss through reduction of stomatal conductance, photosynthesis, and growth rates; thereby minimising water loss and physiological damage, and enabling a relatively fast recovery. The large, fleshy leaves may also postpone desiccation through water storage (Oliver 1930) and high cell wall elasticity that allows preferential water loss from non-essential cells (e.g. Nowak & Martin 1997; Martin 2004). Therefore it is also hypothesised that the large leaves of this species store water to assist in desiccation postponement, allowing *G. lucida* to endure water stress for longer than *G. littoralis*.

In contrast, *G. littoralis* does not regularly inhabit arid canopy climates and consequently avoids the regular water stress that its congener is exposed to. It also has smaller and thinner leaves, indicating less reliance on water storage and cell elasticity than *G. lucida*. Thus, it is expected that *G. littoralis* is a desiccation tolerator that can maintain a higher level of photosynthesis during water stress than *G. lucida* with less reliance on water storage and high cell elasticity.

A drought experiment was undertaken to address these hypotheses. The physiological responses of both *G. lucida* and *G. littoralis* were measured under moderate and severe levels of desiccation.

The plants in this experiment were potted seedlings. In the case of *G. lucida,* these are considered equivalent to a juvenile epiphyte that has not developed a terrestrial root connection.

3.2 Materials and Methods

3.2.1 Plants and glasshouse conditions

Seedlings of the epiphytic *Griselinia lucida* were approximately six months old when sourced from Lyndale Nurseries in March 2010. The seed source for these plants was terrestrial individuals in Whenuapai and Waitakare, northern North Island. Seedlings of *G. littoralis* were nine months old when received from Forevergreen Seedlings in May 2010. The seed source was the Taupo Botanical Gardens, central North Island. The seedlings were 28.1 ± 0.7 centimetres and 19.3 ± 0.6 centimetres tall with 19.2 ± 0.4 and 16.1 ± 0.6 leaves for *G. lucida* and *G. littoralis*, respectively. Both species were re-potted within a week of arrival into 4.5 litre pots (16.5x16.5x19 centimetres) with standard potting mix ("Just" brand, supplied by Daltons Ltd., NZ, with controlled release fertiliser). Leaf thickness was measured with digital callipers modified to measure a single point on the lamina. A total of 80 measurements from four plants of each species were taken at 0.01 millimetre accuracy. Leaf sectioning by hand was undertaken to compare the anatomy of each species. Measurements of cell thicknesses were made using a microscope and a stage micrometer. Plant height and number of leaves were recorded every three weeks for every plant.

The experiment was conducted over the winter and spring months of July-September in a glasshouse with the following range of temperature, relative humidity, and photosynthetically active radiation (PAR) (Table 3.1).

Table 3.1: Mean, minimum and maximum temperature (T), relative humidity (RH), and PAR in glasshouse over duration of experiment.

	T (°C)	RH (%)	PAR (nm)
Mean	22.53	44.72	70.64
Minimum	15.79	27.61	-0.18
Maximum	27.88	72.20	628.30

3.2.2 Experimental design

Seedlings were randomly assigned to thirty blocks, until each block had three randomly positioned seedlings of each species (Martin & Ogden 2005). Each seedling was then randomly assigned to one of three treatments and a subset of 30 plants (five of each species under each treatment) was randomly chosen for monitoring of pot weight using a balance (Denver XL-6100).

Due to the fluctuating availability of canopy water supplies, *in situ* epiphytes are likely to be drought-hardened at a young age which affects future control of water loss and performance under drought (Kozlowski & Pallardy 2002). To reflect this natural condition, all plants were drought-hardened by a three week period without water prior to the beginning of treatments. During treatment, pot weight loss and pre-dawn water potentials were monitored with weekly measurements to establish soil water deficits in each treatment group and estimate the volume of water required to create minimal (1), moderate (2) and severe (3) stress:

- Treatment 1: Control/Minimal stress: watered every seven days with the volume of water required to maintain pot weights at the mean starting weight.
- Treatment 2: Moderate stress: watered every seven days with a volume of water required to maintained moderate levels of stress; estimated to be equivalent to a pre-dawn water potential of -0.2 MPa.
- Treatment 3: Severe stress: water withheld.

The experiment was ended when 50 % of plants undergoing treatment three reached severe predawn wilting (Rahman et al. 1999; Ealson & Richards 2009), at which time all treatments were re-watered to saturation. The total duration was 70 days.

3.2.1 Plant harvest and relative growth rates

Plant harvests were conducted at the beginning and end of the experiment on ten randomly selected plants of each species from each treatment (start: n_{start}=20, end: n_{end}=60). Leaves, stems and roots were separated and cleaned of all extraneous material. Leaf area was measured using a Li-Cor Li-3100 area meter, fresh and dry weights of leaves, stems and roots were measured using a Mettler AE260 balance. Plant leaf areas were calculated from leaf counts and the average leaf areas for each treatment group.

Relative growth rates (RGR) were calculated using the Hunt et al. (2002) software tool and the dry weights of leaves, stems and roots from each harvest. Total leaf dry weight at the end of the experiment was corrected for the number of leaves excised during water potential measurements.

3.2.2 Water relations

Xylem pressure at predawn (ψ_{wPD}) and midday (ψ_{wMD}) were measured every seven days on a randomly selected subset of 18 plants which consisted of three of each species of each treatment. For each measurement a leaf was covered with a humidified plastic bag and then excised. Xylem pressure was measured following Boyer (1995) using a custom-made pressure-chamber (Scholander et al. 1965). For predawn and midday measurements, the leaf weight and pot weight of the plant were recorded. Xylem pressure was assumed to be equivalent to the bulk water potential of the leaf, ignoring the contribution of apoplasmic solutes. Dawn leaf water potentials were regarded as equivalent to the soil water potential. Due to the destructive nature of the pressure-chamber measurements, sampling was distributed between all plants in each treatment group so that no plant lost more than 10 % of its total leaves.

Pressure-volume curves were constructed (Scholander et al. 1965; Boyer 1995; Lenz et al. 2006) for six leaves from each species, in each treatment group (n=36) at the end of the experiment using the youngest fully expanded leaf that had grown since treatment began. The leaf was re-cut under water immediately after excision from the plant and placed in a dark, humidified plastic bag overnight. Water potential and weight loss measurements were made the next day. The first water potential measurement was taken with the leaves enclosed in a humidified bag to minimise transpiration. Subsequent measurements were made periodically while the leaves dried on a lab bench. Leaf weights were measured after each water potential reading. At the end of the procedure, leaves were oven dried at 36 °C and weighed to calculate relative water content (RWC) from:

$$RWC = \frac{FW - DW}{SW - DW}$$

Where FW= Fresh weight of the measured leaf, DW= dry weight of measured leaf and SW= saturated weight of the measured leaf (Smart 1974). Pressure-volume curves were constructed from RWC against the inverse of water potential.

Höfler diagrams were constructed to identify the relationships between water potential (ψ_w), pressure potential (ψ_p), and osmotic potential (ψ_s), and to derive the bulk elastic modulus for each treatment. Osmotic potential was calculated from the formula of the straight line section of the pressure volume curve and pressure potential was calculated as the difference between water potential and osmotic potential.

Bulk elastic modulus (ε) was calculated as per Lambers et al. (2008):

$$\varepsilon = \frac{\Delta\psi p}{\Delta RWC}$$

Where the change in pressure potential is taken from the initial slope of the ψ_p curve, excluding any plateau.

3.2.3 Osmotic potentials

A representative subset of leaves from the beginning and end of treatment (n_{start}= 20, n_{end}=60) were frozen immediately after harvest. When the sampling was complete, the leaves were thawed for sap extrusion using a hydraulic press. The sap was immediately frozen in liquid nitrogen and stored in a -20 °C freezer until measurement with a vapour pressure osmometer (Vapro® 5520, Wescor, Utah). *Griselinia littoralis* leaves exuded very small quantities of highly viscous sap which in some samples was not a sufficient volume; in these cases, the sap of two leaves from the same treatment was combined. The viscous sap also required the use of the “disc immersion” technique as recommended by the osmometer user’s manual. Results from the osmometer were converted to MPa using the Vant Hoff equation (Nobel 2009):

$$\Psi_{\mathrm{s}} = RT \sum_{\mathrm{j}} c_{\mathrm{j}}$$

where $\sum_{\mathrm{j}} c_{\mathrm{j}}$ is the osmolality in mmol kg^{-1}.

3.2.4 Stomatal conductance and photosynthesis

Every seven days stomatal conductance (g_s), and rates of photosynthesis (A) under ambient conditions were measured at midday using a portable photosynthesis system within an integrated light source (Li-6400XT, Licor, Nebraska) on a randomly selected subset of 18 plants; three of each species of each treatment. The first fully expanded leaf was chosen for measurement on each plant. Photosynthetically active radiation (PAR), chamber temperature, and humidity were set to follow natural levels in the glasshouse so as to record actual levels of activity (mean PAR: 282.0±15.5) μmol m^{-2}s^{-1}, mean leaf temperature: 26.3±0.15 °C, mean leaf vapour pressure deficit: 1.81±0.02 kPa).

3.2.5 Cuticular conductance

Cuticular conductance (g_{c}) was calculated (Sack et al. 2003) at the beginning of the experiment from measurements of leaf weight loss from ten leaves of each species. Leaves were left to dry on a lab bench with measurements of leaf weight, relative humidity and temperature every hour for the first seven hours, and then every two hours until changes in weight were negligible. Cuticular conductance was calculated from:

$$g_c = \frac{T}{D_1}$$

Where T is transpiration (moles lost per m^2 per second) estimated from the linear portion of the weight loss curve and D_{l} is the water vapour pressure difference between the leaf and air, in molar units, calculated from air temperature and relative humidity measured using a hygro-thermometer (Extech EasyView™20).

3.2.6 ^{13}C measurements

To compare the water use efficiency of plants under different levels of stress, three fully expanded leaves of each species from each treatment (n_{start}= 6, n_{end}=18) were dried at 36 °C and finely ground for measurement of ^{13}C discrimination by the Waikato Stable Isotope Unit at the University of Waikato. Ratios were determined using a Dumas elemental analyser interfaced to an isotope mass spectrometer.

This method was also utilised to compare water use efficiency of 14 *in situ* plants exhibiting different stages of root development; from fully epiphytic (no roots to the ground) to multiple mature terrestrial roots (Table 3.2). The most recent fully-expanded leaves from *G. lucida* individuals were collected for analysis.

Table 3.2: Number of samples from individual *G. lucida* epiphytes in each root stage that were collected and analysed for ^{13}C.

Root stage	Number
None	4
Early	1
Multiple	6
Mature, multiple	3

3.2.7 Statistical analysis

Physiological data were analysed using Analysis of Variance (ANOVA) and post-hoc Fisher LSD tests. The assumption of homogeneity of variance was checked using the Levene's test and the condition of normal distribution was verified using the Sharpiro-Wilk test. Assumptions were ignored when sample sizes were over 30 as per the central limit theorem. Small data sets that did not meet assumptions were analysed using non-parametric Kruskal-Wallis ANOVA. Correlation between variables was investigated using linear regression and Pearson correlation coefficients. The null hypothesis was rejected and statistically significant results reported when the p-value was less than 0.05; p values are reported with each result.

3.3 Results

3.3.1 Leaf growth

The leaf area of plants of both species shows decreased growth with increased stress (Figure 3.2). The severe treatments have the lowest growth and were significantly less than the control treatments for both species (p<0.03), while the moderate treatment was most comparable to the control.

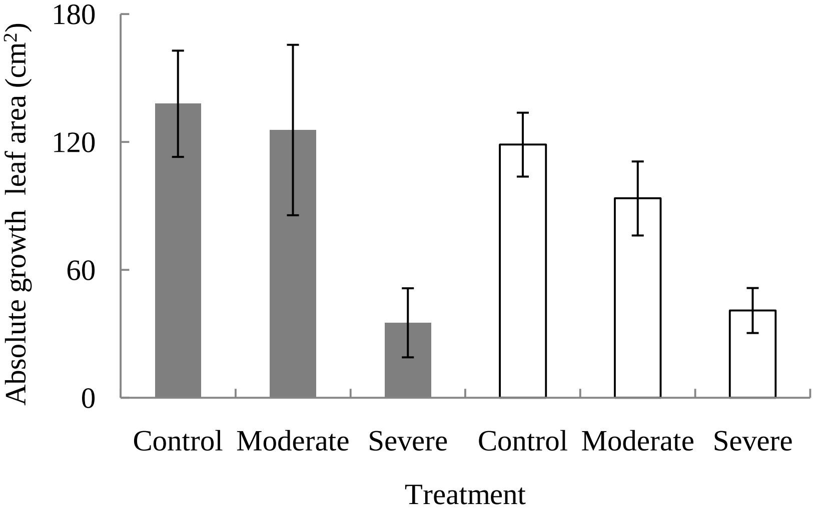

Figure 3.2: Leaf growth (area) for *Griselinia lucida* (closed bars) and *G. littoralis* (open bars) in each treatment group with standard error bars.

3.3.2 Relative growth rates

Relative growth rates of leaf, shoot, and root growth show a similar reduction in growth under severe stress for both species (Figure 3.3), but due to the high variability in plant growth forms and sizes, the data set has high standard error and is thus not significant.

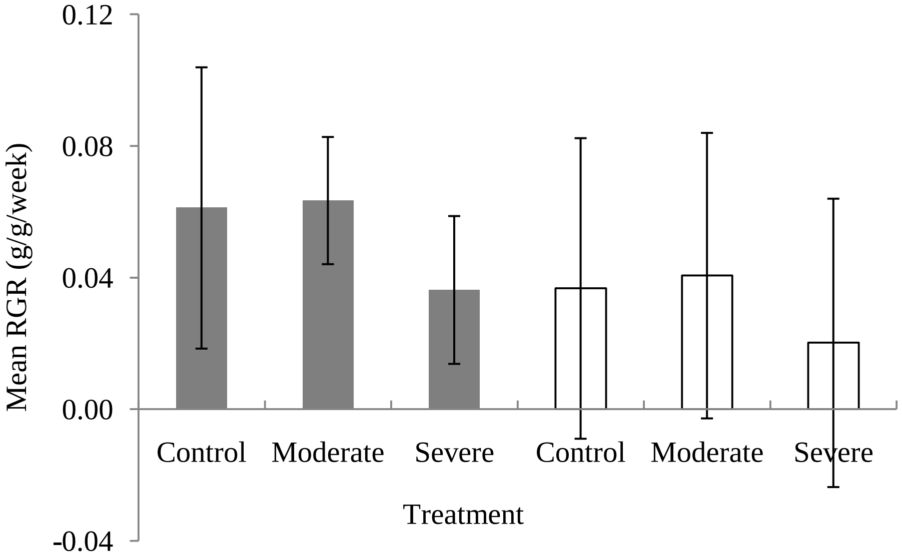

Figure 3.3: Relative growth rates for *Griselinia lucida* (closed bars) and *G. littoralis* (open bars) in each treatment group with standard error bars.

3.3.3 Time course of water potential, stomatal conductance and photosynthesis

Midday water potential, stomatal conductance (g_s) and photosynthesis (A) reduced with time under severe stress (Figure 3.4) for both species but the reductions were the greatest for *G. lucida*. The sharp decline in g_s and A for *G. lucida* under severe stress around week five aligns with a reduction in predawn water potential (not shown). *G. lucida* activity reduced to almost zero until rewatered (shown by dotted line) when it recovered function rapidly. Both species maintain relatively constant or rising levels of g_s and A in the control group (Figure 3.4).

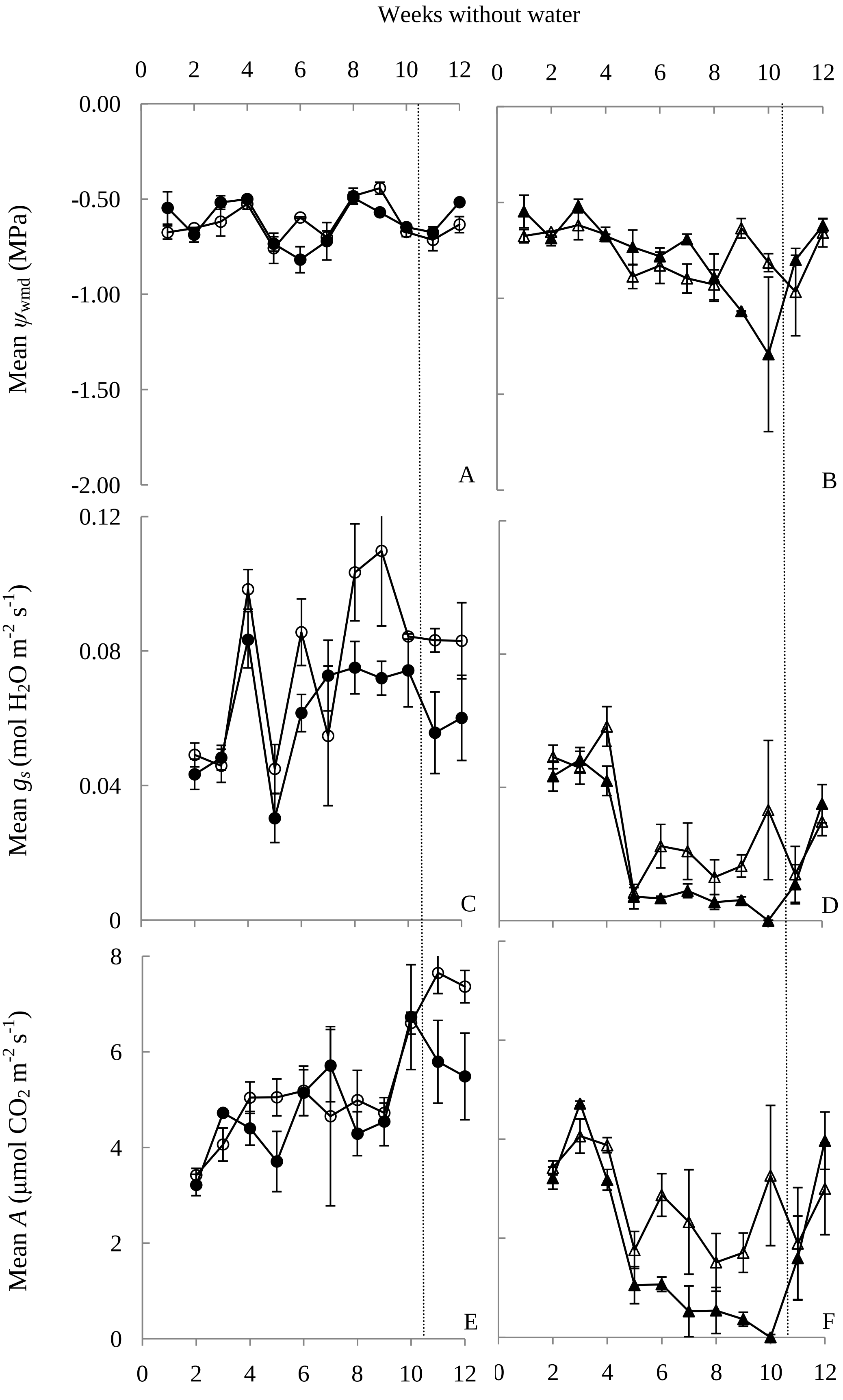

Figure 3.4: Time course of midday water potential (ψ_{wmd}), stomatal conductance (g_s), and photosynthesis (A) for *Griselinia lucida* (closed symbols) and *G. littoralis* (open symbols) in the control (A, C, E) and severe stress (B, D, F) groups. Dotted line shows rewatering (between week 10 and 11) to highlight the rapid recovery by *G. lucida*.

3.3.4 Leaf characteristics

The mean area, thickness, and fresh weight per unit area (per leaf) of *Griselinia lucida* were all significantly higher than *G. littoralis* ($p<0.01$) but specific leaf area was not significantly different (Table 3.3). Measured cuticular conductance of *G. lucida* was significantly lower than that of *G. littoralis* ($p<0.006$) (Table 3.3); two outliers were removed from this analysis because the leaves were not mature and were thus skewing the result.

Table 3.3: Mean leaf area, thickness, specific leaf area (SLA), and cuticular conductance (g_c) per leaf for *Griselinia lucida* and *G. littoralis*. Standard errors are presented in brackets.

Species	Mean area (cm^2)	Mean thickness (mm)	Mean fresh weight (g) per cm^2	SLA (cm^2g^{-1})	g_c ($mol.m^2.s^{-1}$)
Griselinia lucida	624.5 (30.6)	0.45 (0.01)	0.055 (0.001)	80.9 (2.3)	0.00097 (0.00013)
Griselinia littoralis	159.3 (12.2)	0.36 (0.01)	0.042 (0.001)	85.1 (5.0)	0.00166 (0.00016)

3.3.5 Soil moisture

Predawn water potential (ψ_{wpd}) of the control group was held between zero and -0.4 MPa with 25-50 % volumetric water capacity (θ) of soil water. The predawn water potential of moderately stressed plants was kept below -0.17 MPa with *G. lucida* dropping to a minimum of -0.53 MPa and *G. littoralis* reaching -0.34 MPa. The clearest difference between species was under the severe stress treatment, in which *G lucida* dropped to -1.25 MPa after 70 days of no water, while *G. littoralis* reached a minimum of -0.74 MPa (Figure 3.5). This lower ψ_{wpd} in *G. lucida* influences other measured features and thus, stomatal conductance and photosynthesis have been plotted against soil moisture content rather than the time since water was withheld.

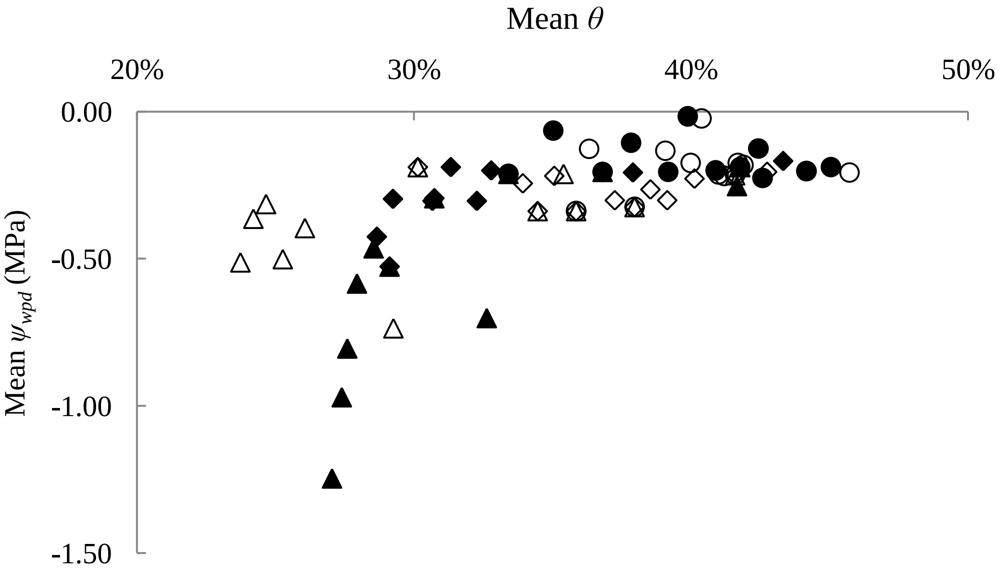

Figure 3.5: Mean volumetric soil moisture (*θ*) against mean predawn water potential (ψ_{wpd}) for *Griselinia lucida* (closed symbols) and *G. littoralis* (open symbols) in control (circles), moderate (diamonds) and severe stress (triangle) treatment groups.

3.3.6 Stomatal conductance

The stomatal conductance of both species decreased in response to reduced water potentials with *G. lucida* reaching a minimum of zero and *G. littoralis* reaching 0.008 mol H2O m^{-2} s^{-1}. While the stomatal response to drought appeared similar in the two species, there was some indication that stomatal conductance decreased more abruptly and at higher predawn water potentials in *G. lucida* compared to *G. littoralis* (Figure 3.6).

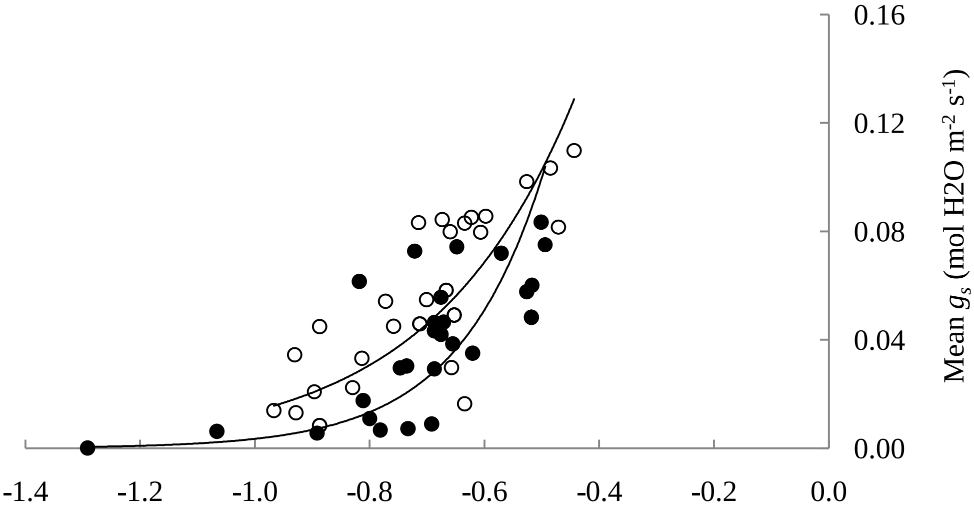

Figure 3.6: Mean midday stomatal conductance (g_s) against mean predawn water potential (ψ_{wpd}) for *Griselinia lucida* (closed symbols) (R^2=0.70) and *G. littoralis* (open symbols) (R^2=0.60). Data sets fitted with exponential trendlines.

3.3.7 Plant photosynthesis

The relationship between midday photosynthesis and stomatal conductance was similar in the two species, with photosynthesis declining linearly with decreasing stomatal conductance in both species (Figure 3.7). The relationship between photosynthesis and soil water potential (not shown) was therefore similar to that observed for stomatal conductance (Figure 3.6), with photosynthesis declining to low levels in both species as predawn water potential approached -1 MPa.

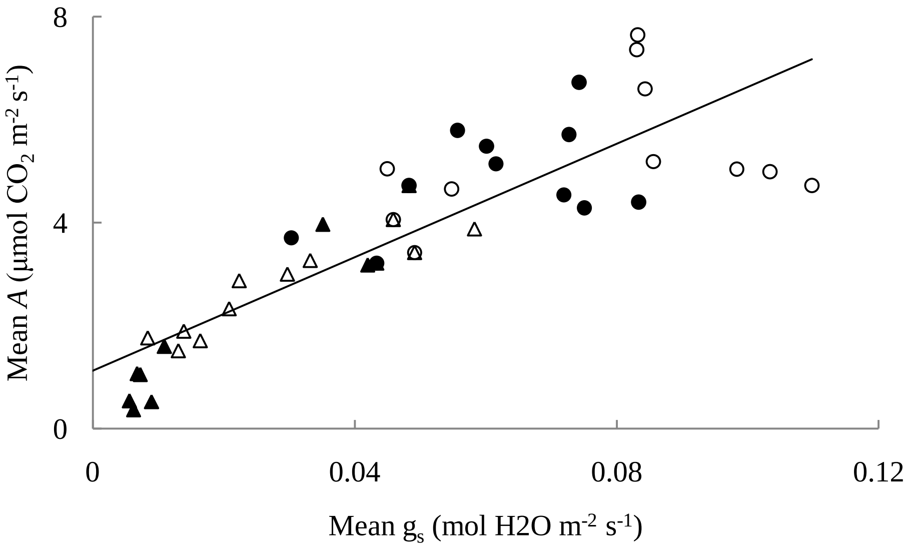

Figure 3.7: Mean midday photosynthesis (*A*) against mean stomatal conductance (g_s) fitted with a linear trendline (R_2=0.74) showing limited *A* with reduced g_s.

3.3.8 Leaf pressure-volume relationships

The bulk elastic modulus for *G. lucida* was significantly higher than *G. littoralis* for the control and moderate treatment groups (Table 3.4) because leaf turgor (pressure potential) in these treatment groups decreased faster with declining relative water content (Figure 3.8). However, the ε for *G. lucida* under severe stress was significantly lower ($p<0.006$) than the moderate and control groups and similar to the range of ε for *G. littoralis* (Table 3.4).

Relative water content and water potential at turgor loss point (TLP) for all *G. lucida* treatments were significantly higher (less negative) than *G. littoralis* ($p<0.05$), and osmotic potential at full turgor was significantly lower (more negative) in *G. lucida* ($p<0.05$). These variables were not significantly different between treatments for either species (Table 3.4).

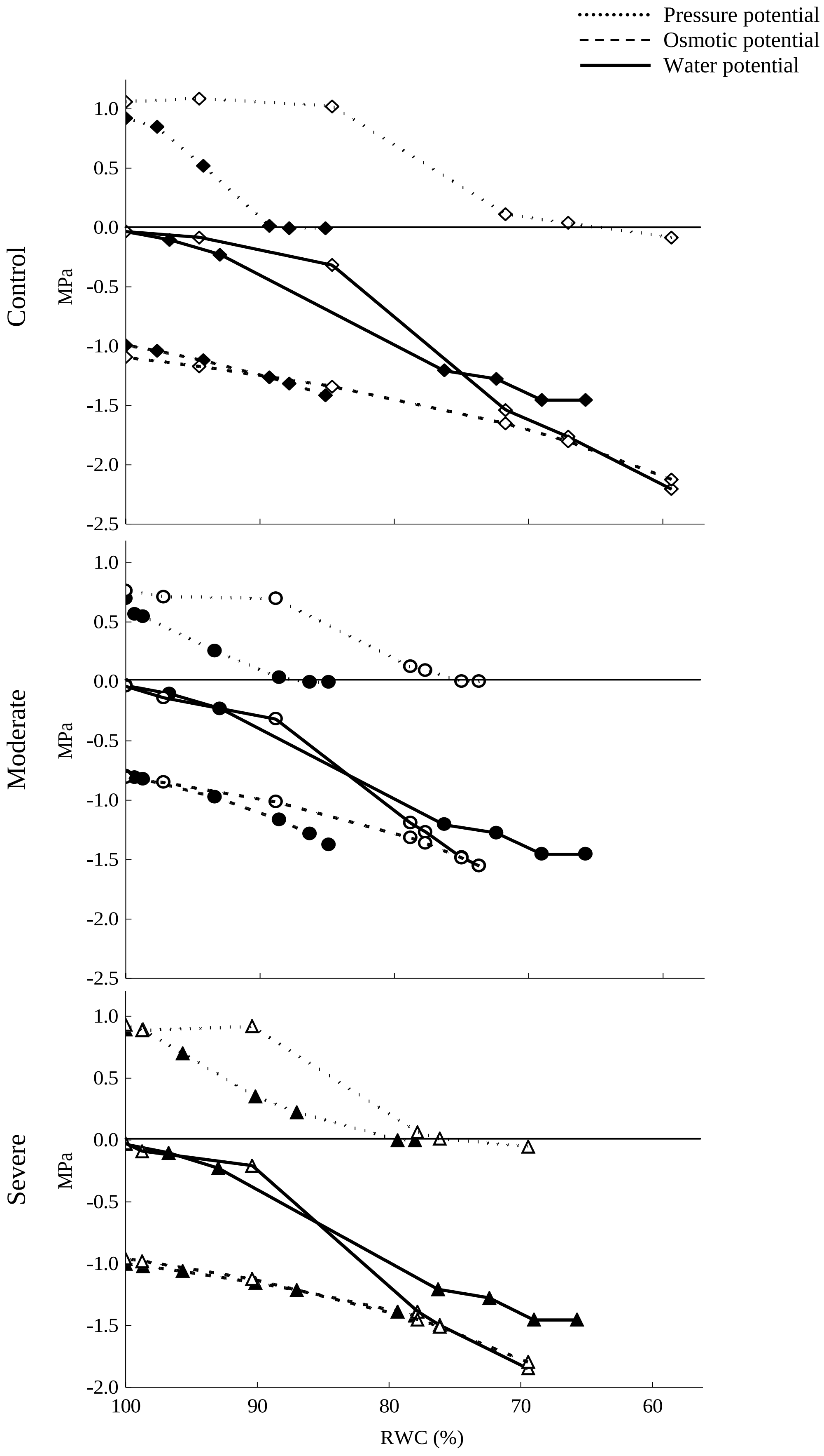

Figure 3.8: Examples of Höfler diagrams for each species and treatment showing reductions in water, osmotic, and pressure potentials with decreasing relative water content. Closed symbols: *Griselinia lucida*, open symbols: *G. littoralis*, circles: control, diamonds: moderate, triangles: severe.

Table 3.4: Mean water relation values (MPa) from pressure-volume analysis of *Griselinia lucida* and *G. littoralis* leaves (n=6 per species) under each treatment: bulk elastic modulus (ε), relative water content (RWC) at turgor loss point (TLP), water potential (ψ_w) at TLP and osmotic potential (ψ_s) at TLP. Standard errors are presented in brackets.

	Control		Moderate		Severe	
	G. lucida	*G. littoralis*	*G. lucida*	*G. littoralis*	*G. lucida*	*G. littoralis*
ε (MPa)	8.09 (0.51)	1.94 (0.62)	6.36 (0.85)	3.25 (0.64)	3.66 (0.61)	3.55 (0.77)
RWC @ TLP (%)	83.52 (1.31)	75.28 (0.82)	83.83 (1.15)	71.93 (3.32)	82.68 (2.19)	77.36 (0.66)
ψ_w @ TLP (MPa)	-1.37 (0.07)	-1.37 (0.10)	-1.39 (0.03)	-1.61 (0.09)	-1.16 (0.09)	-1.56 (0.11)
ψ_s @ sat. (MPa)	-1.17 (1.14)	-0.76 (0.72)	-1.12 (0.07)	-0.95 (0.07)	-0.83 (0.85)	-0.79 (0.85)

3.3.9 Osmotic potential

Osmotic potentials of extracted leaf sap were significantly lower for the pre-treatment group ($p<0.02$), with no significant species or treatment effects (Table 3.5).

Table 3.5: Osmotic potential (MPa) of *Griselinia lucida* and *G. littoralis* leaves (n=4-10 leaves) pre- and post-treatment for each group. Standard errors are presented in brackets.

	Pre-treatment		Control		Moderate		Severe	
	G. lucida	*G. littoralis*	*G. lucida*	*G. littoralis*	*G. lucida*	*G. littoralis*	*G. lucida*	*G. littoralis*
Mean	-0.87 (0.03)	-1.10 (0.13)	-1.16 (0.03)	-1.12 (0.11)	-1.19 (0.03)	-1.25 (0.11)	-1.15 (0.02)	-1.29 (0.06)
Minimum	-0.72	-0.85	-1.03	-0.61	-1.00	-0.54	-1.07	-1.10
Maximum	-1.07	-1.46	-1.30	-1.71	-1.36	-1.59	-1.27	-1.42

Comparison of the mean water potential results (Figure 3.5) with the mean water potential at turgor loss point (Table 3.4) indicates that *G. lucida* plants reached turgor loss point under the severe stress treatments and *G. littoralis* plants did not. Observations during the experiment support this conclusion with earlier and more frequent occurrences of wilting in *G. lucida* than *G. littoralis* plants. However, all *G. lucida* plants had the majority of leaves recover within two or three days after rewatering (Figure 3.9) while *G. littoralis* appeared to take longer to recover (often more than three days).

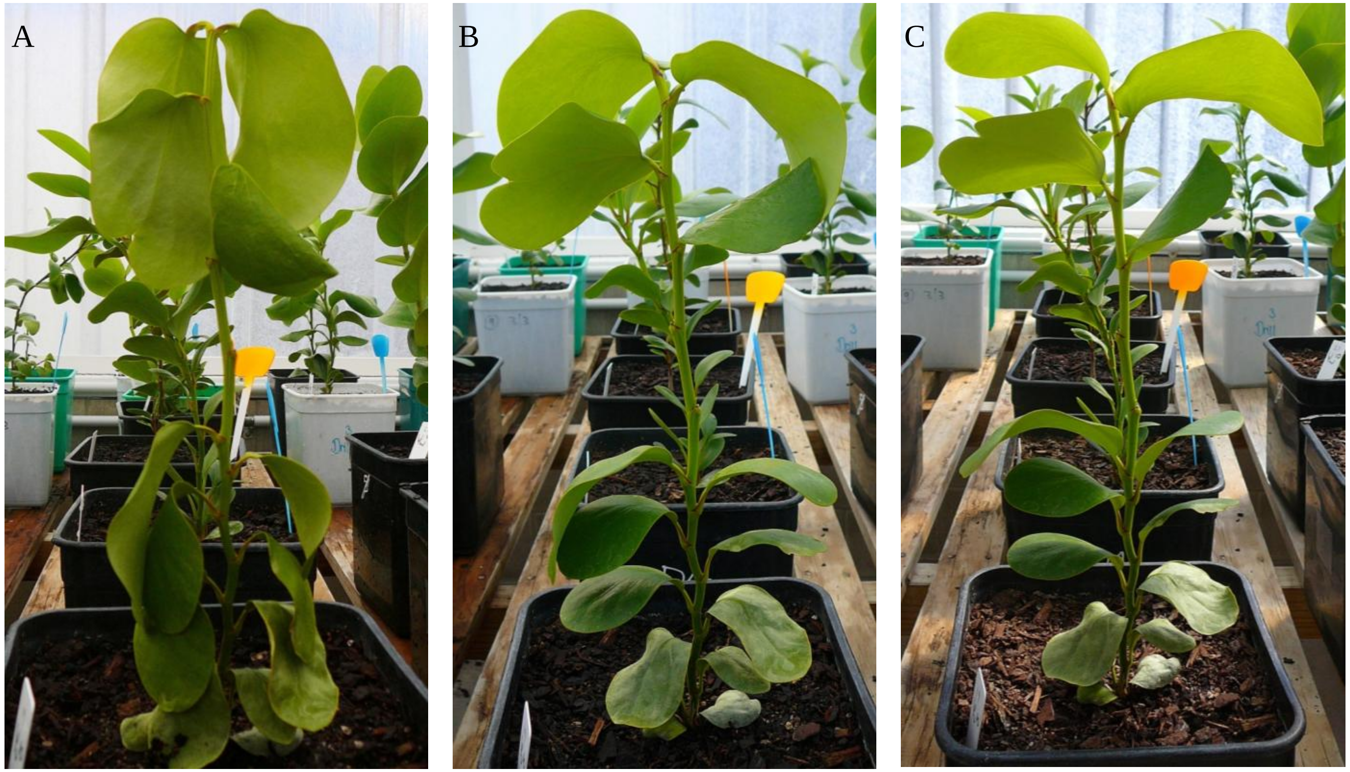

Figure 3.9: A severely stressed *Griselinia lucida* plant showing turgor loss at the end of treatment (A), recovery one day after rewatering (B), and three days after rewatering (C). Note: the leaves missing from centre stem had been excised for water potential measurements.

A small number of *G. lucida* plants (13 %) in the post-treatment harvest exhibited dieback in the distal portions of roots with only the core of the root mass still alive. The leaves and shoots of these plants still appeared turgid. In contrast, the roots of *G. littoralis* were alive under all treatments.

3.3.10 ^{13}C measurements

Delta ^{13}C analysis of *G. lucida* and *G. littoralis* for pre-treatment, control, moderate stress, and severe stress (Table 3.6) showed no significant differences.

Table 3.6: Delta ^{13}C values for *Griselinia* pre-treatment (PT), control, moderate stress and severe stress leaves.

	PT	Control	Moderate	Severe
G. lucida	-27.40 (0.33)	-26.49 (0.60)	-26.57 (0.29)	-26.65 (0.45)
G. littoralis	-26.04 (0.15)	-26.22 (0.54)	-26.60 (0.38)	-25.64 (0.23)

Delta 13C analysis of *G. lucida* individuals with different stages of root growth also showed no significant differences (Table 3.7).

Table 3.7: Delta 13C values for different stages of *Griselinia lucida* root development.

Roots	Mean 13C
None	-28.69 (1.28)
Early	-25.59 (0.00)
Multiple	-26.94 (0.80)
Mature, multiple	-26.58 (0.47)

3.3.11 Plant morphology and anatomy

Leaf sections across the midrib of *Griselinia lucida* and *G. littoralis* leaves showed similar anatomy. The main differences between species was the thickness of cell layers; *G. lucida* has a thicker hypodermis, epidermis and cuticle on both the abaxial and adaxial faces while *G. littoralis* has a thicker layer of palisade cells and a slightly thicker phloem and xylem (Figure 3.10 & Table 3.8).

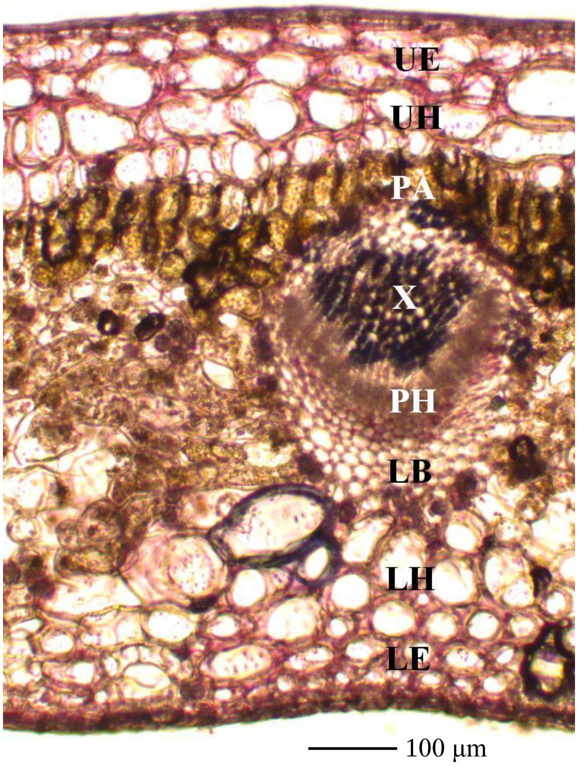

Figure 3.10: Fresh hand section through the midrib of a *Griselinia lucida* leaf stained with toluidine blue. Letters refer to measurements provided in Table 3.8.

Table 3.8: Measurements of cell thickness (µm) in a section of one *Griselinia lucida* and one *G. littoralis* leaf. Letters refer to Figure 3.10.

Cell type	*G. lucida*	*G. littoralis*
Upper cuticle	12.5	6.25
Upper epidermis (UE)	18.75	12.5
Upper hypodermis (UH)	162.5	62.5
Palisade cells (PA)	37.5	100
Upper bundle sheath cells	50	25
Xylem (X)	137.5	143.75
Phloem (PH)	50	62.5
Lower bundle sheath cells (LB)	87.5	62.5
Mesophyll	0	137.5
Lower hypodermis (LH)	200	100
Lower epidermis (LE)	18.75	12.5
Lower cuticle	12.5	6.25
Total	787.5	731.25

3.4 Discussion and conclusions

This drought experiment applied three levels of water stress to seedlings of *Griselinia lucida* and *G. littoralis.* In the severe stress treatment, both species endured more than two months of drought before exhibiting severe wilting. Measurements of acute reductions in stomatal conductance and photosynthesis in severely stressed *G. lucida* plants are consistent with the hypothesis that this species is a desiccation postponer. However, *Griselinia littoralis* also exhibited a similar reaction; contrary to the hypothesis that it is a desiccation tolerator. Both species had relatively high cell elasticity in the severe treatment and it is hypothesised that this response might facilitate tolerance of desiccation in leaves that developed during the onset of drought.

Both species exhibited lower leaf growth with moderate and severe stress than in the control, which confirms that the seedlings were exposed to three distinct levels of desiccation. The greater leaf growth in *G. littoralis* is likely to be due to the significantly smaller leaf sizes of this species.

The observed physiological responses to drought showed that *G. lucida* under severe stress reached lower leaf water potentials, lost leaf turgor at higher relative water contents, and had greater reductions in stomatal conductance than *G. littoralis* (Figure 3.4). This difference can be attributed to the larger leaf surface area and overall larger size of *G. lucida* plants at the beginning of the experiment resulting in greater water use. Thick layers of cuticle, epidermis and hypodermis cells have been suggested to aid different species under stress (e.g. Andrade & Nobel 1997; Helbsing 2000; Zotz & Hietz 2001; Martin 2004), but did not noticeably benefit desiccation postponement in *G. lucida*. The reduction in stomatal conductance of both species under severe water stress effectively restricted photosynthesis and suggests a high sensitivity to tissue desiccation; especially in *G. lucida* (Figure 3.4 & Figure 3.7). A similar sensitivity was found in hemiepiphytes plants that had not yet grown terrestrial roots and thus relied on canopy soil (Holbrook & Putz, 1996b), and also in a range of herbs, shrubs and semi-shrubs that were exposed to severe stress (Galmés et al. 2007).

The bulk modulus of elasticity (ε) in *G. lucida* decreased with increasing stress; representing an increase in the elasticity of cell walls. This adjustment is comparable to the reduced ε in stressed woody terrestrial species reported by Fan et al. (1994), and indicates that elastic adjustment is a key method for maintenance of turgor pressure under desiccation. The mean ε of *G. littoralis* seedlings was consistently low (1.94-3.55 MPa) across all stress levels and comparable to the ε of *G. lucida* under severe stress (3.66±0.61 MPa). This result is contrary to expectations because the thicker leaves of *G. lucida* suggest greater water storage than *G. littoralis.*

In consideration of the epiphytic lifestyle of *G. lucida*, it is appropriate to interpret the ε of the severely stressed group as most relevant to plants in a natural canopy environment. Many authors have noted that water stress is the most limiting factor in canopy habitats (e.g. Zotz & Tyree 1996; Martin 2004; Benzing 1990) and thus, it can be assumed that epiphytic *G. lucida* plants have had some exposure to drought and therefore have adjusted leaf elasticity.

The ε of both *Griselinia* species are comparable to the values reported for relatively elastic species such as the tropical atmospheric epiphyte *Tillandsia utriculata* (3.3±0.4) (Stiles & Martin 1996) and the tropical hemiepiphyte *Clusia minor* (Holbrook & Putz 1996a); while they are much lower than the ε of three tropical epiphytic orchids (8.7-33 MPa) and nine tropical epiphytic ferns (25-60 MPa) (Sinclair 1983; Hietz & Briones 1998). The relatively high cell elasticity of native *Griselinia* species is likely to benefit cell turgor through the preferential loss of water from nonessential cells (Nowak & Martin 1997; Martin 2004) such as the hypodermis which has been described as “water tissue” by Oliver (1930) and as “dedicated water storage” by Hietz & Briones (1998).

Although the severely stressed *G. lucida* plants reached lower water potentials and rates of stomatal conductance and photosynthesis than *G. littoralis*, they recovered faster from severe stress when the water supply was replenished. A similar result was reported by Zhang et al. (2009) in epiphytic ferns that exhibited desiccation postponement characteristics followed by rapid photosynthetic recovery after rewatering and reflects an important strategy for these species to survive the regular drought of epiphytic habitats.

The insignificant differences in osmotic potential between stress treatments indicate that neither *Griselinia* species adjusts leaf solutes to maintain turgor under drought conditions; this is consistent with Lambers et al. (2008) who explain that individual plants are unlikely to exhibit both osmotic and elastic adjustment.

The relatively high (not very negative) osmotic potentials at full turgor for both *Griselinia* species (-1.17 to -0.79) are characteristic of values for epiphytic species (Martin et al. 2004). The significantly lower osmotic potential of *G. lucida* estimated from pressure volume analysis, when compared to *G. littoralis*, is a similar finding to that of Holbrook & Putz, (1996a) who reported that *Clusia minor* had higher osmotic potentials in trees than epiphytes of the same hemiepiphytic species. However, with regards to the current research, this result was not confirmed by the direct measurements of leaf symplasmic osmotic potentials and may be affected by the longer growth period and larger size of *G. lucida* at the time of measurement.

The root dieback exhibited by *G. lucida* may be a pruning response to water stress and is supported by field observations of *G. lucida* shedding leaves during drought (B.D. Clarkson, University of Waikato, pers. comm. 2011). This suggests that *G. lucida* has more severe mechanisms to postpone desiccation than *G. littoralis* due to the demanding microclimate of epiphytic habitats; however, further research is required to test this hypothesis.

Similar relationships between assimilation and stomatal conductance, and analysis of ^{13}C showed that *G. lucida* and *G. littoralis* had comparable water use efficiency which did not change with increased stress for either species. However, because photosynthesis and growth was reduced under stress, the carbon in measured leaves is likely to have been fixed prior to severe stress and any increase in water use efficiency may have been undetected.

The water use efficiency of *G. lucida* with different stages of roots was not significantly different. This result suggests that plants without terrestrial roots have access to sufficient sources of water and thus, similar water use efficiencies. This also aligns with the results of Holbrook & Putz (1996b) who measured comparable water use efficiency in different life forms of strangler hemiepiphytes in Venezuela.

In comparison to epiphyte species across the world, *G. lucida* is relatively sensitive to dehydration with evident prioritisation of desiccation postponement through reduced photosynthetic function. This is particularly apparent when comparing *G. lucida* to the desiccation tolerant epiphytic members of the Bromeliaceae family which can germinate, survive and reproduce in habitats as arid as electricity wires (Stiles & Martin 1996; Bader et al. 2009). This finding supports the observed distribution of *G. lucida* (chapter four) in wet temperate lowland forests and also its absence in small forest fragments that have relatively warm and dry microclimates (chapter two). This is also relevant for the inclusion of this species in restoration ecology as it supports the recommendation that future reintroductions should be focussed in suitably humid habitats (chapter five).

In summary, the highly elastic cell walls and reductions in photosynthetic function indicate that both *Griselinia* species exhibit features of desiccation tolerance in the early stages of drought but primarily rely on desiccation postponement to survive low water supply. Greater stomatal closure, root pruning, thicker leaves, and faster recovery from stress indicate that *G. lucida* has more acute postponement features than *G. littoralis* which is in accordance with the fluctuating water supply of its forest canopy habitat.

Chapter Four: Biological Flora of New Zealand. *Griselinia lucida*, puka, akapuka, akakōpuka, shining broadleaf

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Abstract

Information relevant to the biology and ecology of *Griselinia lucida* (Forst. f.) (Griseliniaceae) available through published and unpublished sources is assembled and reviewed. *Griselinia lucida* is a large shrub hemiepiphyte that grows primarily in trees of wet, lowland forests. It also occurs in open coastal and rocky outcrop habitats. Large, bright green, glossy leaves and grooved terrestrial roots make this species a very conspicuous member of New Zealand's endemic flora. *Griselinia lucida* has a wide geographic range, extending throughout the North Island and much of the South Island. Its distribution is restricted by temperature, rainfall, and humidity as it requires high moisture and warm climates to establish and thrive. *Griselinia lucida* is one of two native members of the *Griselinia* genus which has links to five South American species. *Griselinia lucida* is frequently associated with diverse and abundant epiphyte communities. The conservation and restoration of both epiphytic and terrestrial populations is important to ensure functionally diverse ecosystems and accordingly, it is recommended that this species is included in future forest ecological restoration.

Keywords: *Griselinia*; epiphyte; morphology; taxonomy; distribution; associations; conservation; restoration; nomenclature; microclimate

4.1 Morphological description

Griselinia lucida is a dicotyledonous shrub or small tree, up to eight metres tall that usually occurs as an epiphyte (Alan 1961; Burrows 1999). It is an evergreen perennial with bright green glossy leaves (Figure 4.1B), that can reach spans of eight metres or more in the canopy of a host tree (Cockayne 1910; 1958; Dawson 1986; Burrows 1999). It is classified as a hemiepiphyte because of its large light-brown to grey grooved roots that often descend to the forest floor (Dawson 1966; Burns & Dawson 2005) (Figure 4.3 & Figure 4.4). These unique vegetative features led Dawson (1966) to describe it as “the most conspicuous shrub epiphyte in the New Zealand rain forest”.

Key morphological features are shown in Figures 4.1 - 4.4. Mature leaves are thick (Wylie 1954) obliquely-broadly ovate to oblong and rounded at the apex (Alan 1961). They are usually asymmetrical about the midrib with the proximal portion of each leaf, relative to the branch bearing it, being both shorter and thinner than the distal portion (Dawson 1966) (Figure 4.2). Very young leaves are not asymmetrical (Dawson 1966) and often have a reddish-purple margin (Figure 4.1A).

Leaves are 7-18 cm long, 5-9 cm wide (Dillon & Muñoz-Schick 1993), 0.3-0.7, mm thick, and 240-990 cm^2 in area. They are coriaceous (Cockayne 1958), with uniformly dense stomata extending over the glabrous under-surface; resulting in a whitish opaque appearance (Dawson 1966). Leaf veins are clearly visible on both upper and lower sides, and are slightly raised underneath. The midrib is raised on both sides, especially towards the leaf base. Petioles are 2.5-5 cm long (Dillon & Muñoz-Schick 1993), with varying degrees of reddish-purple colouring and a sheath-like base pressed closely to the stem (Philipson 1967) (Figure 4.1A & Figure 4.2). In mature shoots, the axillary buds are frequently separated from the petiole because of displacement during growth (Philipson 1967; Bell 2008).

Griselinia lucida is dioecious and thus has either male (staminate) or female (pistillate) flowers, in branched inflorescences from October to December. Inflorescences are on the end of branchlets with stems (pendUncles) 10-15 cm long that are covered by apically rounded trichomes. Each small flower in the inflorescence has a stem (pedicel) 1-3 mm long (Dillon & Muñoz-Schick 1993) (Figure 4.1D).

Fruiting occurs in infructescences with berry-like (Oliver 1930), oval fruit that are 4-10 mm long, ca. 5 mm in diameter and ripen a few at a time during winter (June-August) (Dillon & Muñoz-Schick 1993; Sullivan et al. 1995; Burrows 1999) (Figure 4.1C). The thin, oily, tawny to blackish casing contains a single seed ca. 4 mm long and ca. 3 mm wide.

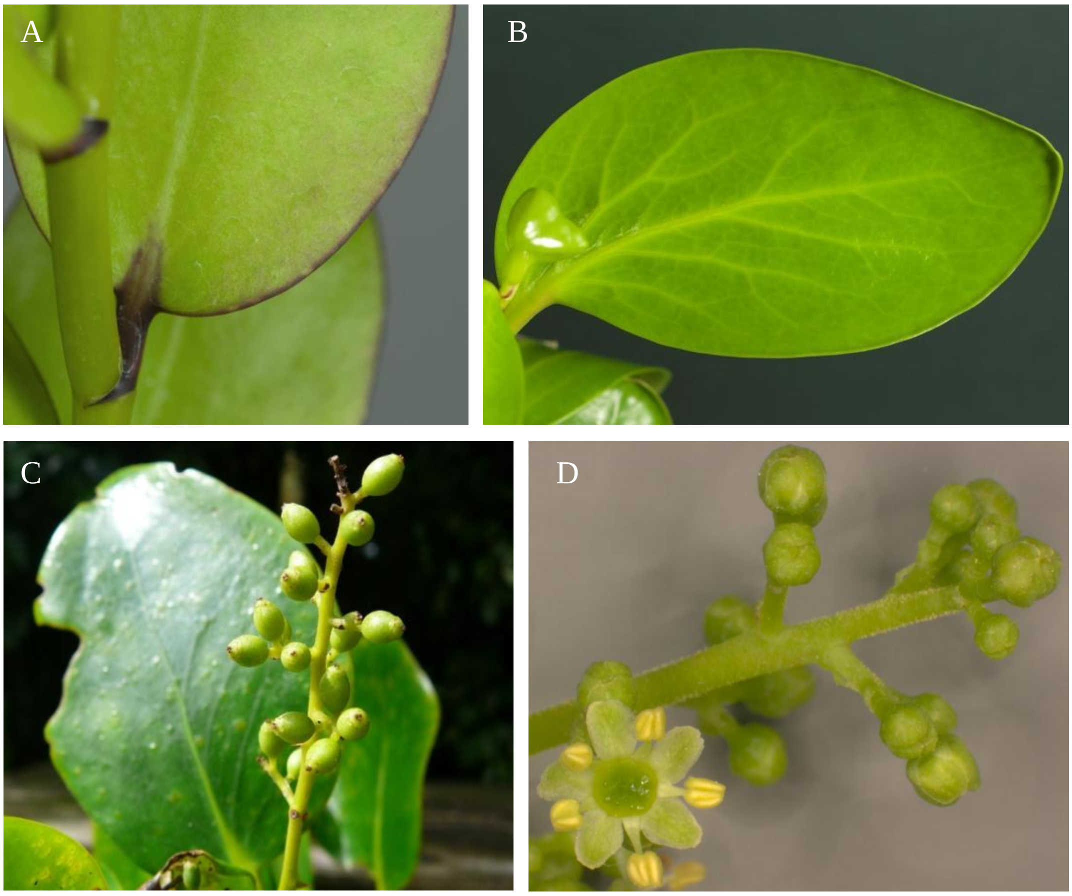

Figure 4.1: Selected key features of *Griselinia lucida*. A: Young leaves showing reddish-purple petiole and leaf margin and sheath-like petiole base (photo courtesy of Barry O'Brien), B: Glossy leaf with asymmetrical base, C: Unripe fruit on infructescence, D: staminate inflorescence showing trichomes, penduncles and pedicels.

Griselinia lucida often establishes terrestrial roots from the canopy to the forest floor when it is growing directly on host bark or in association with a small number of other epiphytic species (Figure 4.3 & Figure 4.4). However, plants that establish within large, diverse epiphyte communities may source resources from canopy detritus with no need for terrestrial connections. When growing on a tree fern, *G. lucida* roots become intimately incorporated into the fibrous trunk of its host.

Rooted plants connect to terrestrial soil during with multiple roots of around three millimetres in diameter that descend the host trunk at a rate of approximately 1.2 m per year (Dawson 1966; Dawson 1986). Young roots have smooth, white tips that anchor into crevices and under bark flakes by means of dense short hairs that start behind the tip (Figure 4.3A). These hairs persist until cork formation begins, at which time the root becomes free hanging (Dawson 1966). Once the root reaches the ground it enlarges evenly and develops longitudinally grooved bark (Oliver 1930; Dawson 1966) (Figure 4.4). Mature roots can become trunk-like with diameters up to 110 cm that often girdle the host using multiple lateral roots (Dawson 1966; Duguid 1990) (Figure 4.3B).

Figure 4.2: Morphological features of *Griselinia lucida.* Illustration adapted from Cheeseman (1914), 1: asymmetrical lamina and sheath-like petiole base, 2: pistillate flower, 3: pistillate inflorescence, 4: staminate flower, 5: staminate inflorescence, 6: seed, 7: infructescence.

4.2 Anatomy

Leaf cross sections show that the tissue of *G. lucida* is markedly differentiated (Figure 4.5). Water retention appears to be an important function with a thick cuticle covering the small, rhomboidal, upper epidermal cells and an adjacent thick layer of hypodermis, or water cells (Oliver 1930; Dawson 1966; Philipson 1967). Beneath the hypodermis is a layer of oblong palisade cells perpendicular to the cuticle. The lower third of the lamina is composed of spongy mesophyll with sclerencymatous idioblasts and many air spaces sitting parallel to the surface (Oliver 1930). The lower epidermis has a thick cuticle that arches over stomata to form stomatal chambers (Oliver 1930; Dawson 1966). In a comparison with its terrestrial congener; *G. littoralis*, *G. lucida* has thicker layers of cuticle, epidermis and hypodermis cells and a thinner layer of palisade (Bryan 2011: chapter three).

Philipson (1967) summarised a range of anatomical features of *G. lucida* including its five-lacunar nodes, and research on wood anatomy by Adams (1949) and Li & Chao (1954), reporting the following features: solitary vessels or vessel groups of two to four running parallel and adjacent to one another with oblique scalariform perforations and an average of 28 bars per perforation plate; rounded, oval or spindle-shaped inter-vascular pits; diffuse parenchyma adjacent to vessels; bordered fibre pits; and thick fibre walls.

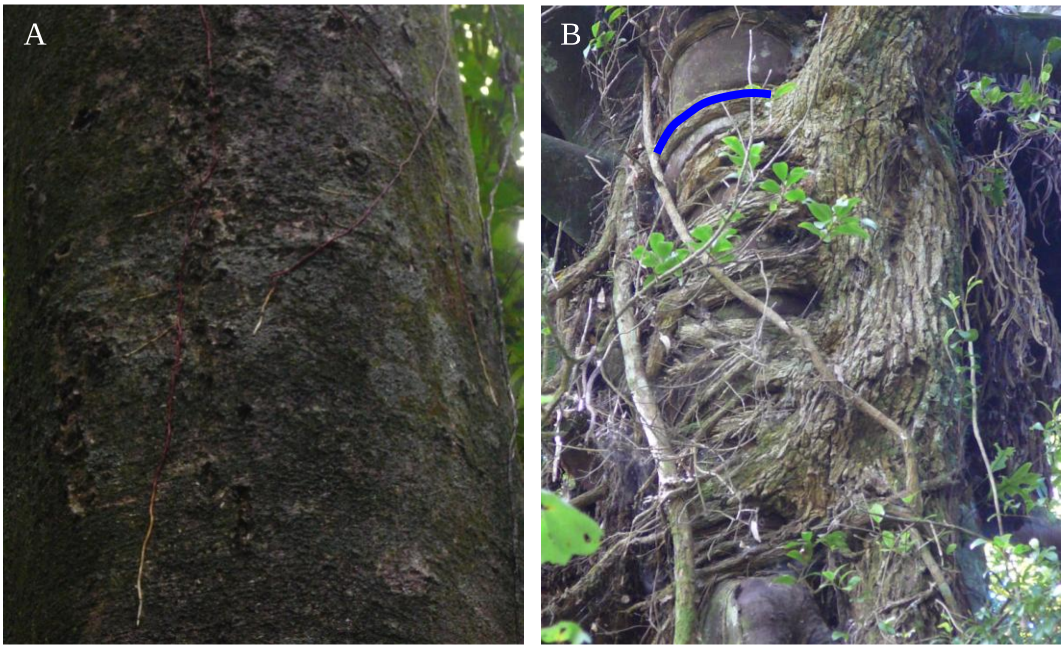

Figure 4.3: A: Young *Griselinia lucida* roots with white tips descending a host tree, B: Lateral roots girdling a host tree (example shown in blue).

Figure 4.4: Mature *Griselinia lucida* roots with longitudinally grooved bark.

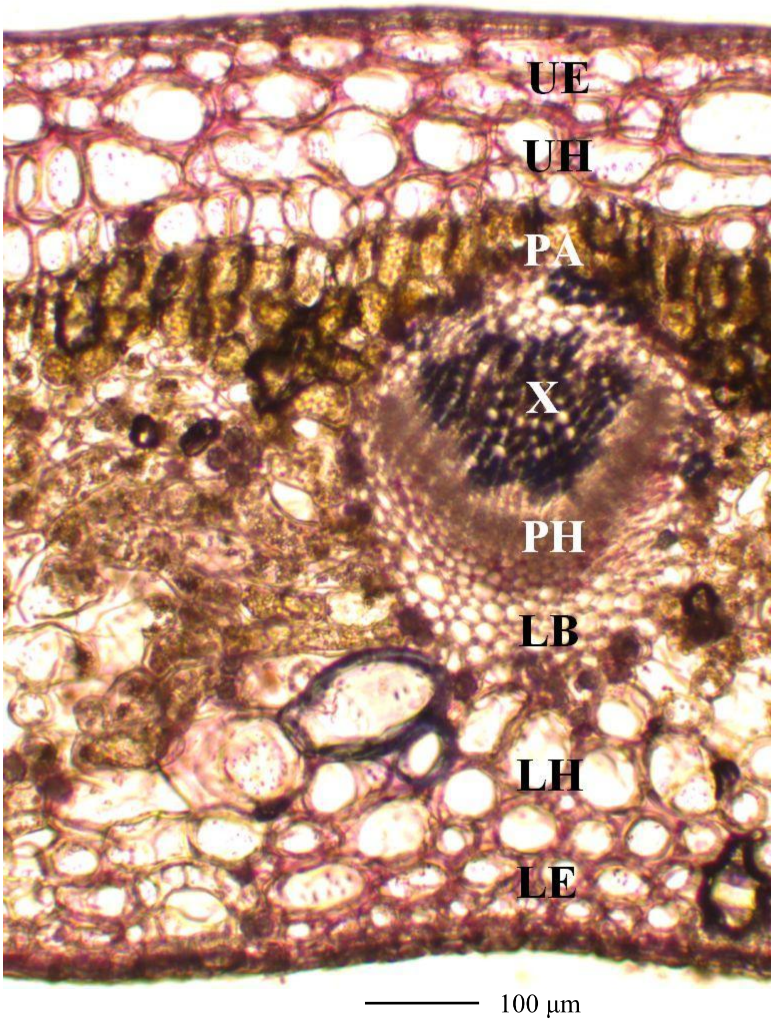

Figure 4.5: Hand section of *Griselinia lucida* leaf at midrib. Letters refer to measurements of cell types in Table 4.1.

Table 4.1: Approximate thicknesses of different *Griselinia lucida* cell types. Letters refer to Figure 4.5.

Cell type	µm
Upper cuticle	12.5
Upper epidermis (UE)	18.75
Upper hypodermis (UH)	162.5
Palisade cells (PA)	37.5
Upper bundle sheath cells	50
Xylem (X)	137.5
Phloem (PH)	50
Lower bundle sheath cells (LB)	87.5
Lower hypodermis (LH)	200
Lower epidermis (LE)	18.75
Lower cuticle	12.5
Overall thickness at midrib	787.5

Dawson (1966) explains the anatomy of *G. lucida* roots to account for the grooved pattern in the root bark. Young roots have 8-14 primary xylem around a wide pith. Mature roots have lignified pith, primary rays leading out from the xylem and secondary xylem with scattered vessels. Secondary phloem layers develop with thin walled tissues, persistent fibres, and eventually cork cambia in each parenchymatous layer that has ceased to function. The bark grooves are formed in mature roots when growing vascular tissues split the bark along the primary rays. There is low cambial activity while the root is growing towards the ground (Dawson 1966).

4.3 Taxonomy and relationships

Griselinia lucida is one of only two New Zealand members of Griseliniaceae, which has family links in South America (Dillon & Muñoz-Schick 1993). The genus name *Griselinia* was first published in 1775 by J.R. Forster and J.G.A. Forster after their first choice of *Scopolia* was unavailable (Dillon & Muñoz-Schick 1993).

Familial placement of *Griselinia* was debated for over two hundred years; the following summarises the history of this genus, as presented by Dillon & Muñoz-Schick, (1993). *Griselinia* has been placed in *Polygamia-Dioecia* (Forster & Forster 1775), *Pentandria trigynia* (Gmelin 1791; Schultes 1820; Sprengel 1825; Dietrich 1839), Euphorbiaceae (Sprengel 1817; Agardh 1823), Juglandaceae

(Kunth 1892), Euphorbiaceae (Reichenbach 1837), Araliaceae (Endlicher 1850), Cornaceae-Aucubeae (Hooker 1852), and Cornaceae (Cronquist, 1981; Thorne, 1968). Philipson (1967) questioned the placement in Cornaceae and suggested in 1977 that it be part of the group Unitegminae. Takhtajan (1980) placed *Griselinia* in the monotypic family Griseliniaceae which was later supported by Thorne (1992), Dillon & Muńoz-Schick (1993), and Chandler & Plunkett (2004).

Ordinal placement has also been complicated with classifications allying *Griselinia* with either Cornales or Apiales because physiological and biochemical features are similar to those in Cornales but floral vasculature and wood anatomy is similar to the Apiales (Chandler & Plunkett 2004). Studies by Plunkett et al. (1996; 1997) and Plunkett & Lowry (2001) strengthened the argument for affinities with Apiales but as part of an out-group or “Apialean alliance” with *Aralidium, Melanophylla, Pennantia* and *Torricellia.*

Therefore, the current taxonomy of the species *Griselinia lucida* is in the small monotypic family Griseliniaceae in the order Apiales, as published by Chandler & Plunkett (2004) and Plunkett et al. (2004). *Griselinia* is suggested to have Paleotropical origins (Dillon & Muńoz-Schick 1993) and the first appearance of both pollen and leaf fossils for this genus are in the Miocene (Mildenhall 1980; Pole 2008).

In New Zealand, the genus *Griselinia* contains *G. lucida* and *G. littoralis*; in Chile there is *G. jodinifolia*, *G. carlomunozii*; while *G. scandens*, *G. racemosa* and *G. ruscifolia* grow in both Chile and Argentina, and *G. ruscifolia* also occurs in south-eastern Brazil. The New Zealand species grow up to 15 metres tall while the South-American species seldom exceed two metres in height (Dillon & Muñoz-Schick 1993). *G. jodinifolia* is cultivated by some nurseries in New Zealand. *G. littoralis* primarily differs from *G. lucida* by its longer petioles and predominantly terrestrial habitat but it also grows epiphytically (Cockayne 1910) in high altitude, wet forests such as the cloud forests of Mount Taranaki (Clarkson 1986).

4.4 Nomenclature

Griselinia lucida was first described in 1786 by J.G.A. Forster in *Florulæ Insularum Australium Prodromus* (75) from a type specimen in Queen Charlotte

Sound, that is stored in the herbarium of the Royal Botanic Gardens, Kew, U.K. (Allan 1961).

The name *Griselinia* was chosen for this genus in honour of Francesco Griselini (1717 - 1783), a naturalist of Venice (Dillon & Muñoz-Schick 1993) and was first proposed by J. R. Forster and J. G. A. Forster in *Characteres Generum Plantarum* in 1775 (Dillon & Muñoz-Schick 1993). The specific epithet *lucida* stems from the word lucidus, meaning shining (Eagle 2006); in reference to its glossy leaves.

The Māori names for this plant are puka, akapuka, akakōpuka, and pukatea (Landcare Research 2011c). The use of "puka" refers to broad leaves (Laing & Blackwell 1907) and "aka" refers to the vine of any climbing plant (Williams 1971); in combination, these words describe a vine with broad leaves. The common English name for *G. lucida* is shining broadleaf (e.g. Matthews 1979).

A variety of *Griselinia lucida*; *Griselinia lucida* var. *marcophylla* was described by Hooker in his *Handbook of New Zealand Flora* (1864, p105) from specimens collected by A. Cunningham in the Bay of Islands and Sinclair in Auckland: "very robust. Leaves almost orbicular, almost cordate at the base (perhaps only young shoots of *G. lucida*)" (Allan 1961). This variety is also noted by Kirk (1869) as "merely a state of the species to which it is referred" that is "usually found growing on pohutukawa and other littoral trees".

4.5 Reproductive Biology

As noted in Morphology, *G. lucida* is dioecious. The small flowers of pistillate inflorescences lack petals (Dillon & Muñoz-Schick 1993) (Figure 4.2) and have unilocular ovaries, three short styles, sepals ca. 2 mm long and 0.2 mm wide, dorsal traces, and ventrals that run up the ovary wall to supply the styles (Philipson 1967). Staminate flowers are reflexed at antheis, have a campanulate hypanthum, and are quick to fall off. They have five yellow to greenish petals 1.2-1.5 mm long, five sepals ca. 0.4 mm long that are opposite the five stamens of 0.5-0.6 mm in length (Dillon & Muñoz-Schick 1993).

There are no documented observations of pollen dispersal mechnisms but given the size of the flowers, wind or insect pollination is most likely. Pollen grains are ellipsoidal, aperturate and striated with a complete tectum. They are flattened at the poles and have a very indistinct pore (Dillon & Muñoz-Schick 1993).

After fertilisation the flower ovules develop into berry-like fruit with one seed per fruit. Seeds are 3.85±0.2 mm long, 2.9±0.2 mm wide and weigh ca. 0.0085 g (Burrows 1999). The seed is adapted to dispersal by birds such as kereru (*Hemiphaga novaeseelandiae*), bellbirds (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*), whiteheads (*Mohoua albicilla*), pied tits (*Petroica macrocephala*), and silvereyes (*Zosterops lateralis*), as it will not germinate until the flesh is removed (McEwen 1978; Moeed & Fitzgerald 1982; Fitzgerald & Fitzgerald 1983; Burrows 1999). Burrows (1999) found that optimal germination is achieved under maximum daylight and moist conditions because the seeds are very sensitive to drying out.

4.6 Geographic distribution

Griselinia lucida is endemic to New Zealand, most commonly occurring as an epiphyte in North Island forests and as both an epiphyte and rupestral in a limited area of the South Island (Cockayne, 1906; Wardle, 1964; Dawson, 1966; 1986; Burrows, 1999). It is also common as a terrestrial shrub on volcanic offshore rocky islands such as Rangitoto, Hen, and Little Barrier (Dawson 1966; Wright 1978; Julian 1992) (Figure 4.6 & Figure 4.7).

The geographic distribution in Figure 4.6 is based on an extensive collation of *G. lucida* records and shows that this species is concentrated on the west coast of New Zealand with relatively low abundances on the east coast of both islands. It penetrates further inland in the North Island because of the less mountainous terrain and warmer temperatures. Figure 4.7 shows the observed and predicted distribution based on presence and absence data from the New Zealand Forest Service Ecosurvey plots in the National Vegetation Survey Database (Landcare Research 2011a). The associated Derived Biodiversity Information database (Landcare Research 2011a) indicates that the probability of *G. lucida* naturally occurring is highest with a mean annual temperature of 14-16 °C, vapour pressure deficits of less than 0.5 kPa, mean solar radiation of around 13 MJ/day/m^2 and a ratio of mean annual rainfall to potential evapotranspiration of 3.9-4.5. The most significant correlate for explaining variation in *G. lucida* distribution is mean annual temperature (Landcare Research 2011a). This observed and predicted distribution (Figure 4.7) is consistent with the collated distribution of *G. lucida* (Figure 4.6) which shows that highest abundances in the warmer areas of New Zealand that have moderate solar radiation and moderate-high rainfall and humidity (low vapour pressure deficit).

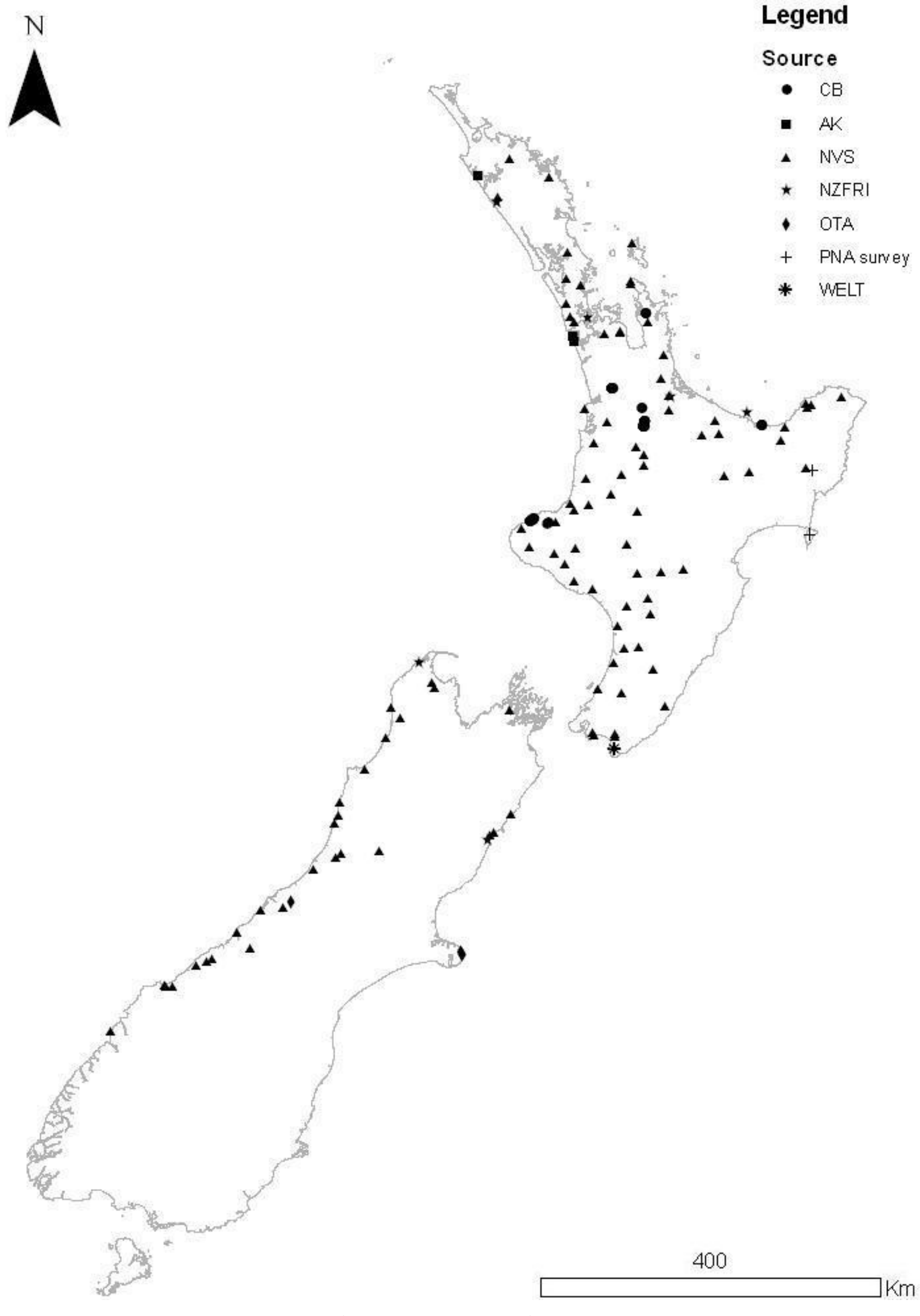

Figure 4.6: Geographic distribution of *Griselinia lucida* from Bryan (2011) (CB), Auckland Museum herbarium (AK), University of Otago herbarium (OTA), Museum of New Zealand - Te Papa Tongarewa herbarium (WELT), National Forestry herbarium (NZFRI), New Zealand Vegetation Survey Databank (NVS), Clarkson & Clarkson (1991) and Whaley et al. (2001) (PNA survey).

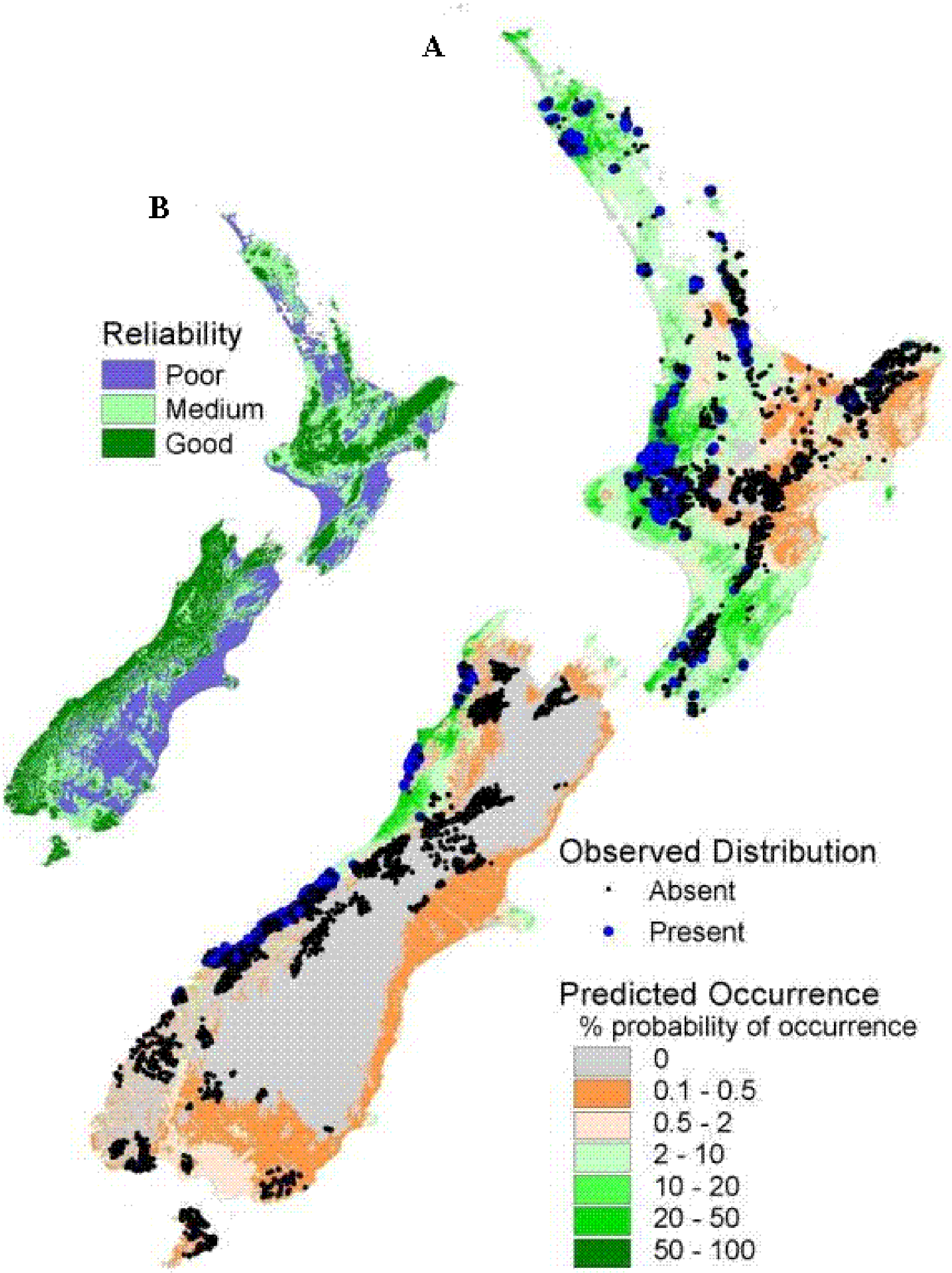

Figure 4.7: Observed and predicted geographic distribution of *Griselinia lucida*. A: Observed distribution of *G. lucida* with predicted natural occurrence based on presence and absence. B: Reliability of predictions in *A*; low reliability is related to a lack of survey data and a lack of forest cover. Figures courtesy of Landcare Research Derived Biodiversity Information (2011a) database.

4.7 Environmental requirements and limitations

Griselinia lucida, like many hemiepiphyte species, has variable establishment modes (Knightbridge & Ogden 1998). It primarily grows epiphytically in the canopy of old growth lowland forests with high rainfall (Oliver 1930; Burrows 1999) but also in coastal cliff and rock habitats (Figure 4.8) (Oliver 1930;

Cockayne 1958; Wardle 1991; Burrows 1999). Epiphytic habitats are often described as severe because of high insolation, vapour pressure deficits, and wind speeds; as well as fluctuating water and nutrient supplies, and poor physical stability (Matelson et al. 1993; Holbrook & Putz 1996a; Benzing 1990). These rigorous conditions are also present in the terrestrial and rupestral habitats of *G. lucida*. This species is uncommon in small forest patches that have been affected by fragmentation and anthropogenic disturbance (Bryan 2011: chapter two). This absence is suggested to be due to the warmer and drier canopy microclimates in these small patches; especially if they are in a matrix of urban landuse. In support of this hypothesis, the results of a nine month monitoring period showed that temperatures in urban forests were in the upper range of those recorded in nonurban and coastal habitats while vapour pressure deficits (VPD) were highest in urban forests (Bryan 2011: chapter two; Clarkson 2011) (Table 4.2).

Table 4.2: Range of mean temperatures and VPD in coastal, urban and nonurban epiphyte habitats.

Habitat type	Mean temperature (°C)	Mean VPD (kPa)
Coastal (n=1)	12.5	0.13
Small urban forest (n=3)	11.8-12.3	0.19-0.23
Large nonurban forest (n=2)	10.5-11.4	0.11-0.12

Corresponding to its open habitats, *G. lucida* has a requirement for high levels of insolation and rarely survives forest floor conditions if it is dislodged from the canopy. Plants growing in coastal habitats, including *G. lucida*, are generally tolerant of wind and salt spray (Cockayne 1958), but can be damaged by “salt scorching” in very strong coastal winds (Gillham 1960). *G. lucida* is sensitive to frost and cold temperatures with a leaf freezing resistance of $^{-}7$°C (Wardle 1991; Burrows 1999). In the Waikato region, it commonly grows in trees on upper hillslopes and ridge tops but is not present in basins where temperature inversions prevail. *G. lucida* is widely considered to be able to withstand drought (e.g. Ogden 1976) and a desiccation tolerance experiment on young *G. lucida* plants (Bryan 2011: chapter three) showed that this species endures water stress through reduced stomatal and photosynthetic activity and increased cell wall elasticity. This desiccation postponement facilitates fast recovering when its water supply is restored. However, in contrast to expectations, *G. lucida* does not exhibit a significantly greater ability to endure water stress than its terrestrial congener *G. littoralis*.

It is speculated that *G. lucida* only extends large roots to terrestrial soil if the resources of its habitat become inadequate for further growth. This hypothesis is supported by water-use efficiency measurements that were not significantly different between plants with and without terrestrial roots; as determined by a ^{13}C discrimination of *in situ G. lucida* (Bryan 2011: chapter three). Terrestrial roots can often be seen when *G. lucida* occurs in small canopy communities or, as shown in Figure 4.8, when it is on rock outcrops adjacent to the mainland. If the terrestrial connection does not form, *G. lucida* relies on regular rainfall, mist, and fog for moisture (Oliver 1930; Burrows 1999).

Figure 4.8: Large *Griselinia lucida* individual shown from above and beneath growing on a limestone outcrop in Raglan harbour, Waikato. White arrows show a large root that extends under the rock stack to the soil of the mainland.

4.8 Plant communities and associations

As mentioned above, *Griselinia lucida* occurs primarily in epiphytic habitats; 96 % of 54 plants recorded in Waikato and Taranaki regions (C.L. Bryan, unpublished data); but it also grows terrestrially along coastlines and on islands (Oliver 1930; Cockayne 1958; Wardle 1991; Burrows 1999). The following provides information about the associated plant communities in each of these habitats.

In an epiphytic habitat, *G. lucida* generally requires a source of "canopy soil" for successful germination and to support its early growth (Oliver 1930). Accordingly, it is commonly found growing amongst other epiphyte species; especially the nest species *Collospermum hastatum* and *Astelia solandri* which have long linear leaves that efficiently trap detritus and water (Burns & Dawson, 2005). These communities frequently occur on large, well-established host trees in relatively undisturbed forests. Large hosts are correlated to diverse and abundant epiphyte communities primarily because they provide a large surface area for epiphytes to perch on, good access to light and moisture, and a long time for species to accumulate (Knightbridge & Ogden 1998; Hofstede et al. 2001; Benzing 2004; Cummings et al. 2006; Flores-Palacios & Garcia-Franco 2006; Laube & Zotz 2006). Comparison of host tree size (diameter) with *G. lucida* abundance shows that large host trees are important for the population abundance of this species (Figure 4.9).

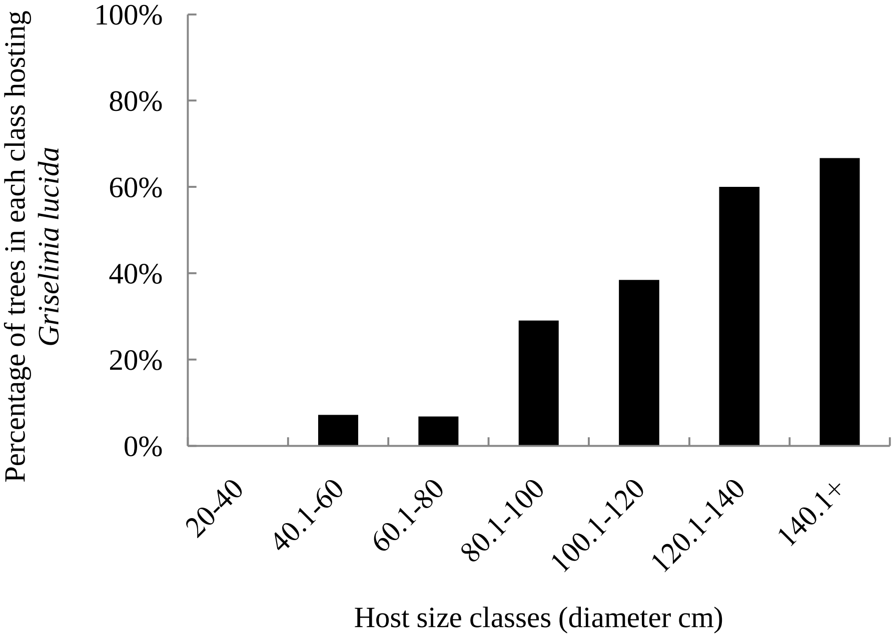

Figure 4.9: Percentage of trees in seven size classes hosting *Griselinia lucida* (n=399).

Epiphytic *G. lucida* was found to be most frequently associated with nest epiphytes (*C. hastatum* and *A. solandri*), and the ferns *Microsorum pustulatum* and *Pyrrosia eleagnifolia* (C.L. Bryan, unpublished data) (Table 4.3). *G. lucida* was found with conspecific individuals on less than six percent of occasions (C.L. Bryan, unpublished data). This may reflect the specialised and scarce nature of the niche that this species occupies and the associated intraspecific competition for habitat and resources that limits the number of plants occurring on each host tree.

Table 4.3: The epiphyte and vine species associated with (occurring on the same host tree) *Griselinia lucida* and the frequency of occurrence (n=54). Species that occurred in less than two percent of records were primarily accidental epiphytes and were excluded from this table.

Associated species	Occurrence with *G. lucida* (%)
Collospermum hastatum	80
Microsorum pustulatum	56
Astelia solandri	43
Pyrrosia eleagnifolia	43
Metrosideros fulgens	39
Asplenium flaccidum	39
Asplenium polyodon	39
Earina mucronata	39
Ripogonum scandens	35
Blechnum filiforme	33
Microsorum scandens	20
Metrosideros diffusa	19
Freycinetia banksii	17
Earina autumnalis	15
Tmesipteris elongata	15
Metrosideros perforata	13
Pittosporum cornifolium	9
Winika cunninghamii	7
Asplenium oblongifolium	7
Hymenophyllum sanguinolentum	7
Huperzia varia	7
Brachyglottis kirkii	6
Griselinia lucida	6
Lygodium articulatum	6

Epiphytic *G. lucida* grows on a range of native and non-native tree species with an evident preference for large branches and wide-branch angles. In the Waikato and Taranaki regions of the North Island, the most frequent host trees for *G. lucida* are pukatea (*Laurelia novae-zelandiae*) and tawa (*Beilschmiedia tawa*) (C.L. Bryan, unpublished data; n=54) (Table 4.4). These host species often support diverse and abundant epiphytic assemblages but on the occasions where *G. lucida* does not grow in such communities it is often directly rooted in the thick stringy bark of trees like totara (*Podocarpus totara*) or the fibrous root mass of tree ferns. *G. lucida* has also been recorded growing on exotic trees such as *Pinus radiata* and *Abies* sp. (Burrows 1994; 1996).

Table 4.4: Frequency of tree species hosting *Griselinia lucida* (n=54).

Host species	%
Laurelia novae-zelandiae	25
Beilschmiedia tawa	22
Knightia excelsa	10
Litsea calicaris	8
Dysoxylum spectabile	6
Alectryon excelsus	4
Dacrydium cupressinum	4
Melicytus ramiflorus	4
Podocarpus totara	4
Tree fern spp.	4
Nestegis spp.	2
Phyllocladus trichomanoides	2
Prumnopitys ferruginea	2
Sequoia sp.	2
Vitex lucens	2

Griselinia lucida is not a parasite or a strangler (see Todzia 1986) but it does affect the long term health and survivability of its host tree. A large epiphytic *G. lucida* can grow to significant weight and cause limb damage or even death to its host if it outgrows the host's capacity for support. This epiphyte also intercepts sunlight, atmospheric nutrients and moisture that would have otherwise benefited the host. However, host trees may also benefit from the presence of *G. lucida* and its associated epiphyte communities, as international research has found host species in both tropical and temperate forests that can access the resources of an epiphyte community through adventitious roots from the branches (Nadkarni 1981). This phenomenom creates an important link between hosts and epiphytes but has not yet been investigated in New Zealand forests.

The rupestral substrates that *G. lucida* inhabits include volcanic basalt on offshore islands such as Rangitoto. A survey of vegetation communities on Rangitoto Island (B.D. Clarkson, University of Waikato, unpublished data) showed that patches dominated by both *G. lucida* and pohutukawa (*Metrosideros excelsa*) frequently supported species that are commonly found as epiphytes in forest ecosystems elsewhere such as *Hymenophyllum* spp., *Microsorum pustulatum, Pyrrosia eleagnifolia,* and *Asplenium oblongifolium* (Table 4.5).

Table 4.5: Species associated with *Griselinia lucida* in vegetation communities dominated by either *Metrosideros excelsa* (M) or *G. lucida* (G) and the frequency (%) of their occurrence in measured plots on Rangitoto Island (n=10). Data from B.D. Clarkson, UoW, unpublished data.

Associated species	M %	G %
Metrosideros excelsa	100	-
Astelia banksii	80	60
Myrsine australis	80	60
Coprosma robusta	60	60
Hymenophyllum spp.	60	60
Leucopogon fasciculatus	60	60
Microsorum pustulatum	60	60
Pyrrosia eleagnifolia	60	60
Asplenium oblongifolium	60	40
Cyathodes juniperina	60	40
Brachyglottis kirkii	60	20
Trichomanes reniforme	40	20
Asplenium flabellifolium	40	-
Ctenopteris heterophylla	40	-
Huperzia varia	40	-
Asplenium flaccidum	40	-
Coprosma lucida	20	-
Earina mucronata	20	-
Geniostoma rupestre	20	-
Olearia furfuracea	20	-

As no systematic survey of plant communities containing *G. lucida* has been undertaken in New Zealand, further examples from published and unpublished sources are provided in the following section. They are presented from north to south in two degree latitudinal divisions to illustrate the country-wide pattern of plant communities and associations.

34-36° S

In forests of the North Cape, *G. lucida* grows epiphytically along with *Asplenium flaccidum*, *A. oblongifolium*, *A. polyodon*, *Hymenophyllum demissum*, *H. dilatatum*, *H. flabellatum*, *H. flexuosum*, *H. rarum*, *H. revolutum*, *H. sanguinolentum*, *Phymatodes diversifolium*, *P. scandens*, *Rumohra adiantiformis*, *Tmesipteris elongata*, *T. reniforme*, *T. venosum*, *Calystegia marginata*, *C. tuguriorum*, *Cassytha paniculata*, *Clematis paniculata*, *Freycinetia banksii*, *Muehlenbeckia australis*, *M. complexa*, *Parsonisa capsularis*, *P. heterophylla*, *Passiflora tetrandra*, *Ripogonum scandens*, *Rubus australis*, *R. cissoides*, *Ichthyostomum pygmaeum*, *Drymoanthus adversus*, *Earina mucronata*, *Earina autumnalis*, *Winika cunninghamii*, *Astelia solandri*, *Collospermum hastatum*, *Pittosporum cornifolium,* and *Pyrrosia eleagnifolia* (Gardner & Bartlett 1980).

36-38° S

In scoria fields of the Auckland volcanoes, *G. lucida* grows abundantly in association with *Litsea calicaris*, *Brachyglottis repanda*, *Alectryon excelsus*, *Pseudopanax lessonii*, *Collospermum hastatum*, *Peperomia urvilleana*, *Astelia banksii*, *Cheilanthes humilis*, *C. distans*, *Pellaea falcata*, *P. rotundifolia*, *Asplenium flabellifolium*, *Anarthropteris lanceolata*, *Hymenophyllum flexuosum* and *Trichomanes endlicherianum* (Esler 1991). On limestone rock outcrops in Raglan harbour, *G. lucida* grows alongside *Pittosporum cornifolium*, *Astelia banksii*, and *Collospermum hastatum* (F.M. Clarkson, University of Waikato, unpublished data).

38-40° S

Griselinia lucida is found epiphytically in forest on the summit of Mount Ngongotaha and adjacent hills, in association with *Pittosporum cornifolium*, and *Astelia solandri*. Prior to the Tarawera eruption (1886), these three species also grew on pohutukawa trees on the shores of Lake Tarawera (Kirk 1872). In semi-coastal forest of Mahia, *G. lucida* is a prominent epiphyte that grows alongside *Freycinetia banksii*, *Metrosideros colensoi*, *M. diffusa* and *Ripogonum scandens* (Whaley et al. 2001). At the Mangaotaki Bluffs and in the wider Waitomo district *G. lucida* has been recorded growing on limestone outcrops. Common associates include *Astelia solandri*, *Collospermum hastatum*, *Hebe stricta*, *Coprosma robusta*, *Phormium cookianum*, and *Pittosporum huttonianum* (B.D. Clarkson, University of Waikato, unpublished data). In the Awakino Gorge *G. lucida* occurs as an epiphyte on pukatea and tawa as well as a rupestral on sandstone and siltstone cliffs. Cliff associates include *Phormium cookianum*, *Coprosma robusta*, *Coriaria arborea*, *Leptospermum scoparium*, *Buddleja davidii*, *Machaerina sinclairii*, *Elatostema rugosum*, and *Freycinetia banksii* (B.D. Clarkson, University of Waikato, unpublished data). In coastal forest of northern Taranaki, *G. lucida* is associated with *Metrosideros* spp., *Melicytus ramiflorus*, *Melicope ternata*, *Dicksonia squarrosa*, *Macropiper excelsum*, *Geniostoma rupestre* var. *ligustrifolium*, *Corynocarpus laevigatus*, *Fuchsia excorticata*, *Dysoxylum spectabile*, *Brachyglottis repanda*, *Ripogonum scandens*, and *Coprosma* spp. (Wilmshurst et al. 2004). The semi-coastal forest of the Kaitake Range exhibits a prominent population of epiphytic *G. lucida* in association with *Collospermum hastatum*, *Freycinetia banksii*, *Astelia solandri*, *Blechnum filiforme*, *Earina mucronata*, *Tmesipteris elongata*, *Asplenium oblongifolium*, *A. polyodon*, *Metrosideros fulgens*, *Microsorum scandens*, *Pyrrosia eleagnifolia*, and *Cardiomanes reniforme* (Clarkson 1985).

40-42° S

Epiphytic *G. lucida* grows in association with *Ripogonum scandens*, *Freycinetia banksii*, *Rubus cissoides*, *Collospermum hastatum*, and *Astelia solandri* in northern Horowhenua forests (Duguid 1990). At Pukerua bay near Wellington, scattered *G. lucida* occur at the foot of coastal greywacke bluffs in association with *Corynocarpus laevigatus* and *Olearia paniculata* (Towns & Elliot 1996). The Marlborough Sounds region hosts *G. lucida*, *Astelia solandri*, *Phormium colensoi*, *Arthropodium cirratum*, *Coprosma repens*, *Entelea arborescens*, *Corynocarpus laevigatus*, and *Hebe speciosa*, on coastal rocks and cliffs (Cockayne 1906; Cockayne 1958). In the Edgecombe Point Scenic Reserve, also in Marlborough, *G. lucida* grows epiphytically in association with *Freycinetia banksii*, *Ripogonum scandens*, *Metrosideros* spp., and *Asplenium oblongifolium*;

and as a rupestral on greywacke and schist with *Olearia paniculata*, *Kunzea ericoides*, *Ozothamnus leptophyllus*, and *Cortaderia turbaria* (Walls 1984). *G. lucida* can also be found on rocky outcrops of Pepin Island, alongside *Drymoanthus adversus, Peperomia urvilleana, Parietaria debilis* and *Dysoxylum spectabile* (McLintock 2001).

42-44° S

Griselinia lucida grows terrestrially in coastal forest near Kaikoura, alongside *Freycinetia banksii*, *Melicope ternata*, *Lophomyrtus bullata*, *Metrosideros colensoi*, *M. perforata*, *Nestegis cunninghamii*, and *Rhopalostylis sapida* (Wardle 1961). In the Napenape reserve of northern Canterbury, *G. lucida* grows on limestone substrate along with *Dodonea viscosa, G. littoralis, Macropiper excelsum*, *Myrsine australis*, *Olearia paniculata*, *Coprosma robusta*, *Hebe salicifolia*, and *Myoporum laetum* (Department of Conservation 2002). On the opposite coast, in the Westland National Park, *G. lucida* occurs epiphytically in warm sites in association with *Earina autumnalis*, *E. mucronata*, *Winika cunninghamii*, *Asplenium polyodon*, *A. flaccidum*, *Ichthyostomum pygmaeum*, *Pyrrosia eleagnifolia*, and *Luzuriaga parviflora* (Wardle 1979). In both Canterbury and Westland, there is a notable overlap of *G. lucida* and *G. littoralis* distributions (Wardle 1977; Department of Conservation 2002).

46-48° S

Griselinia lucida has been reported in Southland (New Zealand Biodiversity Recording Network 2011) but these records are unsupported by herbarium vouchers and are doubtful (B. Rance, Department of Conservation, pers. comm. 2011). Accordingly these records have not been included on the distribution map (Figure 4.6).

4.9 Chemistry

Griselinoside, an iridoid glucoside, is produced by *Griselinia lucida* (Jensen & Nielsen 1980). Iridoid glucosides are glycosides in which the bound sugar is glucose (Crellin et al. 1990). Glycosides have deterrent properties for herbivores but may attract specialist insects (Lüttge 2010). This is supported by many observations of insect herbivory on *G. lucida* and very few of mammalian browsing (see Other biotic and abiotic roles). *G. lucida* also produces the fatty acid petroselinic acid but lacks proanthocyanidins and ellagic acid; features which have been useful in taxanomic classification (Bagci 2007).

4.1 Cytology

The chromosome number of *Griselinia lucida* is *n*=18 (Hair & Beuzenberg 1959; Federov 1969; Dillon & Muñoz-Schick 1993).

4.2 Other biotic and abiotic roles

Biotic resources and abiotic processes

Epiphytes such as *G. lucida* contribute to species richness and play a substantial role in the processes and interactions that make an ecosystem function (Cummings et al. 2006). *G. lucida* and its associated epiphytic communities provide habitat, nectar, water, fruits and nesting materials for invertebrates and birds (Nadkarni 1989; Benzing 1990; Gentry 1991; Nadkarni 1992; Affeld 2008; Cruz-Angón et al. 2009). Affeld (2008) found 397 invertebrate species in a survey of 120 epiphytic assemblages in forests of the west coast of the South Island, while O’Donnell & Dilks (1994) found that up to nine percent of observed feeding by birds in South Westland was on epiphytes. Epiphytes can also constitute a large proportion of photosynthetically active material (Hofstede et al. 2001) and contribute to abiotic processes such as water fluxes and nutrient cycling (Gentry 1991; Holscher et al. 2004). However, because research on the role of epiphytes in ecosystems is limited, especially in New Zealand (Zotz 2005; Affeld 2008), the extent of their biotic and abiotic interactions is likely to currently be unrealised.

Predation

The North Island kokako browses on *G. lucida* leaves and buds (Powlesland 1987) but insects appear to cause more frequent damage (Figure 4.10) as they are more abundant than the kokako. Insects that have been reported in association with this species include the mite *Tropacarus bakeri* (Collyer 1966), the Australasian green shield bug *Glaucias amyoti* (Martin 2010a), members of Hemiptera, Coleoptera, Blattodea, and Araneae orders (Michel et al. 2008), the exotic leaf miner

Phyllonorycter messaniella (Brockerhoff et al. 2010), and the native leaf miner *Peristoreus discoideus*; which only attacks *Griselinia* species (Kuschel 1971).

The moth larvae of *Apoctena spatiosa* browse only on *Griselinia* (Dugdale 1990), while the trunk and branches of *G. lucida* can be damaged by the burrowing and grazing of the puriri moth *Aenetus virescens* (Kirk 1872; Martin 2010b). Also, seed predation by larvae of the native moth *Heterocrossa gonosemana* has been documented in two cases; one with a minimal effect (6 % of the sample) (Sullivan et al. 1995), and the other with "a moderate number in each panicle damaged" (Burrows 1999). Possums (*Trichosurus vulpecula)* do not prefer *G. lucida*; possibly due to natural deterrents (see Chemistry, above) (Julian 1992). No primary literature was found with mention of browsing by goats (*Capra hircus*) or deer (*Cervus* spp.).

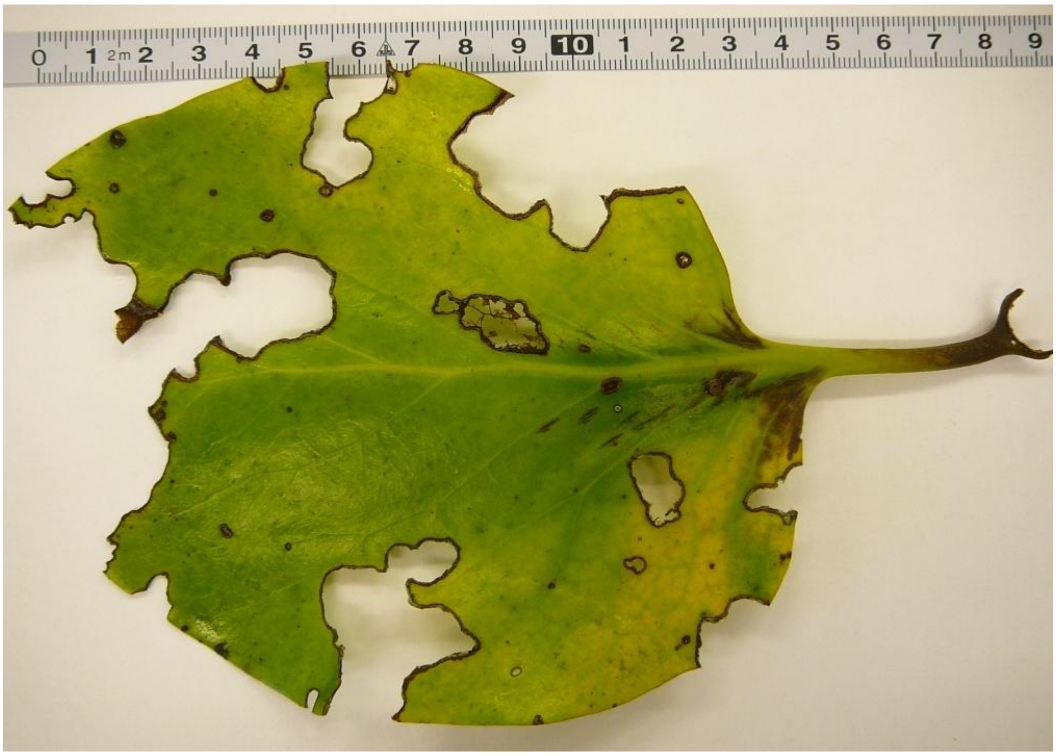

Figure 4.10: Leaf of epiphytic *Griselinia lucida* showing insect herbivory. Scale is in centimetres.

Mycorrhizae

Endotrophic mycorrhizas were reported by (Baylis 1959) in the congener of *G. lucida*; *Griselinia littoralis*, which was found to lead to higher phosphorus and lower nitrogen levels than that of non-mycorrhizal plants.

4.3 Human uses

Historically, Māori used the tough wood of *G. lucida* for making cartridge holders (Best 1907), and the inner bark has been suggested to have soothing characteristics, similar to those of *G. littoralis*, for skin rashes and eruptions (Stark 1979). *G. lucida* is popular for cultivation in gardens, often alongside *G. littoralis*; Cockayne (1910) described *G. lucida* as “a most handsome shrub for the open border”.

4.4 Conservation and restoration

Griselinia lucida should be considered in both conservation and restoration projects because it is a part of New Zealand’s considerable diversity and abundance of epiphytes (Zotz 2005; Affeld 2008), that contribute to the biotic and abiotic processes of functional ecosystems (Burns & Dawson 2005; Bryan 2011: chapter one).

The lowland and coastal habitat of *G. lucida* has been significantly reduced and transformed, and while the species is still well represented in public conservation land, national parks and scenic reserves, the small, disturbed forest patches that are scattered throughout the country generally do not support epiphytic *G. lucida* populations. This absence is likely due to the young second-growth nature of these forests and their relatively high temperatures and low humidity. These disturbed conditions inhibit the development of epiphytic communities and canopy soil (Bryan 2011: chapter two). Forest restoration within, and revegetation between these small patches will improve the microclimates for all epiphytes and aid the natural recovery of *G. lucida* populations, however, direct reintroductions may be needed to accelerate the return of *G. lucida* in isolated forest remnants (*sensu* Cummings et al. 2006).

Currently, *Griselinia lucida* has been recommended and used in terrestrial restoration plantings (e.g. Gay 1999; Auckland Regional Council 2004; Blaschke et al. 2009) but there are no documented records of restoring epiphytic populations of this shrub species. Further research and experimentation is required to establish efficient reintroduction techniques for *G. lucida* (e.g. Burns et al. 2009). The most suitable trial forests are those that are undergoing ecological restoration and have existing nest epiphyte populations (Bryan 2011: chapter five). Examples of such sites in Hamilton include Hammond Bush and Claudelands Bush.

Griselinia lucida has the potential to be used as a bioindicator (see Barthlott et al. 2001) because it generally grows as a part of epiphyte communities that occur in old growth forests with low levels of disturbance. Therefore, the presence of *G. lucida* in a forest indicates environmental suitability for a range of epiphyte and vine species. Also, the successful reintroduction of *G. lucida* would indicate that populations of associated species could also be restored. Setting targets and monitoring progress of *G. lucida* reintroductions would be crucial for understanding how to successfully return this species to appropriate forest ecosystems (*sensu* Lake 2001; Cummings et al. 2006), and could lead to the widespread inclusion of *G. lucida* and other epiphytes in ecological restoration.

4.5 Conclusions

The epiphytic status of *Griselinia lucida* has been discussed since 1930 when Oliver classified it as a typical epiphyte, i.e. a species which is habitually epiphytic. The rupestral and terrestrial populations of the South Island mean that this species does not meet the obligate classification of Benzing (2004); "every member of a population of an "obligate" epiphyte roots on bark", or Ibisch (1996, *in* Zotz 2005); "> 95 % of all individuals of a species in a particular region are growing epiphytically". Most recently Burns (2010) has provided a null model to test whether epiphytes are obligate, facultative or accidental and demonstrated that *G. lucida* meets the definition of obligate at Otari-Wilton's bush in Wellington. On the basis of regional and national scale analyses (Bryan 2011), *G. lucida* can be classified as an obligate because (1) it most frequently occurs as an epiphyte, (2) the rupestral and terrestrial environments that it inhabits have harsh conditions similar to that of its canopy habitat (Dawson 1986), and (3) it does not meet the criteria of facultative species that commonly occur on both the forest floor and in the canopy (Benzing 2004; Burns 2010).

To conclude, *Griselinia lucida* is a conspicuous member of New Zealand's endemic flora that frequently grows as a hemiepiphyte in old growth lowland forests and as a terrestrial or rupestral shrub in coastal and rocky environments. *G.*

lucida establishes in the canopy soil of epiphytic communities and often accesses the resources of the forest floor through large, grooved roots that descend the trunk of its host tree. Under water stress, this species exhibits a desiccation postponement strategy through reductions of stomatal conductance and highly elastic cell walls. *G. lucida* is an important component of ecosystems as it provides resources for forest fauna and flora and contributes to abiotic processes. For these reasons, it is recommended that *G. lucida* is included in the future ecological restoration of degraded ecosystems.

Chapter Five: Synthesis

5.1 Discussion

This research has enhanced our understanding of the ecology of New Zealand's vascular epiphytes and provided important information for the inclusion of epiphytes in forest restoration. The case study on the water relations and desiccation tolerance of *Griselinia lucida* provides specific details about the requirements and limitations of this shrub epiphyte that support and extend the recommendations from the ecological study.

When compared to nonurban Waikato and Taranaki forests, urban Waikato (i.e. Hamilton City) forests have relatively depauperate vascular epiphyte and vine populations. Hamilton forests are predominantly comprised of early and mid arrival species, and the average number of species per host tree is less than one. Because epiphytes and vines contribute to biodiversity, these forests are consequently expected to have reduced function, resilience, and ecosystem services. The underlying reason for the low species diversity and abundance in Hamilton City is the fragmented and disturbed nature of this urban habitat.

Diverse epiphyte and vine populations are associated with a range of biotic and abiotic factors, many of which are altered or even lost when forests are fragmented by anthropogenic development. Through monitoring of canopy microclimates, this study showed that urban Waikato forests have higher temperatures and vapour pressure deficits than nonurban Waikato forests. It is speculated that these conditions are inhibiting the accumulation of epiphyte and vines species and thus restricting habitat suitability for late arrival species such as *Griselinia lucida*, *Brachyglottis kirkii*, and *Winika cunninghamii*.

This study has also highlighted the importance of host tree characteristics for epiphyte establishment and survival. Host size, bark type, and architecture were associated with the diversity of epiphyte populations. The highest species counts were recorded on large host trees with non-peeling bark and wide branch angles. These characteristics are frequently absent in the variable assemblages of host trees in Hamilton City; further reducing the suitability of urban epiphyte habitat. It is also speculated that large dispersal distances between urban and nonurban Waikato forests is restricting the arrival of seed into Hamilton City.

The microclimate differences between urban and nonurban Waikato forests were supported by the finding that *Griselinia lucida*, a late arrival shrub epiphyte, is relatively sensitive to dehydration. Under three levels of stress, the water relations of *G. lucida* indicate that it employs a desiccation postponement strategy through the reduction of stomatal conductance and photosynthesis. This species also exhibits high cell elasticity that has been shown in other species to provide tolerance of the early stages of drought through the preferential loss of water from nonessential cells, such as the hypodermis. These physiological mechanisms evidently allow *G. lucida* to postpone desiccation and thus tissue dehydration, then recovery rapidly when water becomes available. However, despite this ability, *G. lucida* is absent from urban Waikato forests; indicating that the microclimate is too severe.

A review of published and unpublished information on *Griselinia lucida* found that, along with its lowland epiphytic habitat, it also commonly grows in open rocky and coastal environments. This habitat range has similar environmental conditions to epiphyte habitat; such as irregular water supply, limited substrate, high exposure to insolation and wind, relatively warm temperatures, and a lack of frost. These commonalities indicate that the ability to postpone desiccation under water stress allows *G. lucida* to grow in a range of environments with intermittent water supplies. Microclimate monitoring in large forests and coastal environments indicates that, although rigorous, these habitats still have higher mean humidity than urban forest patches (chapter four). It is speculated that through drought-hardening, mature *G. lucida* plants would exhibit an even greater ability to postpone desiccation than the seedlings used in the desiccation experiment of this study (chapter two). Desiccation postponement is therefore likely to have been important for the establishment of *Griselinia lucida* populations throughout lowland New Zealand (chapter four).

5.2 Recommendations for restoration ecology

After studying the epiphytes of pine-oak forests in Mexico, Wolf (2005) stated that “more insight in the response of epiphytes to anthropogenic disturbance is particularly needed to facilitate the incorporation of the epiphytic component in forest management." The research presented in chapters two, three, and four has addressed this need in the North Island of New Zealand through an investigation into the effects of anthropogenic disturbance on epiphyte populations of urban Waikato, an assessment of the general requirements of vascular species local to the Waikato region, and the development of the following recommendations for the incorporation and management of epiphyte species in ecological forest restoration.

As explained previously, many epiphyte and vines species are absent from urban forest patches (chapter one). The following recommendations are therefore aimed at small forests but will also be applicable to restoration in larger forests remnants.

5.2.1 Trials

The inclusion of epiphyte and vine species in ecological restoration will require species reintroductions through the relocation of juvenile or mature plants, or the introduction of seed into suitable substrate. Before practical recommendations for these reintroductions can be made, trials need to be conducted to identify best practise methodology.

Each epiphyte and vine species will have different requirements for successful establishment. Previous experiments provide some methodology and a good starting point for further investigations. In New Zealand, Burns et al. (2009) had reintroduction success with *Metrosideros robusta*, using large volumes of sphagnum moss under wire mesh on the southern aspect of native host trees. Yam et al. (2010) have had good survival rates of native orchid species in Singapore by raising seedlings on "fern bark" then nailing this substrate to a host tree. Reintroduction trials should be conducted in forest patches that are already undergoing ecological restoration and have some existing epiphyte populations. Potential forests in the Waikato region are Hammond Bush and Claudelands Bush. In the case of forest restoration where host species are planted and epiphytes are completely absent, generalist species should be introduced as soon as canopy closure has been achieved (Cummings et al. 2006), so as to begin the facilitation and species accumulation processes as soon as possible. Waiwhakareke Natural

Heritage Park in Hamilton City will be a suitable forest restoration site to trial epiphyte introductions from scratch.

Initially, epiphytes and vines could be sourced from tree falls in diverse forests. This should be followed by investigations into ecosourcing seed for *ex situ* propagation and possibly even inclusion in nursery stock.

5.2.2 Practical recommendations

Once best practise reintroduction techniques have been developed for the attachment of epiphytes to hosts, the following recommendations will be useful for undertaking a reintroduction program. Where possible, epiphytes should be planted near, or in, existing epiphyte assemblages because they indicate suitable conditions (Yam et al. 2010). As with all aspects of ecological restoration, setting targets and monitoring progress is essential for the long term viability of the project (Society for Ecological Restoration International Science & Policy Working Group 2004).

Microclimate

The microclimate of a forest is likely to be the most important factor in determining the success or failure of epiphyte reintroductions. The key aspect of microclimate suitability is relative humidity (e.g. Yam et al. 2010). Along with temperature and wind speed, relative humidity is an important factor in the rate of water loss from plants (Stuntz et al. 2002). Suitable humidity for diverse and abundant epiphyte communities in lowland forests can be indicated by mean vapour pressure deficits less than 0.15 kPa (chapter two). These conditions are found in forests that have relatively large edge:area ratios; from the measurements in chapter two it is speculated that a ratio of over 100 may be required to provide suitable conditions. Nearby water bodies are also likely to increase relative humidity. Planting near or in existing epiphyte communities will increase survivability because they create a buffered microclimate (Freiberg 2001; Stuntz et al. 2002). In forests that have low edge:area ratios and high vapour pressure deficits, reintroduction efforts should be focussed on colonising, generalist species that have a greater tolerance for harsh conditions; examples include *Pyrrosia eleagnifolia*, *Microsorum* species, and *Earina mucronata* (chapter two).

Host selection

Choosing an appropriate host tree will increase survivability of reintroduced species. The first host characteristic to consider is size; with the goal of restoring large, diverse epiphytic communities, hosts over 50 cm in diameter that reach the canopy should be targeted because they provide a greater source of light and water, and a larger surface area to inhabit (see chapter two). Secondly, the bark type of a host tree should be considered (Yam et al. 2010) because the texture, degree of peeling, water-storage capacity, and the presence or absence of alleochemicals all influence epiphyte survival. From this research, it is recommended that fibrous and smooth bark types are targeted (chapter two). Finally, the host architecture is relevant for many epiphytes and vines; host species such as titoki with large branch angles and wide limbs are good hosts for many epiphytes, including large nest species (chapter two).

Epiphyte or vine species

The selection of epiphyte species for reintroduction should be based on the condition of the forest and any existing epiphyte and vine populations. If very few species are present in the target forest, the microclimate is likely to be relatively harsh and thus, early arrival, generalist species are appropriate (chapter two). However, if the goal is to enhance an existing epiphyte community, later arrival species that require more specialist habitat with higher humidity may be appropriate. The differentiation between these types of epiphytes and vines is important because the survival and growth response of a reintroduced species will depend on the availability of habitat or niches that suit its ecological and physiological requirements (Nöske et al. 2008). If the species is a generalist, it has a wider range of niches and will thus be easier to reintroduce, while more specialist species that arrival late in the process of epiphyte accumulation, such as *Griselinia lucida*, need particular conditions to survive and successfully reproduce (Alvarenga et al. 2009). Chapter two provides relevant classification of lowland epiphytes species.

Education and awareness

Once practical recommendations for epiphyte reintroductions are developed they need to be disseminated to the wide range of restoration practitioners across New Zealand. This could include government and council staff, community group members, and private landowners. Workshops and newsletter features would also be a useful method to share information and get people involved. It is crucial that this link between restoration ecology research and the practise of ecological restoration is made in order to ensure the best outcomes for restored ecosystems (Cabin et al. 2010). In the future, it will also be important to celebrate reintroduction successes and share information about the unique nature of this plant guild in a way that educates and engages people; especially those who live near urban forest patches (chapter one).

5.2.3 Goals and conclusions

The ultimate goal of these ecological restoration recommendations is to increase awareness of New Zealand's unique epiphyte and vine species and provide the first steps towards including them in restoration projects. Epiphytic communities and the habitats that they occupy are complex and dynamic. Although we cannot hope to fully restore systems through plant reintroductions, we can aim to establish diverse populations from which resilient communities can develop.

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Appendices

Appendix one: family, genera and species counts in Waikato forests

Number of families occurring in Waikato forests

Families (28)	Total	Nonurban	Urban
Apocynaceae	1	1	0
Araliaceae	1	0	1
Aspleniaceae	3	3	3
Asteliaceae	4	4	1
Blechnaceae	1	1	1
Convolvulaceae	1	0	1
Ericaceae	1	1	1
Griseliniaceae	1	1	0
Hymenophyllaceae	1	1	0
Laxmanniaceae	1	1	0
Loganiaceae	1	1	1
Myrsinaceae	1	0	1
Myrtaceae	4	4	3
Oleaceae	2	0	2
Orchidaceae	5	5	4
Pandanaceae	1	1	1
Passifloraceae	1	1	1
Piperaceae	1	1	1
Pittosporaceae	1	1	0
Polygonaceae	1	0	1
Polypodiaceae	3	3	3
Psilotaceae	1	1	1
Ranunculaceae	1	1	0
Ripogonaceae	1	1	1
Rosaceae	1	0	1
Rubiaceae	2	2	1
Schizaeaceae	1	1	0
Violaceae	1	1	0
Total	44	37	30

Number of genera occurring in Waikato forests

Genera (34)	Total	Nonurban	Urban
Asplenium	3	3	3
Astelia	2	2	1
Blechnum	1	1	1
Clematis	1	1	1
Collospermum	2	2	2
Convolvulus	1	1	0
Coprosma	2	2	1
Cordyline	1	0	1
Drymoanthus	1	1	0

Earina	2	2	1
Freycinetia	1	1	1
Geniostoma	1	1	1
Griselinia	1	1	1
Hedera	1	1	0
Hymenophyllum	1	1	0
Ichthyostomum	1	1	0
Jasminum	1	0	1
Leucopogon	1	1	0
Ligustrum	1	0	1
Lygodium	1	1	0
Macropiper	1	1	0
Melicytus	1	1	0
Metrosideros	4	4	3
Microsorum	2	2	2
Muehlenbeckia	1	1	1
Myrsine	1	1	1
Parsonsia	1	1	0
Passiflora	1	1	1
Pittosporum	1	1	0
Pyrrosia	1	1	1
Ripogonum	1	1	1
Rubus	1	0	1
Tmesipteris	1	1	1
Winika	1	1	1
Total	44	40	29

Number of species occurring in Waikato forests

Species (44)	Total	Nonurban	Urban
Asplenium flaccidum	116	92	24
Asplenium oblongifolium	9	5	4
Asplenium polyodon	54	41	13
Astelia banksii	1	1	0
Astelia solandri	70	66	4
Blechnum filiforme	87	73	14
Clematis paniculata	1	1	0
Collospermum hastatum	82	77	5
Collospermum microspermum	8	7	1
Convolvulus sp.	2	0	2
Coprosma grandifolia	1	1	0
Coprosma robusta	2	0	2
Cordyline banksii	1	1	0
Drymoanthus adversus	6	5	1
Earina autumnalis	28	28	0
Earina mucronata	74	72	2
Freycinetia banksii	33	22	11
Geniostoma ligustrifolium	2	1	1

Griselinia lucida	18	18	0
Hedera helix	9	0	9
Hymenophyllum sanguinolentum	32	32	0
Ichthyostomum pygmaeum	10	9	1
Jasminum polyanthum	1	0	1
Leucopogon fasciculatus	3	3	0
Ligustrum sinense	1	0	1
Lygodium articulatum	13	13	0
Macropiper excelsum	2	2	0
Melicytus micranthus	1	1	0
Metrosideros albiflora	1	1	0
Metrosideros diffusa	54	50	4
Metrosideros fulgens	94	93	1
Metrosideros perforata	59	52	7
Microsorum pustulatum	112	76	36
Microsorum scadens	88	70	18
Muehlenbeckia australis	12	0	12
Myrsine australis	1	0	1
Parsonsia spp.	6	6	0
Passiflora tetrandra	2	1	1
Pittosporum cornifolium	3	3	0
Pyrrosia eleagnifolia	244	153	91
Ripogonum scandens	78	70	8
Rubus fruticosus	1	0	1
Tmesipteris elongata	18	14	4
Winika cunninghamii	20	19	1
Total	1460	1179	281

Species life form and growth form in Waikato forests

Species	Life form	Growth form
Asplenium flaccidum	holo	pendant
Asplenium oblongifolium	holo	pendant
Asplenium polyodon	holo	pendant
Astelia banksii	holo	nest
Astelia solandri	holo	nest
Blechnum filiforme	herb. vine	-
Clematis paniculata	liana	-
Collospermum hastatum	holo	nest
Collospermum microspermum	holo	nest
Convolvulus sp.	liana	-
Coprosma grandifolia	accidental	-
Coprosma robusta	accidental	-
Cordyline banksii	accidental	-
Drymoanthus adversus	holo	mat
Earina autumnalis	holo	pendant
Earina mucronata	holo	pendant
Freycinetia banksii	liana	-

Geniostoma ligustrifolium	accidental	-
Griselinia lucida	hemi	shrub
Hedera helix	liana	-
Hymenophyllum sanguinolentum	holo	mat
Ichthyostomum pygmaeum	holo	mat
Jasminum polyanthum	liana	-
Leucopogon fasciculatus	accidental	-
Ligustrum sinense	accidental	-
Lygodium articulatum	holo	pendant
Macropiper excelsum	accidental	-
Melicytus micranthus	accidental	-
Metrosideros albiflora	liana	-
Metrosideros diffusa	liana	-
Metrosideros fulgens	liana	-
Metrosideros perforata	liana	-
Microsorum pustulatum	herb. vine	-
Microsorum scadens	herb. vine	-
Muehlenbeckia australis	liana	-
Myrsine australis	accidental	-
Parsonsia spp.	liana	-
Passiflora tetrandra	liana	-
Pittosporum cornifolium	holo	shrub
Pyrrosia eleagnifolia	holo	mat
Ripogonum scandens	liana	-
Rubus fruticosus	liana	-
Tmesipteris elongata	holo	pendant
Winika cunninghamii	holo	pendant

Appendix two: family, genera and species counts in Taranaki forests

Number of families occurring in Taranaki forests

Families (21)	Total	Nonurban	Urban
Apocynaceae	1	1	0
Aspleniaceae	3	3	3
Asteliaceae	4	3	4
Asteraceae	1	1	0
Blechnaceae	1	1	1
Cyatheaceae	1	0	1
Griseliniaceae	1	1	1
Hymenophyllaceae	1	1	1
Loganiaceae	1	0	1
Lycopodiaceae	1	1	1
Myrsinaceae	1	0	1
Myrtaceae	3	3	3
Oleandraceae	1	1	1
Orchidaceae	4	2	3
Pandanaceae	1	1	1

Passifloraceae	1	0	1
Pittosporaceae	1	1	1
Polypodiaceae	3	3	3
Psilotaceae	1	1	0
Ripogonaceae	1	1	1
Violaceae	1	1	1
Total	33	26	29

Number of genera occurring in Taranaki forests

Genera (25)	Total	Nonurban	Urban
Arthropteris	1	1	1
Asplenium	3	3	3
Astelia	2	1	2
Blechnum	1	1	1
Brachyglottis	1	1	0
Collospermum	2	2	2
Cyathea	1	0	1
Drymoanthus	1	0	1
Earina	2	2	1
Freycinetia	1	1	1
Geniostoma	1	0	1
Griselinia	1	1	1
Huperzia	1	1	1
Hymenophyllum	1	1	1
Ichthyostomum	1	0	1
Melicytus	1	1	1
Metrosideros	3	3	3
Microsorum	2	2	2
Myrsine	1	0	1
Parsonsia	1	1	0
Passiflora	1	0	1
Pittosporum	1	1	1
Pyrrosia	1	1	1
Ripogonum	1	1	1
Tmesipteris	1	1	0
Total	33	26	29

Number of species occurring in Taranaki forests

Species (33)	Total	Nonurban	Urban
Arthropteris tenella	5	3	2
Asplenium flaccidum	17	9	8
Asplenium oblongifolium	10	5	5
Asplenium polyodon	30	12	18
Astelia banksii	1	0	1
Astelia solandri	19	8	11
Blechnum filiforme	44	19	25
Brachyglottis kirkii	1	1	0

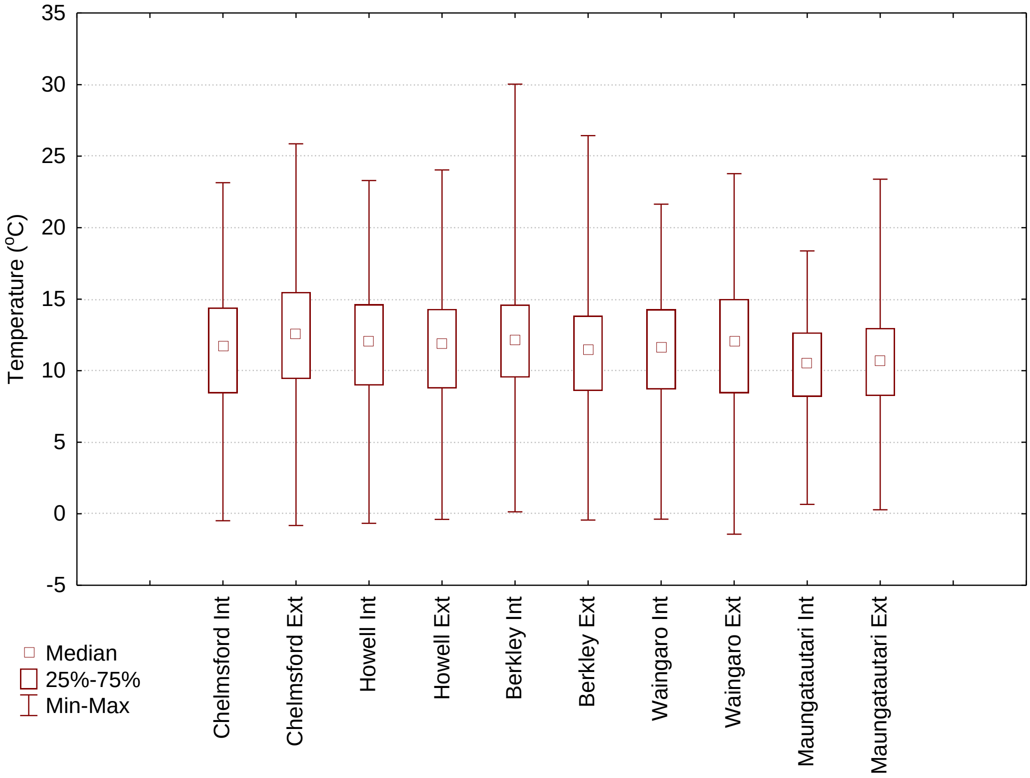
Collospermum hastatum	59	23	36
Collospermum microspermum	16	7	9
Cyathea spp.	1	0	1
Drymoanthus adversus	2	0	2
Earina autumnalis	2	2	0
Earina mucronata	32	16	16
Freycinetia banksii	16	4	12
Geniostoma ligustrifolium	2	0	2
Griselinia lucida	17	6	11
Huperzia varia	4	1	3
Hymenophyllum sanguinolentum	20	13	7
Ichthyostomum pygmaeum	1	0	1
Melicytus ramiflorus	2	1	1
Metrosideros diffusa	4	2	2
Metrosideros fulgens	33	10	23
Metrosideros perforata	33	15	18
Microsorum pustulatum	34	20	14
Microsorum scandens	54	28	26
Myrsine australis	1	0	1
Parsonsia heterophylla	3	3	0
Passiflora tetrandra	2	0	2
Pittosporum cornifolium	2	1	1
Pyrrosia eleagnifolia	49	21	28
Ripogonum scandens	30	14	16
Tmesipteris elongata	4	4	0
Total	550	248	302

Species life form and growth form in Taranaki forests

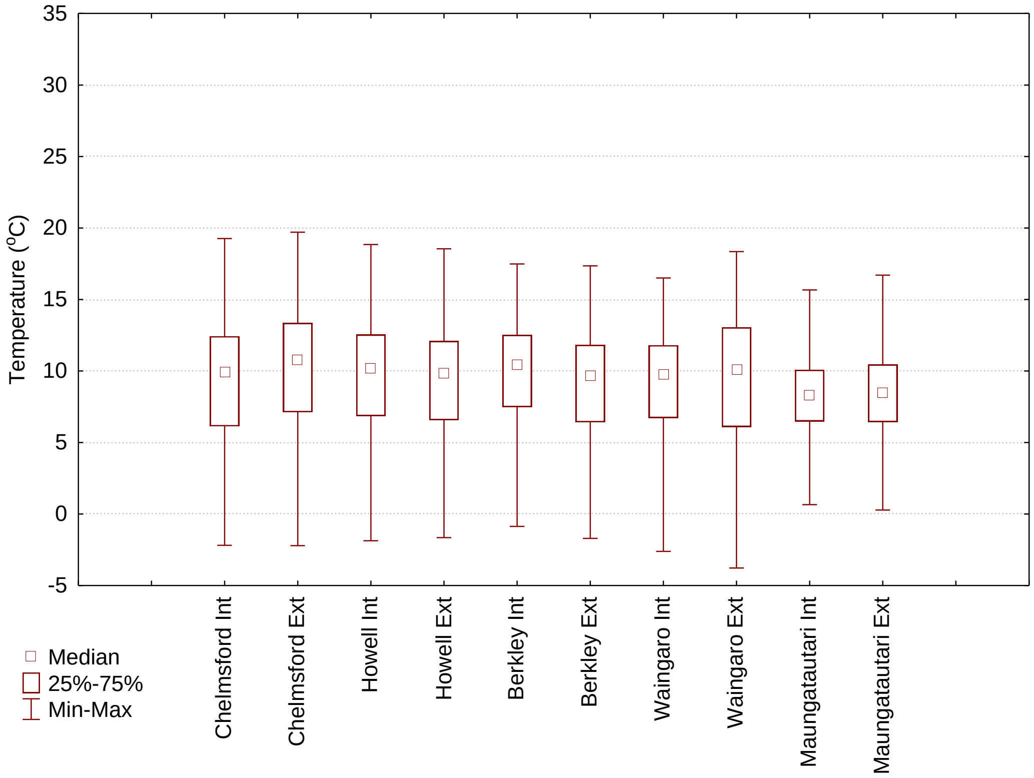
Species	Life form	Growth form
Arthropteris tenella	herb. vine	-
Asplenium flaccidum	holo	pendant
Asplenium oblongifolium	holo	pendant
Asplenium polyodon	holo	pendant
Astelia banksii	holo	nest
Astelia solandri	holo	nest
Blechnum filiforme	herb. vine	-
Brachyglottis kirkii	holo	shrub
Collospermum hastatum	holo	nest
Collospermum microspermum	holo	nest
Cyathea spp.	accidental	-
Drymoanthus adversus	holo	mat
Earina autumnalis	holo	pendant
Earina mucronata	holo	pendant
Freycinetia banksii	liana	-
Geniostoma ligustrifolium	accidental	-
Griselinia lucida	hemi	-
Huperzia varia	holo	pendant

Hymenophyllum sanguinolentum	holo	mat
Ichthyostomum pygmaeum	holo	mat
Melicytus ramiflorus	liana	-
Metrosideros diffusa	liana	-
Metrosideros fulgens	liana	-
Metrosideros perforata	herb. vine	-
Microsorum pustulatum	herb. vine	-
Microsorum scandens	accidental	-
Myrsine australis	accidental	-
Parsonsia heterophylla	liana	-
Passiflora tetrandra	liana	-
Pittosporum cornifolium	holo	shrub
Pyrrosia eleagnifolia	holo	mat
Ripogonum scandens	liana	-
Tmesipteris elongata	holo	pendant

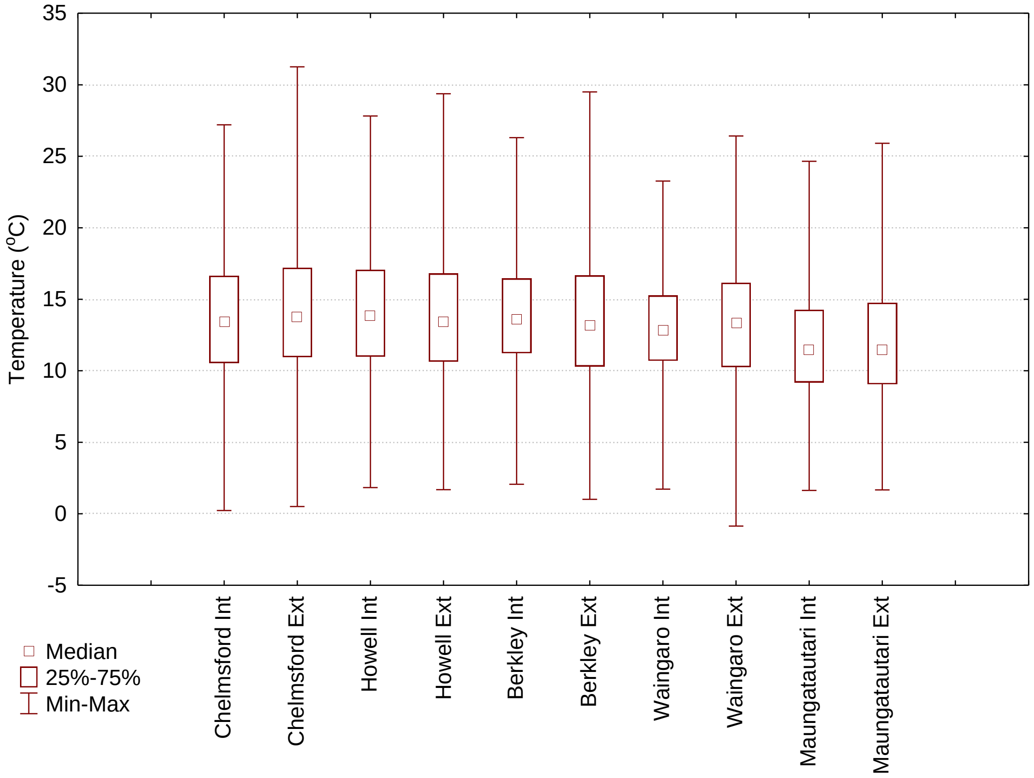
Appendix three: temperature (°C) and vapour pressure deficit (kPa) records from interior (Int) and exterior (Ext) loggers at all sites for each season



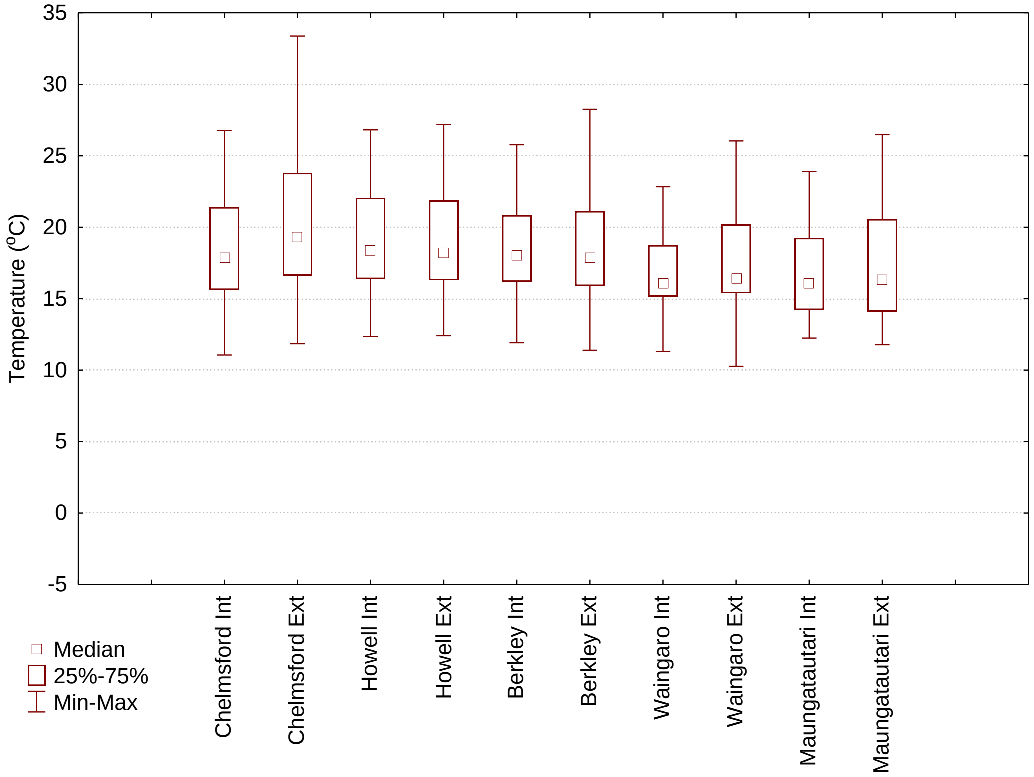
Autumn temperature (°C) for interior (Int) and exterior (Ext) loggers at all sites. Note: data set incomplete.



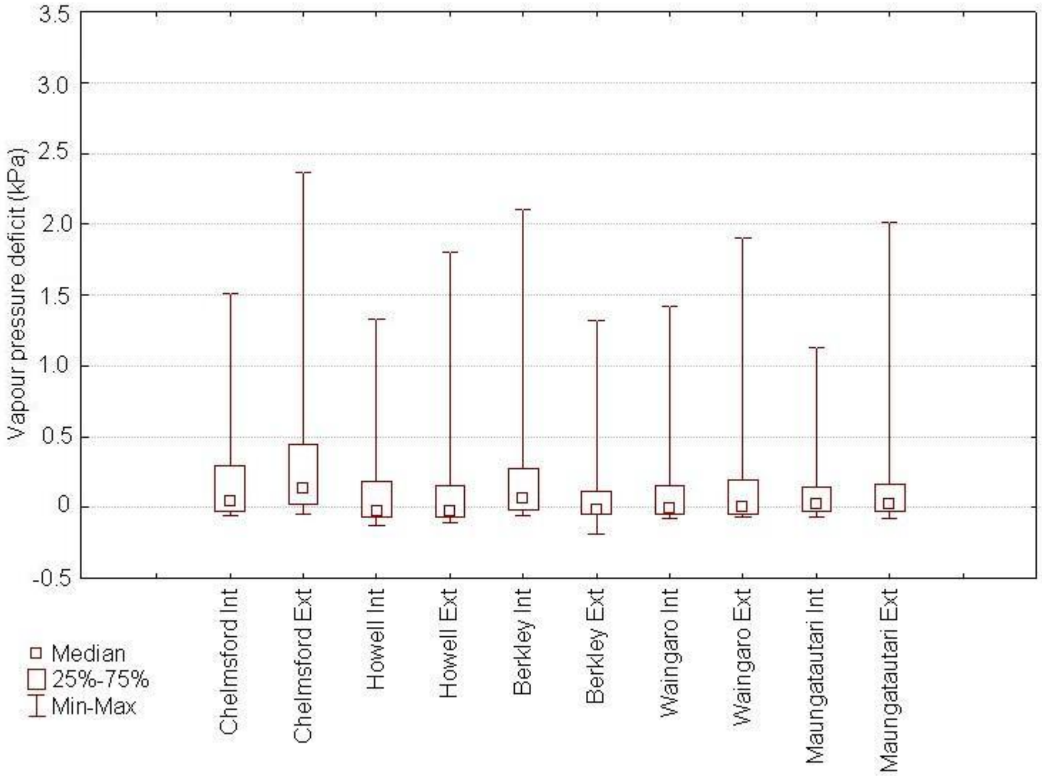
Winter temperature (°C) for interior (Int) and exterior (Ext) loggers at all sites.



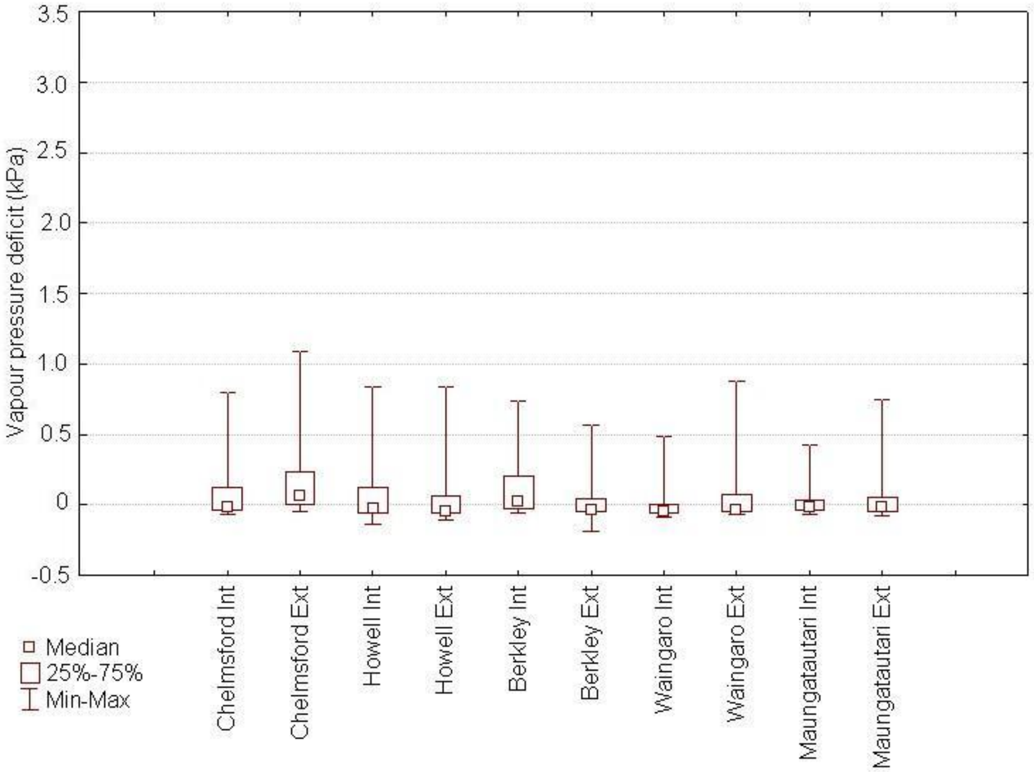
Spring temperature (°C) for interior (Int) and exterior (Ext) loggers at all sites.



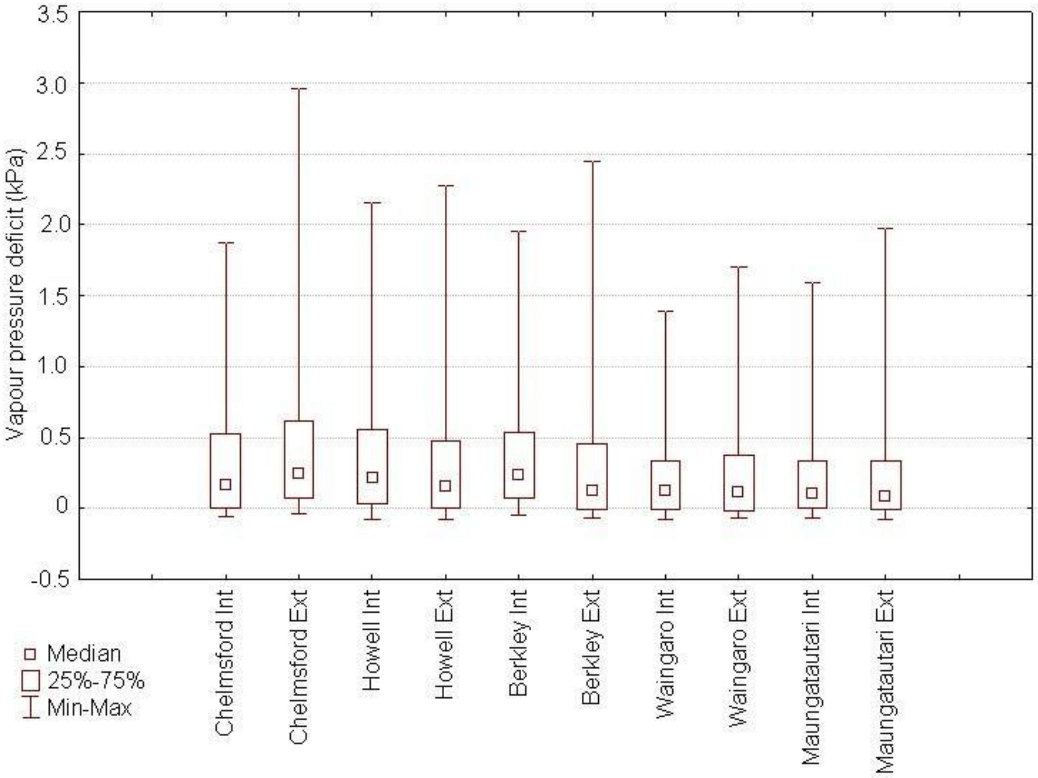
Summer temperature (^{o}C) for interior (Int) and exterior (Ext) loggers at all sites. Note: data set incomplete.



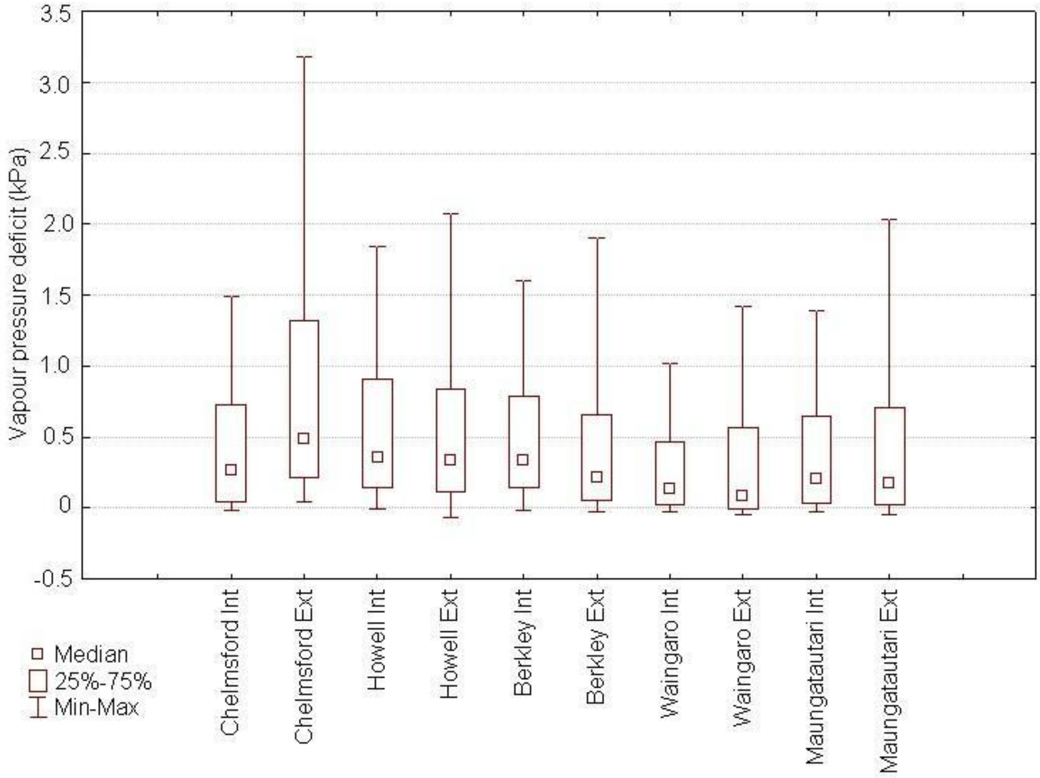
Autumn vapour pressure deficits (kPa) for interior (Int) and exterior (Ext) loggers at all sites. Note: data set incomplete.



Winter vapour pressure deficit (kPa) for interior (Int) and exterior (Ext) loggers at all sites.

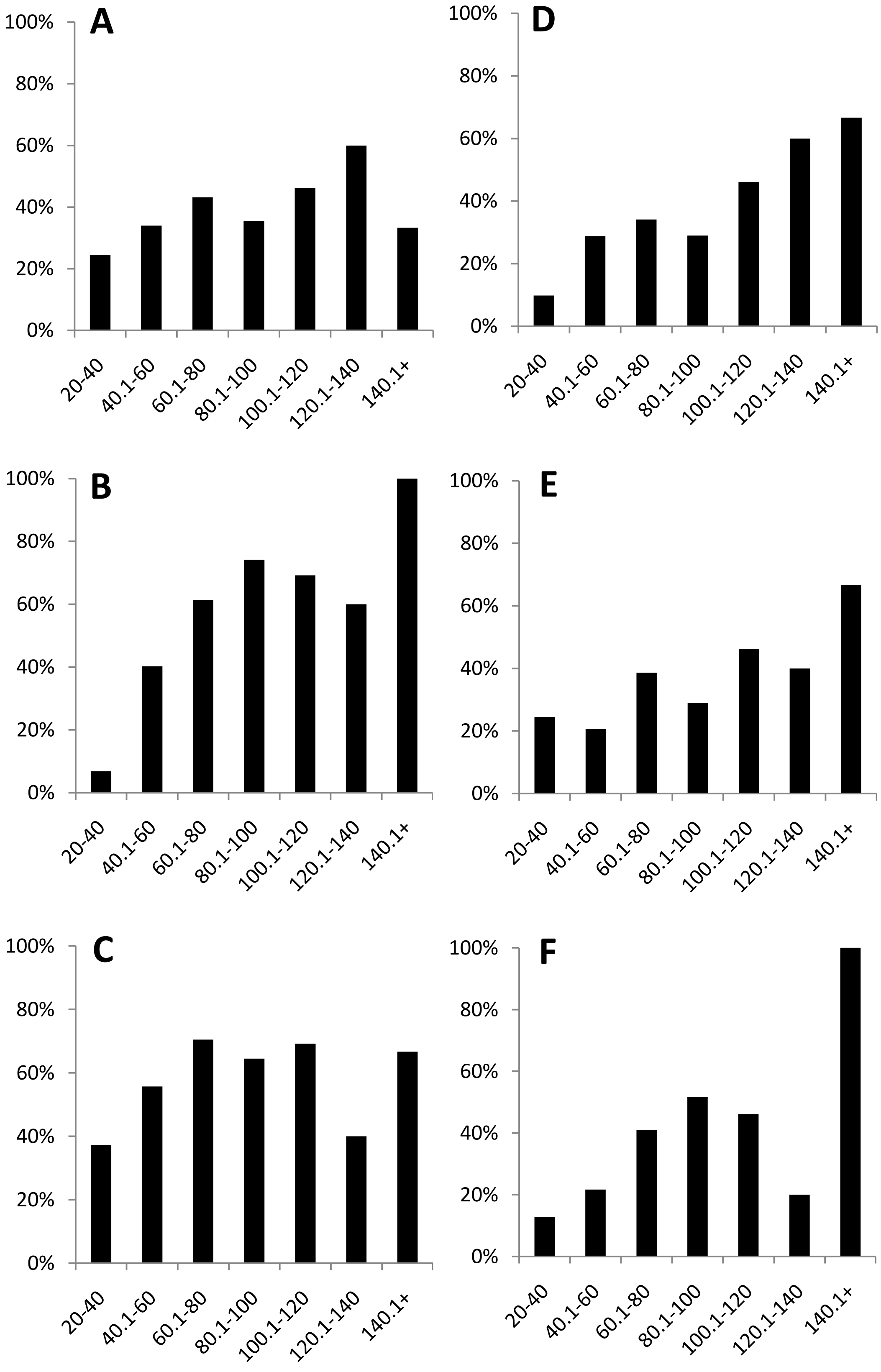


Spring vapour pressure deficit (kPa) for interior (Int) and exterior (Ext) loggers at all sites.

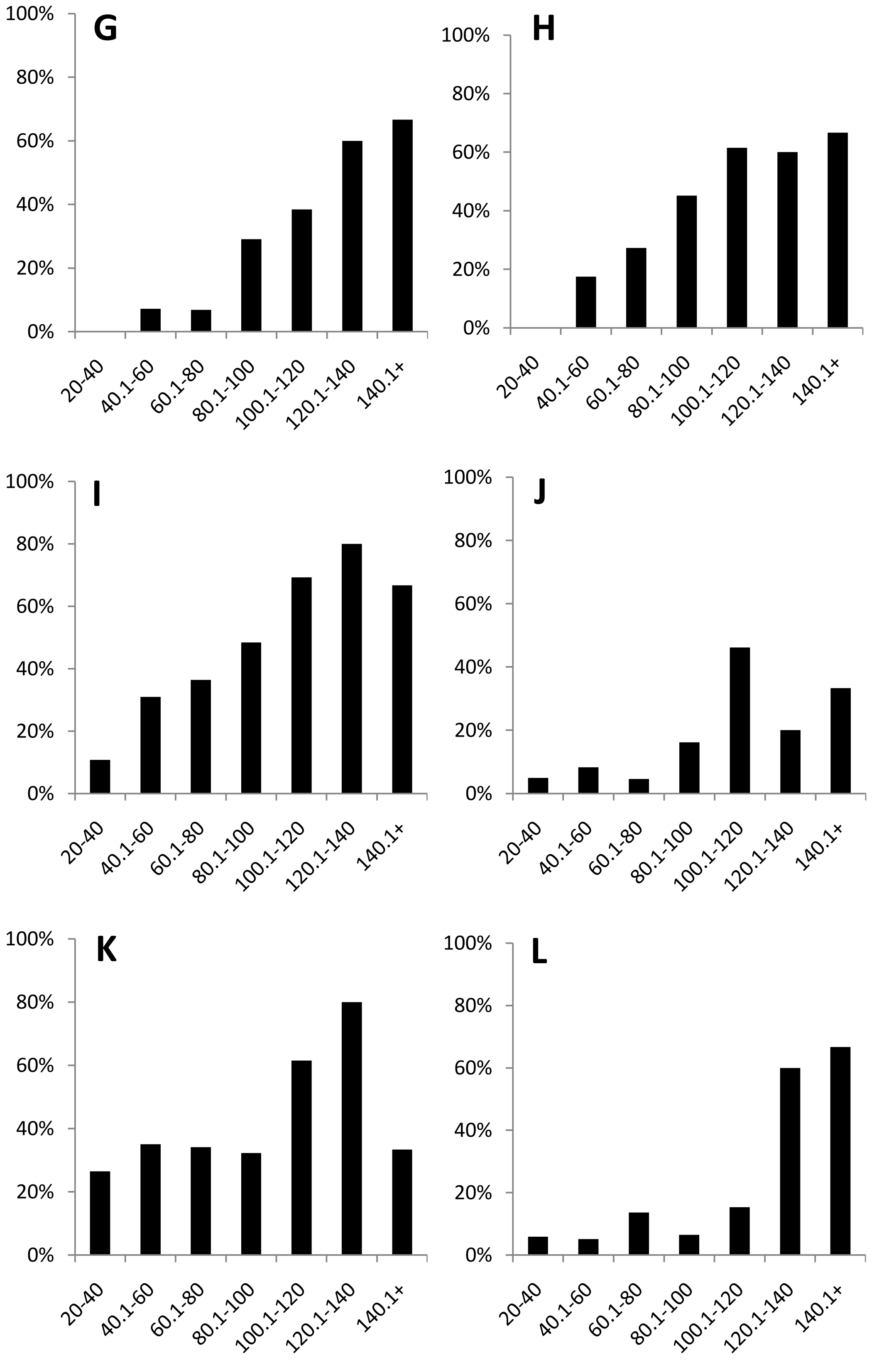


Summer vapour pressure deficit (kPa) for interior (Int) and exterior (Ext) loggers at all sites. Note: data set incomplete.

Appendix four: percent of trees in seven size classes that host each epiphyte or vines species



A: *Microsorum scandens*, B: *Collospermum hastatum*, C: *Pyrrosia eleagnifolia*, D: *Asplenium flaccidum*, D: *Ripogonum scandens*, F: *Earina mucronata*.



G: *Griselinia lucida*, H: *Asplenium polyodon*, I: *Microsorum pustulatum*, J: *Earina autumnalis*, K: *Blechnum filiforme*, L: *Freycinetia banksii*