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***Pittosporum kirkii*: autecology of an endemic shrub
epiphyte**

A thesis submitted in partial fulfilment
of the requirements for the degree

of

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at

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by

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THE UNIVERSITY OF
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***“The most striking and beautiful of the New Zealand
[Pittosporum] species” - Kirk (1899)***



Bird's eye view of a female epiphytic *Pittosporum kirkii* at the top of a rimu snag. Photo taken by A. Hawcroft (Department of Conservation 2009) during an aerial foliar browse survey of the Matemateaonga Range, inland Taranaki.

Abstract

This research investigated the autecology of the New Zealand endemic shrub epiphyte *Pittosporum kirkii* (Pittosporaceae). *Pittosporum kirkii* most frequently displays an epiphytic lifestyle, perched amongst nest epiphytes in the canopies of emergent or canopy trees in old-growth forest. The main objective of this research was to enhance the understanding of *Pittosporum kirkii*, with a focus on ecological, morphological and physiological characteristics.

Ecological characteristics were investigated in field surveys of five key *Pittosporum kirkii* populations that encompass its known latitudinal extent. Survey results showed that *P. kirkii* is late successional epiphyte commonly found in the inner crown of large canopy and emergent hosts amongst nest epiphytes, it has a short flowering season and shows clinal patterns in leaf length with increasing latitude. *Pittosporum kirkii* meets the definition of a facultative epiphyte as it grows in rupestral, terrestrial and epiphytic lifestyles. The most common host species for *P. kirkii* is *Dacrydium cupressinum*.

Flowering was concentrated between November and December and individuals in the populations examined were functionally dioecious with a preponderance of males; flower pollinators and seed dispersers are uncertain.

Field data and supplementary data sets (e.g. herbarium records) were combined to develop a predicted environmental distribution map. *Pittosporum kirkii* has an abrupt distribution with strong habitat preferences restricting it to the upper North Island, in upper lowland and lower montane old-growth forest ecosystems. High vapour pressure deficits (>0.39 kPa) and low annual rainfall (<1172 mm) restrict environmental distribution.

Investigations into the physiological and morphological characteristics of *Pittosporum kirkii* were focussed on water relations because water availability is speculated to be the most limiting factor across all of the habitats that *P. kirkii* occupies. In a glasshouse experiment *P. kirkii* seedlings were subjected to three levels of desiccation stress alongside epiphytic congener *P. cornifolium*. In the context of international literature, the stress strategies of each species were identified from analysis of morphological adaptations and physiological responses.

Pittosporum kirkii has small relative leaf area, thick coriaceous upper leaf cuticles, substantial hypodermal tissue, and under desiccation stress, exhibited rapid reductions in stomatal conductance and photosynthetic activity with stress (ceased function at mean pre-dawn water potentials of -0.8 MPa). This evidence aligns *P. kirkii* with a desiccation postponement strategy. In contrast *P. cornifolium* has thinner cuticle hypodermal tissue, larger relative leaf area and maintains photosynthetic function under greater stress (ceased function at mean pre-dawn water potentials of -1.7 MPa), and as a result, lost water potential faster than *P. kirkii*. Therefore *P. cornifolium* is concluded to align with a desiccation tolerance stress strategy. Both species recovered within 3 days after re-watering, an important response for the drought-prone epiphytic, terrestrial and rupestral environments that both species inhabit.

Under the current threat classification *Pittosporum kirkii* is listed as *in decline* and is considered to be a data poor species. The threats to this species are uncertain; although possum browsing and forest clearance have been proposed, all available evidence is anecdotal and circumstantial. The abundant presence of *P. kirkii* on possum-free Great Barrier Island suggests relief from possum browse but other browsers are also restricted. Regenerative failures were not evident in mainland or offshore island populations and possum herbivory was not detected in mainland populations, likely because numbers were controlled. However, there may be other factors that may be potentially causing the decline of *P. kirkii* which could be identified with further research into pollinators, seed dispersal and sexual expression.

Pittosporum kirkii then is a distinctive member of New Zealand's small guild of endemic shrub epiphytes but overall has the narrowest distribution, narrowest environmental profile, greatest habitat specificity and is the least abundant.

To present the key findings of this research alongside existing information, one chapter is presented in the format of the New Zealand Journal of Botany Biological Flora Series.

Key words: Biological flora; *Pittosporum kirkii*; epiphyte; morphology; taxonomy; distribution; associations; conservation; restoration; New Zealand

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Chapter one: Introduction

1.1 Overview

This thesis presents research on the autecology of *Pittosporum kirkii* Hook. f. ex. Kirk (Pittosporaceae: Apiales)* based largely on ecological surveys of five natural populations, and nursery sourced individuals, along with a water relations experiment. Field survey data sets were extended with supplementary data to enhance quantitative ecological assessments, and to construct national scale environmental profiles.

Pittosporum kirkii is an endemic shrub which is listed as data poor and in decline (Brandon et al. 2004; Forester & Townsend 2004; de Lange et al. 2009). It most frequently displays an epiphytic lifestyle, perched amongst nest epiphytes in the canopies of emergent or canopy trees. Terrestrial and rupestral lifestyles are less frequent, especially on mainland New Zealand, but are common on several offshore islands. *Pittosporum kirkii* is primarily found in upper lowland and lower montane ecosystems, which are subject to extreme weather variations; including significant periods of drought in the canopy microhabitat (Lüttge 1989; Benzing 2004; Moore 2008). *Pittosporum kirkii* possesses xeromorphic adaptations and physiological responses to survive in these extreme environmental conditions (Oliver 1930; Dawson 1986a).

Pittosporum kirkii was the last of four endemic epiphytic shrubs to be discovered and described, and to date little has been published on the biology and ecology of this species. Thus, the primary goal of this research is to enhance the depauperate knowledge of *P. kirkii* populations. This is addressed by investigating the species autecology in key populations that encompass its known latitudinal extent. Further, the water relations under desiccation stress are investigated in comparison to epiphytic congener, *Pittosporum cornifolium*, as adaptations to drought are likely to be critical to the species' success as an epiphyte. The ultimate research goal is to inform essential conservation management, and facilitate the inclusion of *P. kirkii* into regional and local restoration strategies.

* Nomenclature follows NZPCN (2012).

1.2 Conservation biology and restoration ecology

The on-going impetus and requirement for ecological restoration and conservation of species in New Zealand has stemmed from the increasing knowledge of the devastating damage caused by introduced mammalian pests, and large scale forest clearance across the country (Saunders & Norton 2001; Norton 2009). Restoration ecology is a relatively new discipline, exponentially increasing in popularity since its inception in the early nineties (Hobbs & Norton 1996). Ecological restoration, the active component of restoration ecology, is described as the intervention and management to restore biotic communities of both animals and plants, and to restore the associated abiotic environment to fully functioning and sustainable ecosystems (Hobbs & Norton 1996). In parallel, conservation biology is an older discipline which focuses on preserving species or specific habitats, is intensely focused over a relatively short period of time to halt the loss of species or habitat, and does not often include a restorative or long term approach, nor involves large numbers of interested communities (Young 2000; Berkes 2004). Both disciplines are complementary, and elements of each are used in combination because the foundations of both recognise the detrimental impact that anthropogenic activities have had by altering the environment, and causing the extinction of native fauna and flora. These disciplines recognise the need for action in the face of the continual biodiversity loss (Young 2000), and in New Zealand they have become synonymous with the introduction, and subsequent attempts to eradicate invasive pests (Norton 2009).

1.3 Vascular epiphytes in New Zealand

Epiphytism is a highly specialised plant lifestyle (habit) that is present in every major plant division (Benzing 1990). An epiphyte is a plant with specialised adaptations to enable survival above ground. In New Zealand there are around 77 – 89 vascular species which often, or usually, adopt an epiphytic lifestyle (Robertson 1964; Dawson 1986a). The term epiphyte is derived from ‘epi’ meaning on, and ‘phyte’ meaning plant (Moffett 2001). Hence, by definition epiphytes are plants that use other plants for mechanical support (Laube & Zotz 2006), growing independently on a host (phorophyte) (Benzing 1990) in arboreal

(canopy) soil and out of other epiphytic species in the ramosphere (Moffett 2001). Epiphytes obtain nutrients from the air, rain, decomposing detritus, humus and leachate (Benzing 1990).

Vascular epiphytes have been categorised based on several criteria (Lüttge 1989). The primary classification is based on their relationship to their host (life history) (Figure 1.1), but they have also been classified by humidity and light preferences (Figure 1.2), the requirement and type of rooting medium, and the frequency of nutrient and water supply (continually or pulse) (Benzing 1987; Lüttge 1989; Benzing 1990).

Life history categorisation is widely used in autecological vascular epiphyte research. Obligate or 'true' epiphytes primarily live in canopies and do not often grow in terrestrial or rupestral habitats (Benzing 2004). Obligate epiphytes can be classed as either hemi-epiphytes or holo-epiphytes. Holo-epiphytes carry out their entire life cycle on a host (Schimper 1903; Benzing 1990), and hemi-epiphytes live half their life as true epiphytes and the other half as a terrestrial plant (Putz & Holbrook 1986; Holbrook & Putz 1996; Nieder et al. 2001). Hemi-epiphytes are further divided into primary and secondary, then into strangler and non-strangler categories. Secondary hemi-epiphytes are not present in New Zealand forests (Bryan 2011). Facultative epiphytes can be epiphytic, terrestrial, or rupestral interchangeably, when favourable growing conditions within, and beneath the canopy converge (Dawson & Sneddon 1969; Benzing 1990). Occasional and ephemeral epiphytes are vascular epiphytes that are most commonly found growing in terrestrial or rupestral habitats. Occasional epiphytes are those that survive to reproductive maturity on a host, while ephemeral (accidental) epiphytes do not survive past the seedling stage (Oliver 1930; Dawson 1986a). Epiphytic parasites have also been included by several researchers (Figure 1.1). These species typically have chlorophyll, are not dependent on the host for nutrients, but rather for a source of water via haustoria (Dawson 1986a).

Classifications based on light and humidity separate vascular epiphytes into sun epiphytes which grow in exposed canopy locations and shade tolerant epiphytes which grow in more sheltered canopy locations. Sun epiphytes are further

differentiated into mat, nest and shrub epiphytes, reflecting their different growth forms (Oliver 1930; Dawson 1986; Lüttge 1989; Benzing 1990) (Figure 1.2).

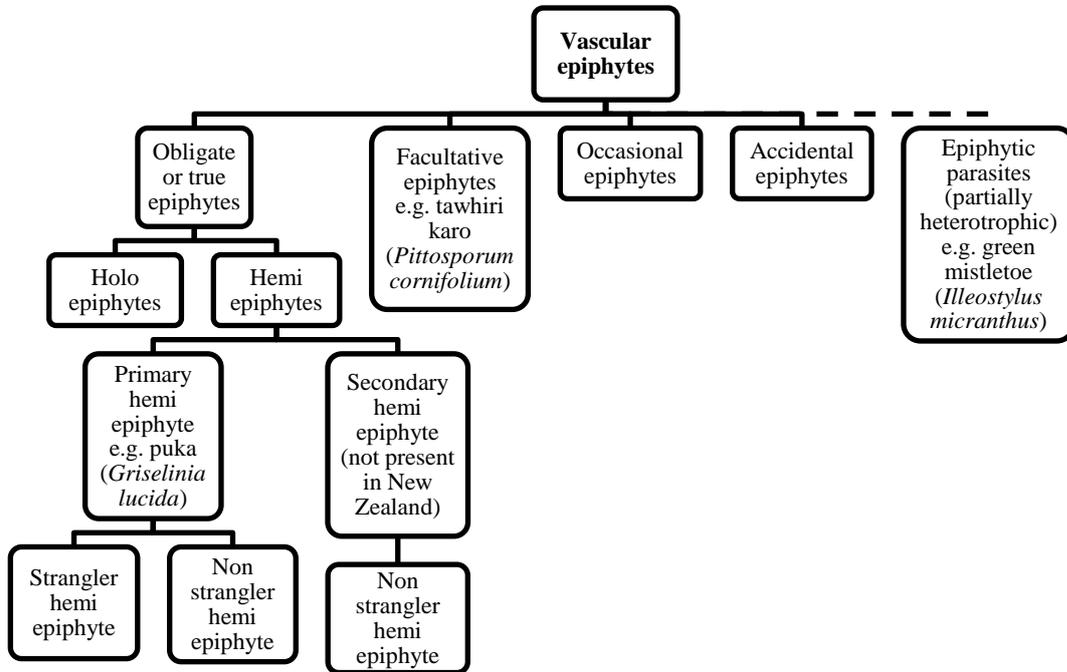


Figure 1.1 Vascular epiphyte life history classification based upon epiphyte-host relationship. Adapted from Bryan (2011), with modifications from Bannister et al. (1999); Benzing (1987,1990); Clarkson et al. (*In press*); Dawson (1986a); Holbrook & Putz (1996); Lüttge 1989; Oliver (1930); Putz & Holbrook (1986). The dashed line represents the conflicting views concerning the inclusion of epiphytic parasites in classification schemes.

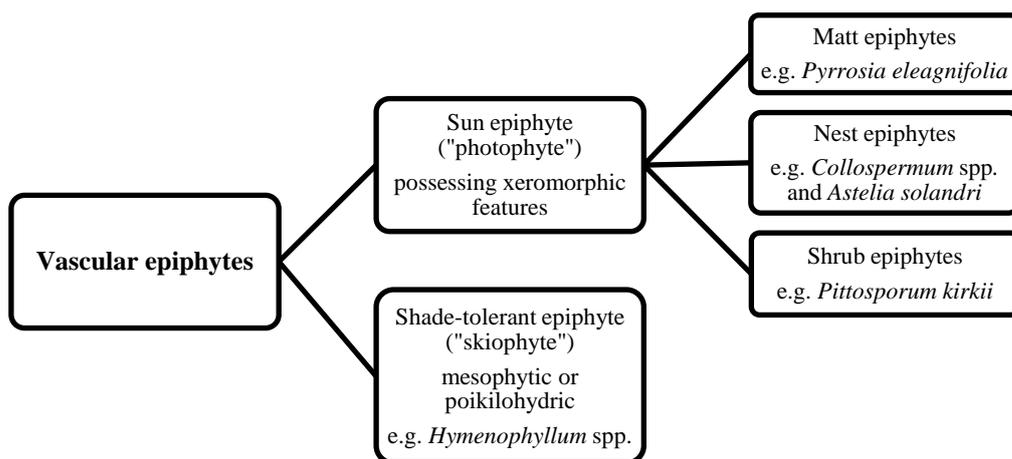


Figure 1.2 Vascular epiphyte Light and humidity classification compiled from Light and humidity classification compiled from Benzing (1990); Dawson (1986b); Lüttge (1989); Oliver (1930).

Vascular epiphytes are a conspicuous component in tropical and temperate New Zealand rainforests, representing ten percent of global vascular plant species (Kress 1986). However, the bulk of literature stems from research undertaken in tropical rainforests. Consequently, the current body of knowledge about epiphyte ecology and the role that epiphytes play in forest ecosystems is largely limited to the tropical rainforests (Hofstede et al. 2001; Zotz 2005). Resultantly, little is known about epiphytic communities in temperate rainforests and even less is known about the role they have in ecosystem processes.

Studies have shown that the biomass of epiphytes (epiphyte loads) can exceed that of host tree foliage in tropical rainforests by up to 44 tonnes per hectare (Hofstede et al. 1993) and that, in temperate and tropical rainforest, vascular epiphytes make up of 25 – 50 percent of vascular flora (Gentry & Dodson 1987; Nieder et al. 2001). Comparatively, in temperate New Zealand rainforests, 2.9 percent of the vascular flora is represented by epiphytes (*cf.* Oliver 1930). The percent held by non-vascular epiphytes (mosses, liverworts and lichens) is unknown, but is likely to constitute the greatest element of total epiphyte richness in New Zealand forests and is thus crucial to the ecological succession of vascular epiphytes (Oliver 1930; Affeld et al. 2008). The biomass that vascular and non-vascular epiphytes hold highlights the significance they have in forest ecosystems (Benzing 1990). Despite this, the importance vascular epiphytes have in ecological processes and the ecological relationships involved have rarely been studied.

Epiphyte ecologists agree that the role played by water, humidity and nutrients is vital to the distribution and diversity of epiphytes on both a global and local scale, within both temperate and tropical rainforests (Scott 1970; Hietz 1999; Laube & Zotz 2003). Epiphytes divorced from terrestrial soil are limited by the availability and irregular supply of water and nutrients (Benzing 1990; Moore 2008). These restrictions are thought to be the main cause of slow growth rates that epiphytes commonly exhibit (Benzing 1990; Heitz 1999; Nieder et al. 2001; Zotz & Hietz 2001; Zotz 2005; Burns 2008). Further, these slow growth rates seem to be related to host preference and diversity patterns; older, larger trees are known to be rich in epiphyte species (Oliver 1930; Burns & Dawson 2005; Díaz et al. 2010). On the other hand, epiphytic intra- and interspecific competition are equally relevant and

also an understudied topic (Hietz & Hietz-Seifert 1995c). Hence, it is crucial to investigate all relevant interactions to understand how epiphyte communities are structured and contribute to the function of forest ecosystems.

The significance of epiphytic biomass in tropical and temperate forests has been confirmed by earlier distribution studies (Oliver 1930; Kress 1986; Benzing 1990; Hofstede et al. 1993; Zotz 2005). Recent studies have recognised that epiphytic biomass influences the microclimate in the canopy and is important to the ecological function of forests (Freiberg 2001; Díaz et al. 2010). Epiphytic biomass in the canopy is integral to nutrient and water cycles and plays an important role in photosynthetic productivity in both tropical rainforests and temperate New Zealand forests (Nadkarni 1984a, b; Hofstede et al. 1993; Hofstede et al. 2001; Alvarenga et al. 2010). These studies report that the biomass of vascular epiphytes is important in procuring nutrient and water over a long period of time, resulting from physiological adaptations to conserve water and nutrients in the often drought stressed ramosphere (Oliver 1930; Freiberg 1996b). Therefore, in order to understand temperate rainforest ecosystems, the role epiphytes play in ecosystem function and processes must be further investigated (Gentry & Dodson 1987; Díaz et al. 2010). Moreover, vascular nest or tank epiphytes (e.g. *Collosporum* species) are vital elements in the forest food chain, through providing a food source and habitat for invertebrates and vertebrates in the canopy (Dawson & Sneddon 1969; Zotz 1997b; Nadkarni et al. 2004; Yanoviak 2006; Krömer et al. 2007; Affeld et al. 2009; Díaz et al. 2012).

1.4 *Pittosporum kirkii*

The type locality of *Pittosporum kirkii* (Kirk's kōhūhū, thick-leaved kohukohu) is Great Barrier Island (New Zealand). This species is one of four endemic shrubs that are commonly epiphytic throughout the country (Kirk 1869; Oliver 1930; Dawson 1986a). It was the last epiphytic shrub to be officially discovered and described by Thomas Kirk (Kirk 1869, 1871). *Griselinia lucida*, the most conspicuous epiphytic shrub was the first, described in 1776 as *Scopolia lucida* (Allan 1961). Widespread congener *P. cornifolium* was described in 1832

(Hooker 1832), followed by, with several name changes, *Brachyglottis kirkii* var. *kirkii* in 1839 (Allan 1961).

Pittosporum kirkii is distinct from other members of the genus *Pittosporum* in New Zealand because of stout reddish-purple branchlets and petioles, and thick coriaceous leaves which are alternate, crowded, or whorled. Flowers are umbels, yellow to yellow-pink in colour, and capsules are notably larger than other New Zealand members of *Pittosporum*, being up to 4 cm long and 2.5 cm wide (Poole & Adams 1994) (Figure 1.3). Similar to other *Pittosporum*, capsules dehisce to reveal seeds in viscid fluid (Poole & Adams 1994). *Pittosporum kirkii* is predominantly epiphytic. However, terrestrial and rupestral individuals have been recorded commonly in open sites with podzolised kauri soil, well drained volcanic soil and on rocky outcrops, such as those found on Mount Hobson (Great Barrier Island) and on ridges of the Coromandel range (Kirk 1869; Cheeseman et al. 1914; Oliver 1930; Young 2010). It is most frequently found in primary forest, growing amongst epiphytic nests (perching lilies) consisting of *Astelia solandri* and *Collospermum hastatum* and, at higher altitudes (above 300 m a.s.l), with *Collospermum microspermum* (Oliver 1930). It occupies a narrow geographical range compared to widespread species such as rimu (*Dacrydium cupressinum*) and hemi-epiphytic shrub puka (*Griselinia lucida*). This range extends from Puketutu near Mangonui in Northland and the Matemateaonga Range of inland Taranaki, including offshore islands; Aotea/Great Barrier Island and Hauturu/Little Barrier Island. Within this range, it is restricted to upper lowland to lower montane old-growth ecosystems.

Pittosporum kirkii is listed as in decline and is nowhere common throughout its range (de Lange et al. 2009; Young 2010). It has been anecdotally reported that herbivory by the introduced brushtail possum (*Trichosurus vulpecular*) and forest clearance have led to the decline of *P. kirkii* (Brandon et al. 2004; Forester & Townsend 2004; Waitakere Threatened Species Management Policy 2009). However, beyond these anecdotal reports no evidence has been presented in the scientific literature. Forest clearance has undoubtedly removed habitat occupied historically by *P. kirkii*. However, because this species is mainly found in the montane bioclimatic zones, the majority of its habitat may still be intact as most

of the uplands of New Zealand are in land reserves (Prof. B. D. Clarkson, pers. comm. The University of Waikato 2012). This issue is further compounded by its data poor status (de Lange et al. 2009), as very little is known about its autecology, or, the extent of browsing by introduced pests.



Figure 1.3 *Pittosporum kirkii*. A: three-flower umbel, yellow corolla tube with white calyx, Purangi, Taranaki (Photo: C. Ogle). B: three metre (in height) male terrestrial individual growing in podzolised kauri soil directly beneath epiphytic individuals, Waitakere Ranges (Photo: S. Edwards). C: female epiphytic individual (capsules visible) growing amongst a 'nest' epiphyte, *Collosporum microspermum* and a moss clump, Erua Forest (Photo: C.L Bryan). D: rupestral individual growing on a rhyolitic rocky outcrop, Windy Canyon, Great Barrier Island (Photo: R. Thomson).

1.5 Study sites

Population study sites were chosen to encompass the known latitudinal range of *P. kirkii* and to enable comprehensive environmental and geographical analysis. Potential study sites were chosen using information gathered from botanical experts and herbarium records: Allan herbarium (CHR), Auckland herbarium (AK), New Zealand Forest Research Institute herbarium (NZFRI), Te Papa herbarium (WELT) and The University of Waikato herbarium (WAIK). Relevant reviews of local floras and ecological reports (published and un-published) were also utilised (e.g. newsletters from botanical societies). Due to the restrictive and time consuming nature of tree climbing, information on individuals was recorded by ground observation and, depending on lifestyle, either via binocular inspection or direct observation. Collection from epiphytic individuals was aided by a slingshot (Daisy B52).

Study sites surveyed were located at Erua Forest (near the known southern latitudinal limit), Mount Hobson (offshore island population), Mount Taranaki, Waipoua Kauri Forest (near the known northern latitudinal limit), and Waitakere Ranges (Figure 1.4). Table 1.1 highlights the number of individuals recorded in each population.

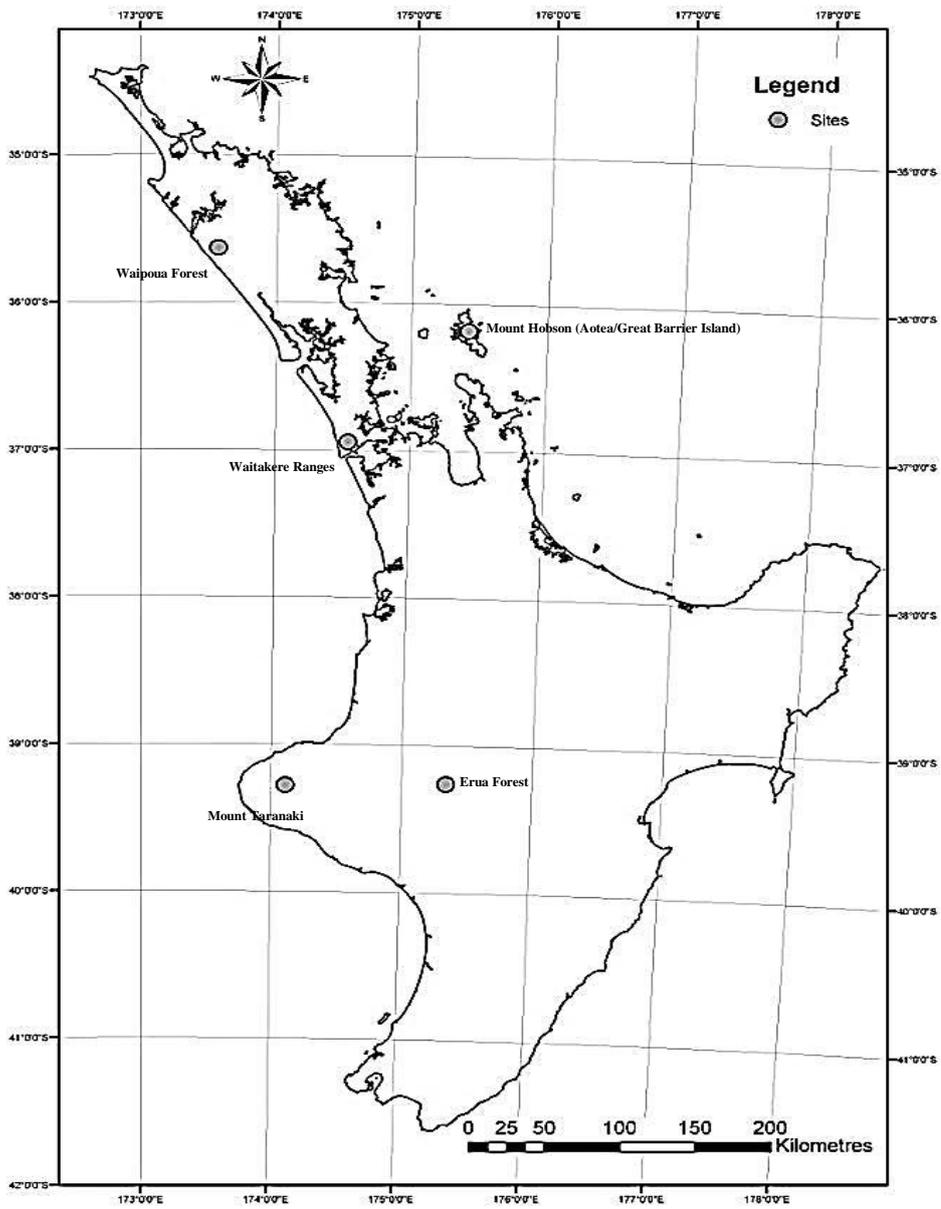


Figure 1.4 Location of the five *Pittosporum kirkii* populations (study sites) surveyed in this research.

Table 1.1 *Pittosporum kirkii* populations surveyed; four mainland populations and an offshore island population (Mount Hobson, Great Barrier Island).

Population	Region	District	Number of individuals recorded
Erua Forest	Tongariro	Tongariro	44
Mount Hobson	Coromandel	Great Barrier	56
Mount Taranaki	Egmont	Egmont	28
Waipoua Kauri Forest	Western Northland	Tutamoe	30
Waitakere Ranges	Auckland	Waitakere	23

1.5.1 Erua Forest

Erua Forest Conservation Area (hereafter, Erua Forest), covers 11,060 ha, has a highest point of 838 m a.s.l and represents the southern latitudinal limit of *P. kirkii*. Forty-four epiphytic individuals were recorded within 50 m of Erua Road, 578 – 78 m a.s.l (Figure 1.5 A; Table 1.1). One individual was recorded on a fallen host, two on standing dead snags and another on a fibrous wheki (*Dicksonia squarrosa*) trunk. All other individuals were associated with nest epiphytes; *Astelia solandri* and *Collospermum microspermum*.

The vegetation consists of scattered emergent northern rata (*Metrosideros robusta*) and rimu (*Dacrydium cupressinum*), reaching up to 30 m in height. The canopy predominantly consists of podocarp species: rimu, mountain totara (*Podocarpus cunninghamii*), miro (*Prumnopitys ferruginea*) and mataī (*P. taxifolia*). Beech (*Nothofagus*) species were notably absent. Other hardwood-broadleaved species present include tawa (*Beilschmiedia tawa*), hinau (*Elaeocarpus dentatus*), pokaka (*Elaeocarpus hookerianus*), pāhautea (*Libocedrus bidwillii*), mahoe (*Meliccytus ramiflorus*), toro (*Myrsine salicina*), and black maire (*Nestegis cunninghamii*). Fallen and dead standing snags of canopy species were prevalent, with regenerating hinau, mountain horopito (*Peudowintera colorata*) and kāmahi (*Weinmannia racemosa*) present throughout.

Erua Forest is marketed as a place to hunt (Conservation 2011), particularly for feral deer (all *Cervus* and *Odocoileus* species), feral goats (*Capra hircus*), and feral pigs (*Sus scrofa*) which are present in high densities. The brushtail possum, ship rats (*Rattus rattus*), and mustelids are also present and controlled via 1080 (sodium fluoroacetate) aerial drops.

1.5.2 Mount Hobson (Hirakimata)

Situated at the outer edge of the Hauraki Gulf, Aotea/Great Barrier Island (hereafter, Great Barrier Island) is New Zealand's largest offshore island (ca. 28,500 ha). Mount Hobson (Hirakimata) is the highest point (627m a.s.l) in a chain of steeply dissected mountains of volcanic origin that span the length of the island (McEwen 1987) (Figure 1.5). The vegetation has been extensively modified by Māori and European colonisation. Initial colonisation by Māori resulted in destruction of forests by fire, while later Europeans cleared forest for farming and timber. As a result, secondary vegetation predominates, with small pockets of original forest mostly restricted to lower montane areas such as Mount Hobson (McEwen 1987). Consequently, epiphyte searches were confined to Mount Hobson, as it is known that *P. kirkii* is a late successional epiphyte (*cf.* Oliver 1930) predominantly restricted to intact forest remnants and primary forest (Cheeseman 1906).

Mount Hobson was the largest population surveyed, with 56 recorded individuals (Table 1.1), consisting almost entirely of rupestral or terrestrial plants. These individuals were confined to regenerating kauri (*Agathis australis*), and podocarp forest with monoao (*Halocarpus kirkii*) and tāwari (*Ixerba brexioides*), remnant mature kauri forest, and on rhyolitic rocky outcrops between 360–600 m a.s.l. Great Barrier Island has remained relatively pest free, as no deer, feral goats, hedgehogs (*Erinaceus europaeus*), mustelids or brushtail possums reside there (Ogden et al. 2010). This may indicate why *P. kirkii* has remained relatively abundant there.

1.5.3 Mount Taranaki

Mount Taranaki (2518m a.s.l.), is an eroded andesitic volcano surrounded by a ring of lahar, debris flow and tephra deposits (Figure 1.5 C). Indigenous vegetation forms an altitudinal zonal sequence. Lowland tawa forest exists to 350–450 m a.s.l, above this beech species are noticeably absent and rimu with scattered northern rata and kāmahī, mahoe, wineberry (*Aristotelia serrata*), tree fuchsia (*Fuchsia excorticata*) and patē (*Schefflera digitata*) are present to 760 m a.s.l, where montane forest begins (Clarkson 1986). Between 760 m a.s.l to the tree line at 1066 m a.s.l, kāmahī, mountain totara and pāhautea dominate, above this subalpine shrub and moss-herbfields dominate till the barren alpine zone (Clarkson 1986).

Twenty-eight individuals (Table 1.1) were recorded in forest dominated by emergent rimu and northern rata reaching up to 25 m, with a canopy and understorey of rimu, kahikatea (*Dacrycarpus dacrydioides*), mahoe, miro, black maire and *Raukaua edgerleyi* between 564–463 m a.s.l, and in forest dominated by mountain totara, kāmahī, miro and toro reaching up to 13 m in height between 638–665 m a.s.l. All individuals were epiphytic: four were present on a fallen host; six were growing from moss, with all others associated with nest epiphytes.

Pests such as the brushtail possum, feral deer, feral goats, mustelids, and the European rabbit (*Oryctolagus cuniculus*) are actively hunted and controlled to different degrees (Taranaki Regional Council 2009).

1.5.4 Waipoua Forest

The Waipoua Forest Sanctuary and Waipoua Kauri Management and Research Area (hereafter, Waipoua Forest) cover approximately 13,000 hectares (Figure 1.5 D). Waipoua Forest was New Zealand's first forest to be designated as a sanctuary, and, as a result, large tracts of indigenous forest remain intact. Most well-known for containing large remnants of dense kauri, Waipoua Forest also contains large tracks of taraire (*Beilschmiedia tarairi*) dominated forest, and high altitude rimu-tōwai (*Weinmannia silvicola*)-tāwari forest with swamp maire (*Syzygium maire*) (McEwen 1987).

Thirty individuals were recorded in two main forest types (306 – 450m a.s.l) (Table 1.1); kauri dominant with tāwheowheo (*Quintinia serrata*), tāwari, cutty grass/māpere (*Gahnia xanthocarpa*) and mountain totara, and in forest dominated by rimu-taraire-tōwai with *Ackama rosifolia*, tree ferns and emergent northern rata reaching up to 30 metres. Two individuals were terrestrial beneath the canopy of 30 – 40 metre tall kauri; two others were on a dead standing kauri snag, while the remaining individuals were associated with nest epiphytes. Pig eradication within Waipoua Forest is limited, as evident by pig rooting (*cf.* Young 2011) under terrestrial individuals in kauri dominant forest, thus possibly destroying terrestrial seedlings. However, brushtail possums are actively controlled by 1080 (Thomas 1995).

1.5.5 Waitakere Ranges

The Waitakere Ranges covers 16,000 ha of native forest (Esler 1983), and is predominantly over 300 m a.s.l, with the highest point being Te Toiokawharu at 474 m a.s.l (McEwen 1987) (Figure 1.5 E). The vast majority of original forest has been logged, and only small patches of un-logged and lightly logged areas remain (Esler 1983). Hence, the forest generally consists of cut-over vegetation dominated by secondary growth forest species (McEwen 1987); kānuka (*Kunzea ericoides* var. *ericoides*) and mānuka (*Leptospermum scoparium.*), with regenerating, and remnant old-growth, kauri and podocarp species.

Twenty-one individuals were recorded across the ranges between 421–421 m a.s.l (Table 1.1). One individual was recorded on a fallen northern rata alongside nīkau (*Rhopalostylis sapida*), kiekie (*Freycinetia banksii*), and rewarewa (*Knightia excelsa*) in regenerating podocarp forest. Two others were recorded growing terrestrially amongst *F. banksii* in *K. ericoides* var. *ericoides* and rimu secondary growth forest. A further three were terrestrial, growing directly beneath an epiphytic female on a 30 m tall kauri. All other individuals were associated with nest epiphytes in unlogged and lightly logged areas, or on canopy and emergent remnants in logged and secondary growth forest. A range of pests are controlled,

including mustelids and the brushtail possum, by 1080 and trapping methods
(Waitakere Threatened Species Management Policy 2009)

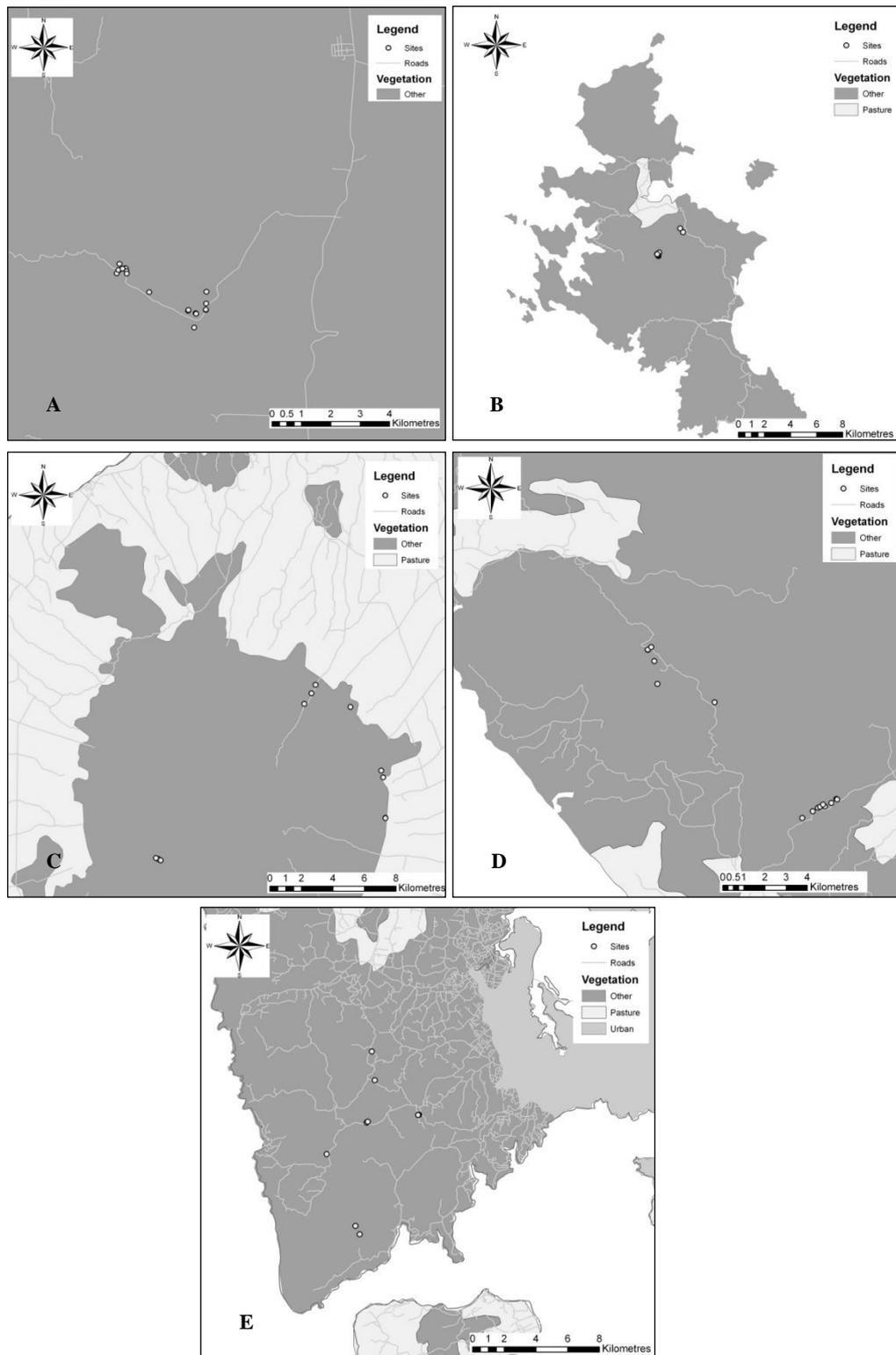


Figure 1.5 The five *Pittosporum kirkii* populations showing surveyed points. A: Erua Forest. B: Mount Hobson, Great Barrier Island. C: Mount Taranaki. D: Waipoua Forest. E: Waitakere Ranges.

1.6 Research objectives and questions

The objectives of this research were to enhance the depauperate knowledge of the understudied epiphytic shrub, *Pittosporum kirkii*, focusing on: 1) quantitative autecological research across its known geographical range; 2) quantifying the vegetation types that *P. kirkii* inhabits, including associated vascular epiphytes and vine species and 3) the water relations in comparison to epiphytic congener *P. cornifolium* under desiccation stress.

These objectives are addressed with the following research questions:

1. What are the autecological characteristics of *P. kirkii*, and what is the current ecological status of *P. kirkii* populations?
2. Can autecological data sources be utilised for predictive environmental modelling?
3. What is the habitat and host preferences of *P. kirkii* and what vascular epiphytes (and vines) are found in association with *P. kirkii*?
4. How can autecological information inform conservation management and restoration opportunities and strategies for *P. kirkii* and vascular epiphytes?
5. What are the physiological responses and stress strategies utilised by *P. kirkii* under desiccation stress, and how does this compare to the epiphytic congener *P. cornifolium*?

1.7 Thesis structure

The results of the research are presented in five chapters:

Chapter One: Introduction

This chapter provides background information on conservation biology and restoration ecology with a specific focus on vascular epiphytes. A literature review on the state of vascular epiphyte research in New Zealand is presented, before introducing the endemic shrub epiphyte to be researched, *Pittosporum kirkii*. Five study sites (populations) are outlined. It concludes with research objectives, questions and a thesis structure.

Chapter Two: Autecology of *Pittosporum kirkii*

This chapter presents the autecology based primarily on ecological surveys across five populations. National data sets, including herbaria and National Vegetation Survey Databank (NVS) records, are assessed with ecological survey data to evaluate the ecological status of each population. Species specific analysis, population structure, habitat preferences (including associated vascular epiphyte and vine species), phenology and distribution are described and analysed. Conservation and restoration implications are discussed.

Chapter Three: Water relations of *Pittosporum kirkii* and epiphytic congener *Pittosporum cornifolium* under desiccation stress

This chapter reviews the literature on morphological features and physiological responses and strategies in periods of desiccation stress, with specific reference to vascular epiphytes. The results of a drought experiment are presented, analysing the water relations of *P. kirkii* in comparison to epiphytic congener *P. cornifolium* under three levels of desiccation stress. The desiccation stress strategy and morphological features that each *Pittosporum* species exhibits are outlined and discussed.

Chapter Four: Biological Flora of New Zealand. *Pittosporum kirkii*, Kirk's kōhūhū, thick-leaved kohukohu

This chapter assembles, analyses, and presents the results from previous research and the present study. It includes a comprehensive evaluation of published and

non-published literature. The format follows the New Zealand Biological Flora Series (e.g. Bryan et al. 2011) in order to submit this research for future publication.

Chapter Five: Synthesis

This chapter summarises key findings and proposes future research directions. Conservation management requirements, and recommendations for inclusion into restoration strategies are outlined.

Chapter two: Autecology of *Pittosporum kirkii*

2.1 Introduction

Chapter two investigates the autecology and the current ecological status of *P. kirkii* populations across its known geographical range. *Pittosporum kirkii* is one of four shrubs endemic to New Zealand, which commonly inhabits an epiphytic lifestyle (Dawson & Sneddon 1969). This species was first listed in the 2004 threatened plant list as in serious decline, with the qualifiers data poor and conservation dependent (de Lange et al. 2004); this threat status has changed to in decline and data poor in the most recent classification (de Lange et al. 2009). It has been suggested that forest clearance and the herbivorous brushtail possum (*Trichosurus vulpecula*) are the main decline agents (Brandon et al. 2004; Forester & Townsend 2004; Taranaki Regional Council 2009). Brushtail possums have been recorded consuming young shoots, leaves and flowers of other *Pittosporum* species in New Zealand (Ridley 1930; Ecroyd 1994; Townsend 1999; de Lange et al. 2011) but only anecdotal records of browsing of *P. kirkii* have been found. This is compounded by a paucity of autecological publications since the species was discovered by Thomas Kirk in 1869. To address this knowledge gap, field surveys were carried out at five populations, including an offshore island population, and the results were assembled and collated with herbaria records, National Vegetation Survey (NVS) databank records, and reliable published and unpublished botanical records. The goal of this chapter is to rectify our limited quantitative and qualitative autecological knowledge, so as to accurately inform essential conservation management and enable inclusions of the species in ecological restoration projects.

Autecology is the biology and ecology of a single species, and its inter-relationship with its abiotic environment at one population, or across a number of populations (Daubenmire 1974). The focus of autecological studies is usually at the population level, with some authors treating autecology as an archaic term, preferring the more widely used term of population ecology. However, autecology is a useful term because it is somewhat broader in scope. Autecological studies are significant in the conservation management and restoration of threatened species. In order to successfully conserve and restore threatened species it is important to

gain understanding on myriad factors causing their threatened status, so as to focus conservation practices and to better place them with suitable restoration programmes (Primack 2008). In New Zealand only a limited number of nationally iconic plant species have undergone extensive autecological assessment. These species include: kauri (Stewart & Beveridge 2010), rimu (Norton et al. 1988), kahikatea (Wardle 1974), kōwhai ngutukākā (*Clianthus puniceus*) (Shaw & Burns 1997), *Olearia hectorii* (Rogers 1996), *Pittosporum obcordatum* (Clarkson & Clarkson 1994) and *Pittosporum patulum* (Rogers & Walker 2005). Recent autecological publications have focussed on the epiphytic shrubs, *Pittosporum cornifolium* (Clarkson et al. *In press*) and hemi-epiphytic shrub, puka (*Griselinia lucida*) (Bryan et al. 2011).

Five population study sites were chosen to encompass the known latitudinal range to enable comprehensive environmental and geographical analysis of *P. kirkii*. These sites included offshore island population, Mount Hobson (Great Barrier Island) and four North Island populations spanning from Waipoua Forest (near the known northern limit), Waitakere Ranges, Mount Taranaki and Erua Forest (near the known southern limit). The aims of this research were to quantify the autecological characteristics of *P. kirkii* and specifically to 1) assess the current ecological status (impact of mammalian herbivores, demography, and dieback) of populations across the known latitudinal range, 2) utilise distribution data to undertake predictive distributional and environmental modelling, 3) characterise habitat and host preferences and the vascular epiphytes species found in association, and 4) utilise autecological information to inform a species specific management and restoration plan.

This research will address the following hypotheses, 1) the narrow niche requirements of *P. kirkii* coupled with a declining ecological status are detrimentally impacting on abundance and regeneration at mainland populations, but not in possum-free populations, 2) due to the relative inaccessibility of the epiphytic lifestyle, populations are overlooked rather than in decline and 3) morphological differences exist across *P. kirkii* latitudinal range and between mainland and offshore island populations. The final intended outcome was to assemble and analyse existing research with new information gathered from the

present research in order to submit a publication in the New Zealand Biological Flora Series. This will address the paucity of comprehensive biological floras published on New Zealand species, as currently only 12 floras have been published, including the recent publication on puka (*Griselinia lucida*) (Bryan et al. 2011).

2.2 Methods

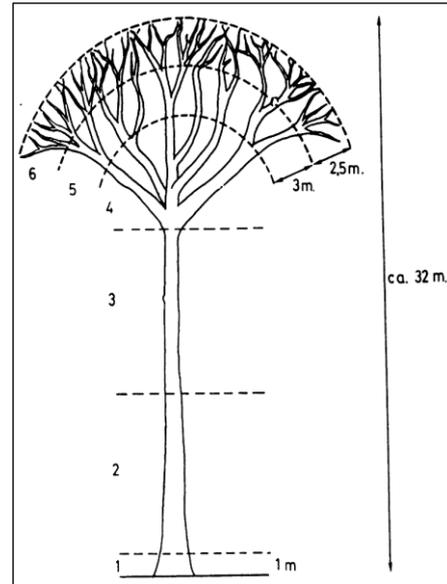
2.2.1 Ecological data collection

Between April and November 2011, field surveys were carried out at five populations as described in Chapter one; Erua Forest, Mount Hobson (Aotea/Great Barrier Island); Mount Taranaki, Waitakere Ranges and Waipoua Forest. The five field sites cover the known distributional range of *P. kirkii*, representing four mainland populations and one offshore island population (Mount Hobson). 181 individuals were comprehensively recorded, and the methodology of this surveying is outlined below.

Epiphytic and rupestral individuals were located using binoculars (10 x 50mm Leupold® Green Ring™ Olympic Series). It was intended that a minimum of 30 individuals were collected from each population, however this was not possible at every population due to low numbers, and highly dispersed individuals in the Waitakere Ranges and Mount Taranaki populations.

To assess population characteristics, habitat requirements and epiphytic associates the following survey methodology were undertaken. For terrestrial and rupestral individuals, lifestyle type, size (length by width), and reproductive stage (presence or absence of capsules, stage of capsule development and flowering) were recorded. In surveying epiphytic individuals the variables above were recorded, in addition to; the height on the host (metres) species, growing substrate, and host zone occupancy, following Johansson Zones (Johansson 1974) (Figure 2.1). Host DBH (diameter at breast height; in centimetres), height (metres) and bark type were also recorded. All associated vascular epiphytes and vine species on each host were recorded along with their host zone occupancy according to the same criteria as above.

For each individual the precise location was recorded via global positioning system (GPS) calibrated to the New Zealand map grid projection. The foliar browse index (Payton et al. 1999) was utilised to assess damage done by herbivorous pests and the degree of dieback on each individual. The surrounding habitat and vegetation type was categorised and tabulated.



Measurements of capsule and leaf morphology were undertaken on specimens collected from each population to establish if there were phenotypic differences between populations. Voucher specimens collected were cross checked, and deposited in the Waikato Herbarium (WAIK).

Figure 2.1 Schematic of height zones. Zones adapted to varying individual host height. 1: base up, 2: lower trunk, 3: upper trunk, 4: lower canopy, forking zone, 5: middle canopy, 6: upper canopy. Modified from Johansson (1974) and ter Steege & Cornelissen (1989)

2.2.2 Supplementary data sets

One-hundred and seventy six *Pittosporum kirkii* records were obtained from the Allan Herbarium (NZCHR), Auckland Museum Herbarium (AK), Forest Research Institute Herbarium (NZFRI), Te Papa Herbarium (WELT) and Waikato University Herbarium (WAIK). Measurements of capsule and leaf morphology and phenology information were taken from AK, NZCHR and WAIK samples.

A further 78 records were obtained from the National Vegetation Survey databank (NVS) and both published and unpublished records from field botanists. These data sets were used in conjunction with field survey data in the analysis of distribution, host species, lifespan, lifestyle, phenology data sets, and vegetation type classification.

2.2.3 Anatomy

Anatomical analysis of tissue layers in the leaf, root and stem of *P. kirkii* were carried out. Four adult individuals grown from seed sourced from epiphytic individuals in the Waitakere Ranges by Oratia Nursery (Auckland) were used. Transverse sections of leaves, roots and stems, were cut by hand and stained with toluidine blue. For the leaf transverse sections, four fully expanded leaves from four separate plants four years in age were chosen. Sections were first cut at the centre of the leaf, and then transverse sections across the midrib were cut.

The depth of each laminae tissue layer was measured via optical microscopy, and photographed using an attached digital microscope camera (Olympus DP70, Olympus America Inc., Melville, New York). Images were ‘stacked’ and processed through Auto-Montage (Syncroscopy©, Cambridge, England) to enhance the focus of the individual tissue layers. Each tissue layer in all three plant structures is classified and presented.

2.2.4 Capsule and leaf morphology

Capsules and leaves were measured from field samples ($n = 32$), and herbarium vouchers ($n = 38$) associated with relevant survey sites (also including Little Barrier Island) (see section 2.2.2). A minimum of ten full grown leaves were randomly selected from each plant, and leaf length and width were measured in millimetres and recorded in the field. However, this was not always possible due to the relative inaccessibility of epiphytic individuals. Epiphytic individuals were sampled via a non-destructive slingshot method (Díaz et al. 2012); a standard hand slingshot was utilised to collect and measure leaf samples. Observations on leaf shape were recorded.

2.3 Data analysis

2.3.1 Data sets and distribution maps

Supplementary data sets were analysed for their accuracy and comprehensiveness for combining with field survey data. A conservative selection approach was applied, and any information that was ambiguous or incomplete was not used. As

a result a limited number of records were available for use, and the sample sizes reported below vary for different data elements.

The GPS co-ordinates from field locations and supplementary data sets were converted to New Zealand map grid projection (NZMG) via Land information New Zealand (Land Information New Zealand 2011). These locations were superimposed on Land Environments of New Zealand (LENZ) environmental surfaces in ArcGIS™ and ArcView version 3.2 (Leathwick et al. 2003; Lehmann et al. 2003), and an appropriate selection of environmental variables was chosen. These variables were elevation/altitude (metres above sea level), mean annual solar radiation (megajoule per square metre, per day), mean annual temperature (degrees Celsius), mean minimum daily solar radiation (megajoule per square metre, per day), mean minimum daily temperature of the coldest month (degrees Celsius), mean October vapour pressure deficits at 0900 hours (kiloPascal) and total annual rainfall (millimetres). The summary statistics of these environmental variables were averaged, then tabulated.

A predicted environmental distribution map was created from the spatial expression of the minimum, maximum and mean of the environmental variables with ArcView version 3.2. An observed distribution map was created with esri™ ArcGIS™ version 9.31 with individual GPS points to compare with the predicted environmental distribution map of *P. kirkii*.

2.3.2 Population structure

Data required to determine the life stage of each *P. kirkii* individual ($n = 181$) was recorded at the five populations to assess population structure, and to analyse each population's ecological status. To assist the classification of life stage, the height and width of each *P. kirkii* individual were converted (multiplied) to a single cover value in square metres. According to size and reproductive stage, individuals were assigned a life stage. Reproductively mature female individuals were used as the baseline for the adult category; hence their size set the precedent for defining class size and thus, the life stage of individuals. Life stage size classes are as follows: seedling size class, individuals under 0.07 m² (reproductively

immature individuals); juvenile size class, individuals between .08 to 0.59 m²; adult size class, individuals over 0.6 m² in size. Size classes and the associated life stage were not completely distinct, as four juvenile size individuals were reproductively mature (adults).

2.3.3 Epiphytic assemblages

The frequency of occurrence of each associated species on *P. kirkii* hosts was combined across four populations, and the most common associated species in each surveyed population were analysed. The Mount Hobson (Great Barrier Island) population was omitted as only one host was recorded. The vertical distribution of the most common associated species in each occupancy zone (Johansson 1974), is presented and interpreted.

2.3.4 Anatomical and morphological analysis

A leaf transverse section is presented with each tissue layer labelled. This is followed by a table of mean laminae tissue depth which were assembled and analysed. Root and stem transverse sections with the distinct tissue layers are also presented and discussed.

Leaf and capsule measurements were compiled and combined from herbaria vouchers and leaves collected in field surveys. The mean width and length measurements of each capsule and leaf were recorded. Scatter graphs were analysed to ascertain distribution-related patterns. Correlations with altitude and latitude were investigated through statistical analysis with p-values presented for statistically significant results.

2.3.5 Statistical analysis

Descriptive statistics were primarily utilised to quantitatively describe, reveal and discuss autecological data. Standard error of the mean are presented where appropriate. When appropriate, Analysis of Variance (ANOVA) or General Linear Modelling with post-hoc Tukey's Honestly Significant Difference test were undertaken to analyse autecological data. The conditions of normality were

assessed with the Shapiro-Wilk test, followed by verifying the assumption of homogeneity of variance with the Levene's test. When sample sizes were over 30 the assumptions of homogeneity were ignored, as data sets met the central limit theorem (Rosenblatt 1956). Hence, data sets with less than 30 samples were analysed using non-parametric Kruskal-Wallis ANOVA. Correlations between variables were investigated using linear regression and Pearson correlation coefficients. The null hypothesis was rejected and statistically significant results were reported when the p-value was significant (<0.05) following Royal Society of New Zealand (2011) publishing guidelines.

2.4 Results

2.4.1 Distribution

Field surveys data sets ($n = 80$), herbarium records ($n = 81$), NVS records ($n = 37$) and reliable published and un-published botanical records ($n = 70$), provided a total of 268 individual grid reference points (GPS locations) that were compiled to produce a presence-only observed distribution map (Figure 2.2). Herbarium records were the least informative data source, with only 52 percent of requested records suitable for full analysis, primarily due to lack of a map reference, and inadequate location details.

Pittosporum kirkii has a restricted environmental and geographical range, occupying upper lowland and lower montane forest near Mangonui in Northland (ca. $35^{\circ}01''\text{S}$) to Raetihi, south of Ohakune, in the central North Island (ca. $39^{\circ}38''\text{S}$) (Figure 2.2). It is also notably abundant in montane bioclimatic zones on the mountainous offshore islands of Great Barrier and Little Barrier. There were no verified records (current or historic) for the South Island. The published record of *P. kirkii* at Karamea (Laing & Blackwell 1907) is probably a mistaken identification of *P. cornifolium* (D.A. Norton, pers. comm. The University of Canterbury 2011).

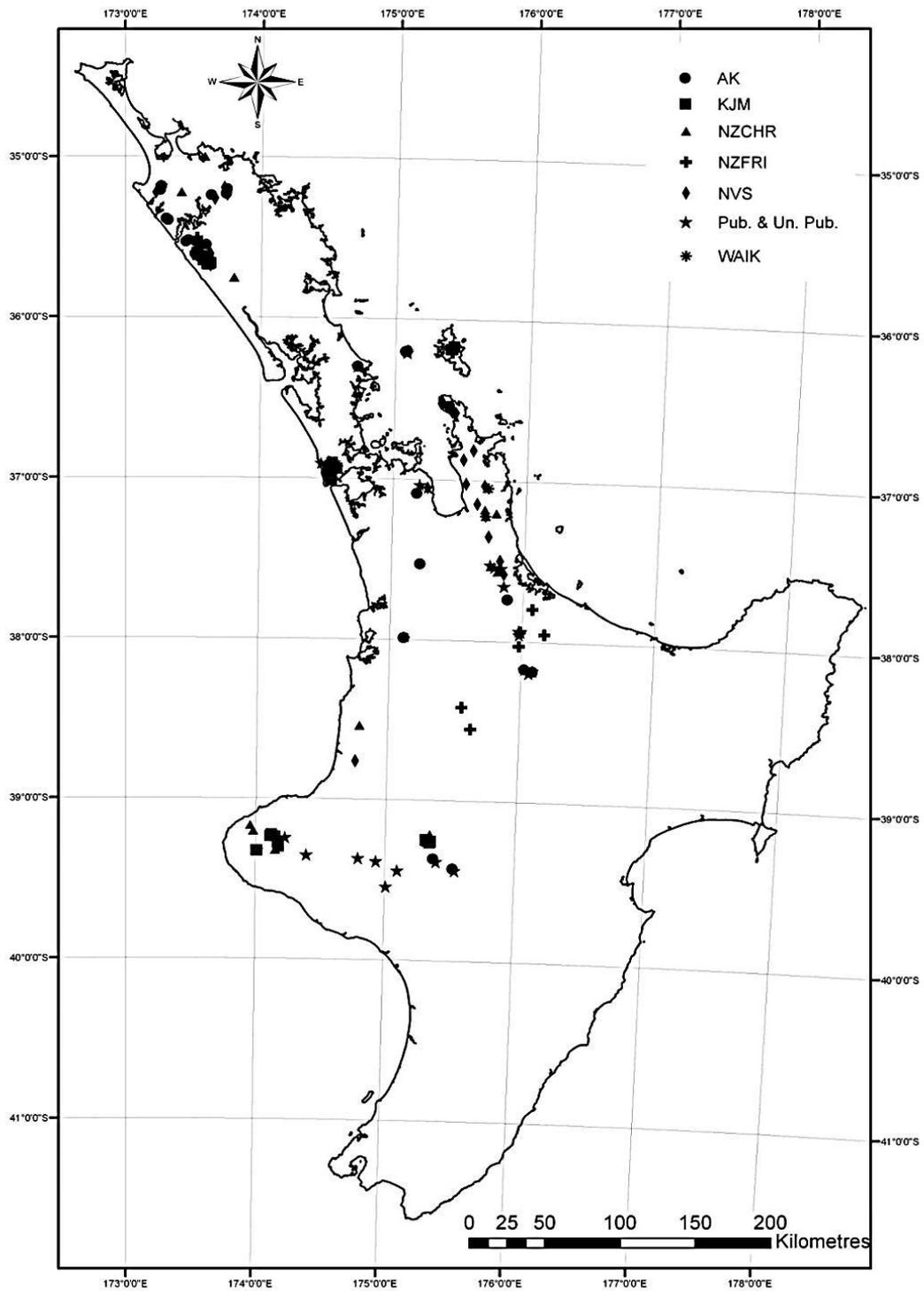


Figure 2.2 Observed distribution of *Pittosporum kirkii* based on GPS plot locations ($n = 268$) obtained from field survey results (KJM), Auckland herbarium (AK), Christchurch herbarium (NZCHR), New Zealand Forest Research Institute (NZFRI), published and unpublished records (Pub. & Un. Pub.) and Waikato herbarium (WAIK).

2.4.2 Predicted environmental distribution

The predicted environmental distribution of *P. kirkii* is presented in Figure 2.3. The summary statistics for the environmental variables utilised are presented in Table 2.1. Mean elevation (altitude) was 473 m a.s.l (± 11), with a wide range from 50-1116 m a.s.l. Mean solar radiation was 14.8 kJ/m² per day (± 0.24) and ranged from 14.0-15.4 kJ/m² per day. The mean annual temperature across observed sites was 12 °C (± 0.09) and ranged from 7.8-15.6 °C. The mean minimum daily solar radiation in the coldest month (June) was 5.9 MJ/m²/day (± 0.04) and had a relatively narrow range of 4.8-6.6 MJ/m²/day, while the mean minimum daily temperature of the coldest month was 4.4 °C (± 0.13) and ranged from 0.3-8.2 °C. The mean vapour pressure deficits at 0900 hours in October were 0.29 kPa with a range of 0.15-0.39 kPa. Mean total annual rainfall was 2104.8 mm (± 25.4), and ranged from 1172-4432 mm.

The predicted environmental distribution indicated *P. kirkii* to be potentially present across most of the upper North Island, except for areas of lower elevation and lower temperatures. This is reflected by the predicted absence of *P. kirkii* from north of its current northern limit near Mangonui (Northland) around the Kaipara Harbour, the Hauraki plains, lowland-coastal areas of the Bay of Plenty, the lowland plains east of Lake Taupo and also from most of the lower North Island (Figure 2.3). However, the predicted absence across the east coast appears to be driven by high vapour pressure deficits (kPa) and low rainfall. The predicted environmental distribution of *P. kirkii* extended to the lower North Island and further south than its known distribution. These areas include higher altitude areas of the Ruahine and Ikawhenua ranges and also the southern area of the Aorangi Range (Wairarapa) (Figure 2.3). In the South Island the predicted environmental distribution is limited to north-west Tasman, across the Wakamarama and Burnett Ranges from around Cape Farewell to Anatori and sites across the Richmond and smaller Gondon Ranges in western Marlborough (Figure 2.3). Hence, in the South Island, low elevation and related environmental variables, lower solar radiation, low temperature and low rainfall appear to be the main limiting factors (Table 2.1).

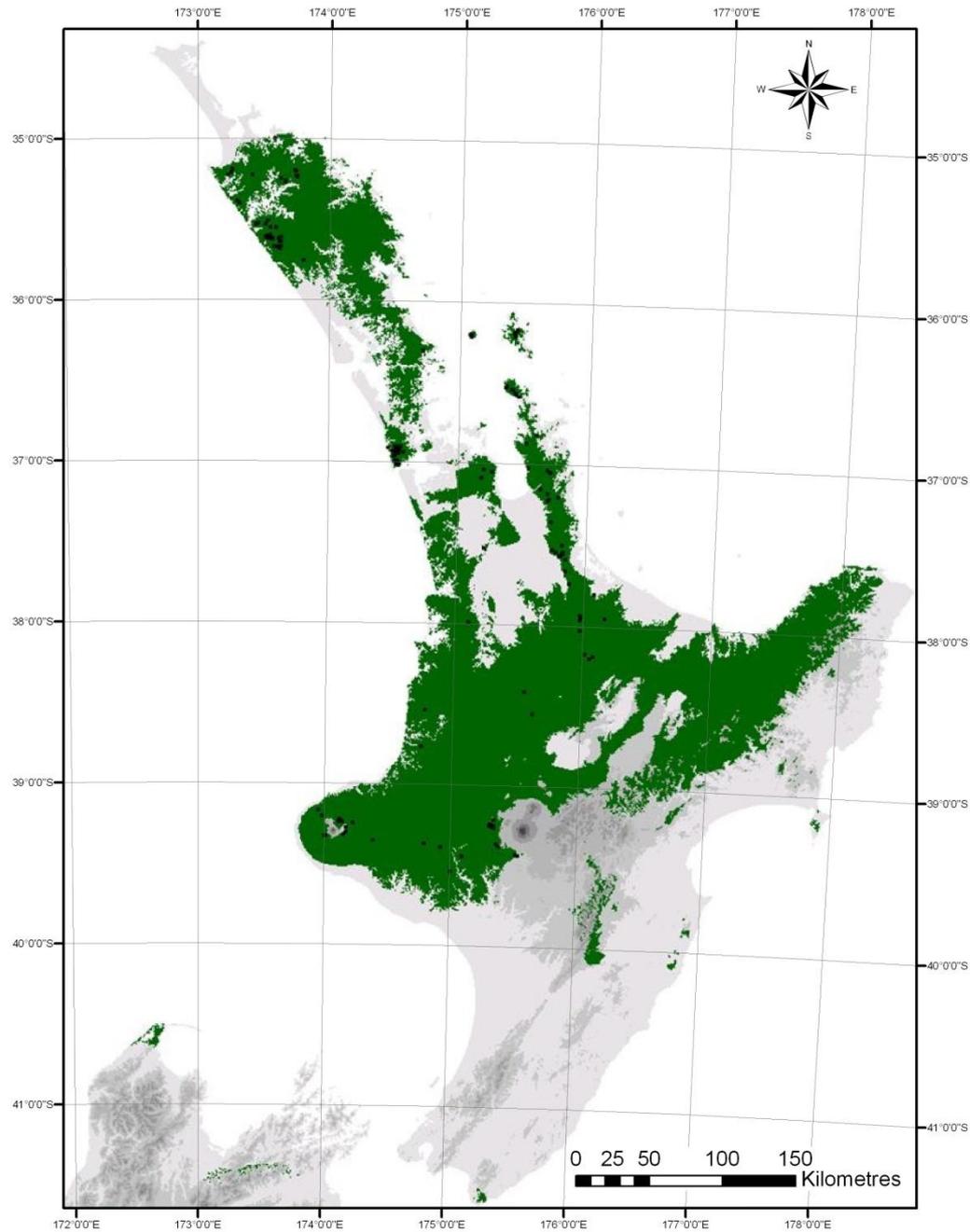


Figure 2.3 Predicted distribution map (environmental envelope) of *Pittosporum kirkii* produced from an ArcView and ArcGIS™ extrapolation of selected environmental variables for sites with *P. kirkii* ($n = 268$). Environmental variables chosen were: elevation; mean annual solar radiation (mas); mean annual temperature (mat); mean minimum daily solar radiation in June (Junes); mean minimum daily temperature of the coldest month (tmin); mean October vapour pressure deficits at 0900 hours (vpd); total annual rainfall (rain). Black points represent current records (on Figure 2.2), and the shaded green areas represent the predicted distribution.

Table 2.1 Summary statistics of key environmental variables produced from selected ArcView and ArcGIS™ extrapolation of current *Pittosporum kirkii* locations ($n = 268$). Environmental variables chosen were: elevation (altitude); mean annual solar radiation (mas); mean annual temperature (mat); mean minimum daily solar radiation in June (Junes); mean minimum daily temperature of the coldest month (tmin); mean October vapour pressure deficits at 0900 hours (kPa); total annual rainfall (rain).

	elevation (m a.s.l)	mas (kJ/m ² /day)	mat (°C)	Junes (MJ/m ² /day)	tmin (°C)	vpd (kPa)	rain (mm)
Mean	471.5	1.48	12	5.9	4.4	0.29	2104.8
Standard Error of Mean	11	0.2	0.09	0.04	0.1	0.0	25.4
Range	1066	1.4	7.8	2	8.4	0.24	3260
Minimum	50	1.4	7.8	4.8	0.3	0.15	1172
Maximum	1116	1.54	15.6	6.6	8.2	0.39	4432
Count	268	268	268	268	268	268	268

2.4.3 Lifestyle (Habit)

Records from the present research ($n = 181$), and supplementary data from herbaria records ($n = 91$), The National Vegetation Survey database (NVS) ($n = 5$) and reports from field botanists ($n = 3$), were compiled to investigate the lifestyle statistics of *P. kirkii*. *Pittosporum kirkii* exhibited three distinct lifestyles (Figure 2.4), with the epiphytic habit being predominant, then terrestrial, and lastly rupestral (Figure 2.4 combined data). Results of the present survey are provided first, followed by those from other sources.

In the montane kāmahi/mixed podocarp forest of Erua, all *P. kirkii* individuals were epiphytic ($n = 44$) (Figure 2.4), with 73 percent of these individuals growing between five and 20 metres above the ground (Figure 2.5). One individual was found on a fallen host, two on standing dead snags and another on a fibrous wheki (*Dicksonia squarrosa*) trunk. All other individuals were associated with nest epiphytes; *Astelia solandri* and *Collospermum microspermum*, and found upon large emergent hosts, northern rata (*Metrosideros robusta*) and rimu (*Dacrydium cupressinum*); these species accounted for 53 percent of hosts at Erua Forest.

The population in lower montane kauri (*Agathis australis*)-mixed podocarp and kauri-mixed broadleaf forest on Mount Hobson, Great Barrier Island, comprised nearly entirely of terrestrial ($n = 46$) and rupestral ($n = 9$) individuals (Figure 2.4). Eighty-two percent were terrestrial, 16 percent were rupestral ($n = 9$) and two

percent were epiphytic ($n = 1$). Terrestrial individuals were found in kauri-mixed podocarp forest in association with species such as kauri grass (*Astelia trinervia*), monoao (*Halocarpus kirkii*), yellow pine (*Lepidothamnus intermedius*), tāwari, tāwheowheo (*Quintinia serrata*), and *Phyllocladus toatoa*. The sole epiphytic individual was located on a thick moss clump on a tāwari (*Ixerba brexioides*) trunk, approximately three metres above the ground (Figure 2.5).

The Mount Taranaki population comprised of entirely epiphytic individuals ($n = 28$) in podocarp-mixed broadleaf lower montane forest (Figure 2.4). Of the individuals present, 39 percent were found between 11 and 14 metres above ground level on their hosts, 21 percent between six and ten metres, 14 percent between 16 and 20 metres, seven percent between one and two metres and 18 percent were found on fallen hosts (Figure 2.5). Additionally, 68 percent of hosts recorded were large emergent trees (up to 25 metres tall), including northern rata at various stages of strangling the trunk of fellow emergent, rimu. Other hosts, included large canopy species miro (*Prumnopitys ferruginea*) and kāmahī (*Weinmannia racemosa*). Except for fallen individuals, all other individuals were found in association with nest epiphytes, with *Collospermum hastatum* being replaced with congener *C. microspermum* at 485 m a.s.l.

At Waipoua Forest 93 percent of individuals were epiphytic ($n = 28$) and seven percent were terrestrial ($n = 2$) in kauri-podocarp and rimu-taraire-tōwai lower montane forest (Figure 2.4). The terrestrial individuals were found growing within one to two metres of the base of two kauri that were four metres in diameter. Epiphytic individuals were growing either, six to ten metres (50 percent), or 11 – 15 metres above the ground (40 percent) (Figure 2.5). These individuals were found on a narrow range of large canopy and emergent host species, 15 to 40 metres in height (kauri, miro, rimu, and tōtara (*Podocarpus totara* var. *totara*), and in association with all three nest epiphytes.

Ninety-one percent ($n = 21$) were epiphytic individuals, and four percent ($n = 2$) were terrestrial in the Waitakere Ranges population (Figure 2.4). They were recorded in kauri-podocarp forest and podocarp-mixed broadleaf (mostly regenerating) lower montane forest. Epiphytic individuals were found across all

height classes, with 38 percent found between 11 – 15 metres above ground and 13 percent of individuals on fallen hosts (Figure 2.5). These individuals were hosted by forest emergents; kahikatea (*Dacrycarpus dacrydioides*), kauri, mountain tōtara and rimu. Terrestrial individuals were growing in kauri detritus beneath a 30 metre tall kauri.

The supplementary data sets revealed that 67 percent of individuals were epiphytic ($n = 64$), while 27 percent were terrestrial ($n = 26$) and six percent were rupestral ($n = 6$) (Figure 2.4). Within these data sets terrestrial individuals were recorded almost exclusively in kauri-podocarp forest. Rupestral individuals were primarily found on greywacke and argillite rock in Northland, and dissected rhyolitic rock on Mount Hobson, Great Barrier Island.

The overall combined lifestyle statistics were 67 percent ($n = 186$) epiphytic, 28 percent ($n = 76$) terrestrial, and five percent ($n = 15$) rupestral (Figure 2.4).

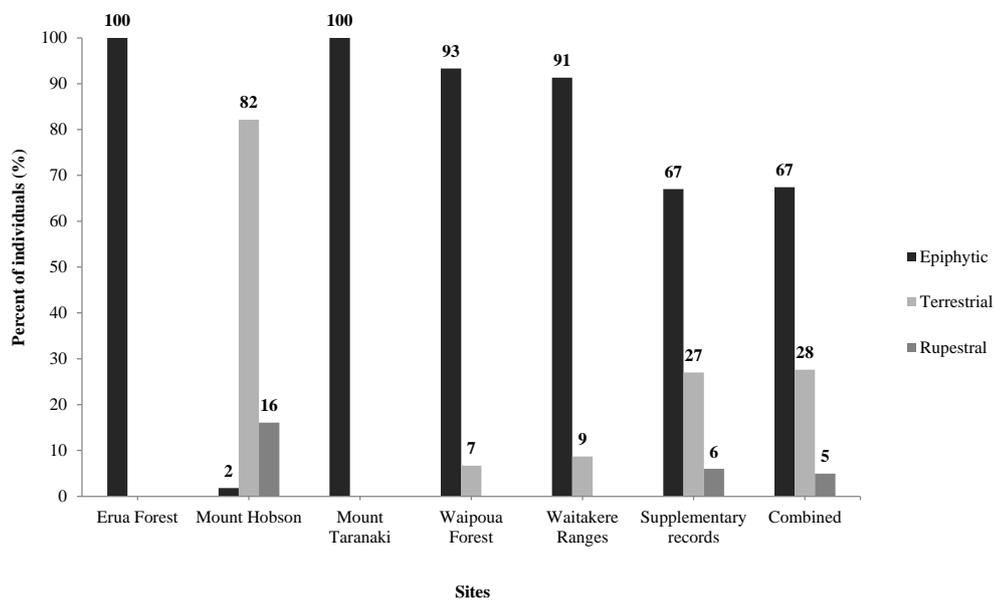


Figure 2.4 Lifestyle profiles exhibited by *Pittosporum kirkii* across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island). Records from supplementary data are shown along with the combined lifestyle ratios for all six data sets.

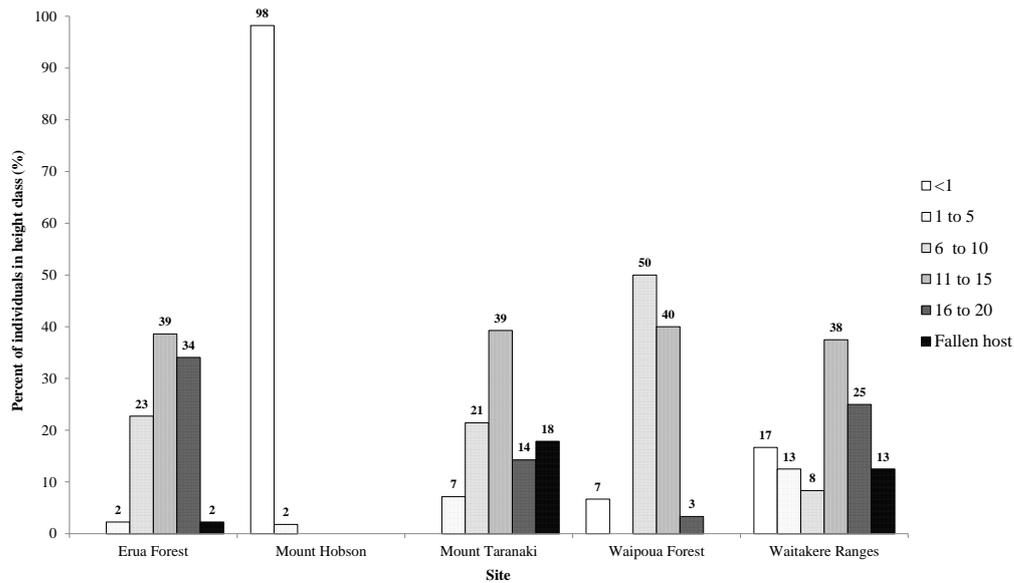


Figure 2.5 Percent of *Pittosporum kirkii* individuals present in each habitat location from the ground (height classes in metres). Individuals recorded less than one metre were rupestral and terrestrial in the Mount Hobson, Great Barrier Island population and terrestrial in all other populations. All individuals located above one metre from ground were epiphytic. The fallen host category represents individuals that were found on hosts that had fallen to the forest floor.

2.4.4 Vegetation classification

Pittosporum kirkii individuals were recorded across 18 different vegetation types (Table 2.2), across two main bioclimatic zones; upper lowland to lower montane. The field survey data from the four North Island, and offshore island population provided 86 percent ($n = 181$) of the vegetation type data analysed. The total data set, including adequate supplementary data, provided 211 records for analysis.

Combining all data sets, showed that rimu forest, co-dominant with mataī (*Prumnopitys taxifolia*) and other hardwoods ($n = 39$) was the forest type that *P. kirkii* most frequently inhabits. This is followed by kauri (*Agathis australis*) forest, where terrestrial individuals primarily occur ($n = 32$) and lastly, rimu (*Dacrydium cupressinum*) and general hardwood forest ($n = 27$). Rupestral individuals were restricted exclusively to rupestral shrublands, and open mānuka/*Kunzea sinclairii* (Great Barrier Island kānuka) shrublands on Mount Hobson, Great Barrier Island (Table 2.2).

Overall, the supplementary records ($n = 30$) revealed a number of unique vegetation types not encountered during field surveys, these include; rimu and beech forest, low moss ‘cloud’ forest, and interestingly, cutty grass/māpere (*Gahnia xanthocarpa*) bog habitat (Table 2.2).

Table 2.2 Vegetation types containing *Pittosporum kirkii*. Types recognised mainly follow Nicholls (1976) forest classification, with personal observation and subsequent re-classification.

Vegetation type	Counts
Rimu-mataī-hardwoods	39
Regenerating kauri-podocarp forest with monoao and tāwari	36
Kauri forest	32
Rimu-general hardwood forest	27
Kauri/softwoods-hardwood forest	16
Rupestral shrublands	12
Taraire-tōwai forest	10
Rimu-tawa forest	9
Softwood dominant forest	6
Softwoods/kāmahi forest	5
Rimu-taraire-tawa forest	4
Regenerating rimu with kānuka shrub	3
Taraire/tawa forest	3
<i>Gahnia xanthocarpa</i> bog	2
Rimu-general hardwoods-beeches	3
Low moss ‘cloud’ forest	1
Mixed shrub with tōwai	1
Open mānuka/Great Barrier Island kānuka shrublands	1

2.4.5 Assemblages of co-occurring epiphytes

Associations and epiphytic composition

Vascular epiphyte and vine species occurring on the same host as *P. kirkii* and their frequency of occurrence are presented in Figure 2.6. Overall, the epiphyte species that most frequently occurred with *P. kirkii* were; nest epiphytes, *Astelia solandri* (85 percent) and *Collospermum microspermum* (54

percent); filmy ferns, *Hymenophyllum* species (62 percent), and ferns, *Asplenium polyodon* (62 percent), *A. flaccidum* (45 percent) and *Microsorium pustulatum* subsp. *pustulatum* (45 percent). *Pittosporum kirkii* individuals were found with conspecific individuals 51 percent ($n = 33$) of instances. Epiphytic congener, *Pittosporum cornifolium* was found 25 percent ($n = 16$) of the time on the same host as *P. kirkii*. The other endemic epiphytic shrubs; *G. lucida* and *Brachyglottis kirkii* var. *kirkii* were found 21 percent ($n = 19$), and 15 percent ($n = 15$) of the time respectively with *P. kirkii* (Figure 2.6).

Appendix one provides the breakdown of associated vascular epiphyte and vine species at each of the populations surveyed. The most common associates at Erua Forest were, nest epiphytes *Collospermum microspermum* ($n = 19$), and *Astelia solandri* ($n = 16$) followed by the fern, *Asplenium polyodon* ($n = 16$). In contrast, on Mount Taranaki *A. solandri* ($n = 12$), the orchid, *Winika cunninghamii* ($n = 10$) and the strangler, *Metrosideros diffusa* ($n = 9$) were the most frequently associated epiphyte species. At the Waitakere Ranges population the nest epiphyte *A. solandri* ($n = 11$) was also the most common associate, followed by the vine (climber), kiekie (*Freycinetia banksii*) ($n = 11$) and the nest epiphyte *Collospermum hastatum* ($n = 9$). Lastly, at the Waipoua Forest population common associates included, *A. solandri* ($n = 16$), filmy fern species, *Hymenophyllum* ($n = 13$) and the hemi-epiphyte, *Griselinia lucida* ($n = 13$).

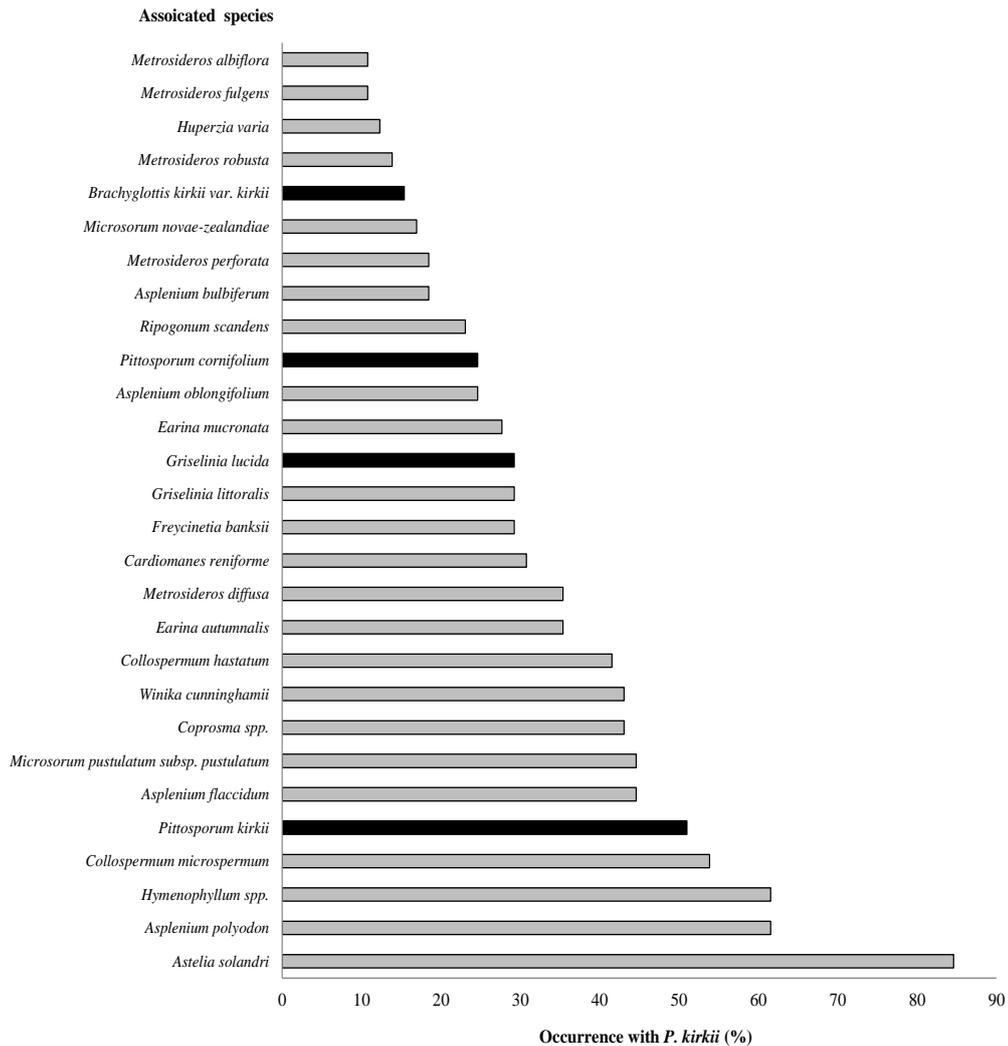


Figure 2.6 The vascular epiphyte and vine species ($n = 28$) associated with *Pittosporum kirkii*, occurring on the same host, and their combined frequency of occurrence (percent) ($n = 575$), across four North Island populations. Bars in black represent the four endemic epiphytic shrubs. Species that had combined frequencies of less than ten percent were predominantly ephemeral (accidental) epiphytes and were omitted from analysis.

Vertical stratification

Vertical distribution (zone occupancy) of the vascular epiphyte and vine species that were most frequently associated with *Pittosporum kirkii* and their frequency of occurrence in each zone is presented in Figure 2.7. Appendix two provides the complete list of associated vascular epiphyte and vine species present in each of the five host occupancy zones combined across the five surveyed populations.

Zone one is composed of an assemblage dominated by *Hymenophyllum* species (25 percent), kiekie (25 percent), and *Metrosideros diffusa* (23 percent). Zone two,

the lower part of the host trunk, is characterised by *Astelia solandri* (37 percent) which starts to become most frequent alongside *Hymenophyllum* species (31 percent) and *M. diffusa* (28 percent). *Pittosporum kirkii* (three percent) first appears in zone two, mainly in open and well-lit kauri forests. Zone three represents the upper half of host trunks, and shows a notable change in composition of associated species to nest epiphytes, *Collospermum microspermum* (34 percent) and *A. solandri* (38 percent) increasing in frequency, alongside *P. kirkii* (15 percent) and *Asplenium polyodon* (22 percent). Zone four is commonly where the primary ramification occurs on hosts, typically forming a branch-trunk fork, and holds the highest abundance of epiphytes (32 percent) (Appendix two). Nest epiphytes, *A. solandri* (42 percent) and *C. microspermum* (38 percent) with *P. kirkii* (44 percent) are most frequent in zone four. Lastly, zone five, which represents branch-branch ramifications, possessed the lowest abundance of epiphytes (Appendix two), however *C. hastatum* occurs in its highest frequency in this zone (15 percent).

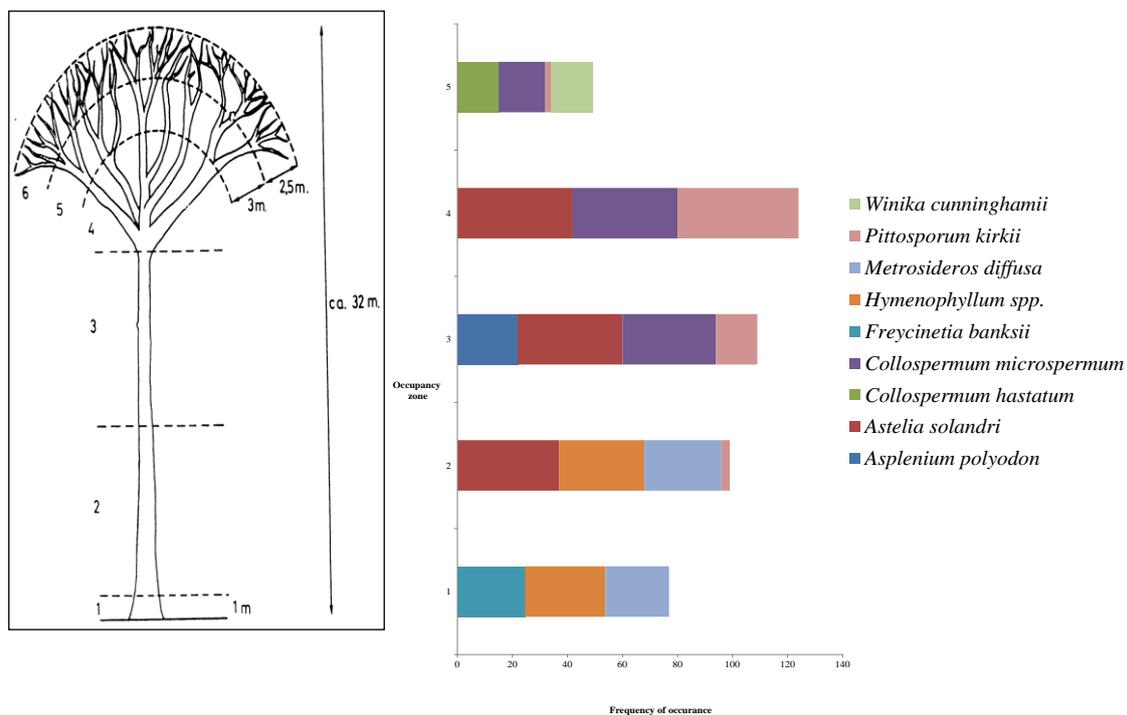


Figure 2.7 The vertical distribution of the nine most common vascular epiphyte and vine (climber) species (n = 566) found in association with *Pittosporum kirkii* (occupying the same host) (n = 121) and their frequency of occurrence in each distribution zone combine.

2.4.6 Host characteristics

Host species

Across all data sets 126 individual trees were recorded as *P. kirkii* hosts (field surveys $n = 59$, supplementary records $n = 67$), these comprised 18 different host species (Figure 2.9). The emergent and canopy layer trees: rimu (*Dacrydium cupressinum*), northern rata (*Metrosideros robusta*), miro (*Prumnopitys ferruginea*) and kauri (*Agathis australis*) accounted for 76 percent ($n = 96$) of *P. kirkii* hosts across all data sets (Figure 2.9).

In the field survey 121 *P. kirkii* individuals were recorded on 59 individual host trees, with the most common host species being rimu ($n = 27$), followed by northern rata ($n = 9$). In contrast, miro ($n = 17$), followed by rimu ($n = 16$), and northern rata ($n = 15$) were the most common host species in supplementary records (Figure 2.9).

The supplementary records ($n = 67$) highlighted the importance of a number of host trees that were not significant in field surveys; tawa (*Beilschmiedia tawa*) ($n = 2$); tāwari ($n = 4$) and tāwheowheo (*Quintinia serrata*) ($n = 2$).

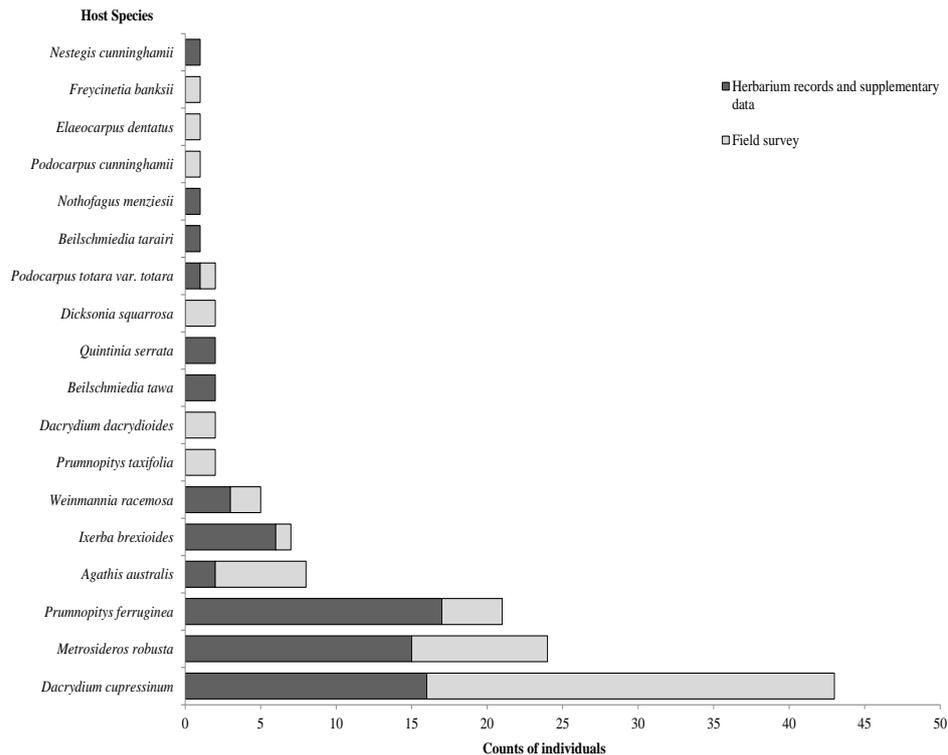


Figure 2.9 Number of *Pittosporum kirkii* host species surveyed ($n = 59$) across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island), and from supplementary records ($n = 67$).

Host height

The combined mean height of host trees was 22.65 ± 0.65 m, with 91% of hosts between 15 and 30 m in height (Figure 2.10) (Figure 2.10). The mean height of hosts did not vary significantly across populations (Table 2.3). However, the height range varied, with Erua Forest and the Waitakere Ranges having the greatest host height range (Table 2.3). This is due to a single short stature tree fern, wheki (*Dicksonia squarrosa*) being host to an epiphytic individual at each population, in addition to tall canopy and emergent trees. At Waipoua Forest, mean host height (23.7 ± 1.5 m) was relatively higher than other populations, due to the greater presence of emergent kauri which reach up to 40 m in height (Table 2.3). The Mount Hobson population only had one epiphytic individual on a 12 metre tāwari (Table 2.3). Statistical analysis did not report significant correlation between the host height and the number of *P. kirkii* individuals.

Table 2.3 *Pittosporum kirkii* host species height mean, minimum and maximum across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island). Standard error of mean in parentheses. N.B: missing values row equates to individuals that were rupestral and terrestrial, or fallen.

	Erua Forest	Mount Hobson	Mount Taranaki	Waipoua Forest	Waitakere Ranges	Combined
<i>n</i>	44	1	23	28	18	114
Mean	21.7 (1.4)	-	21.8 (0.9)	23.7 (1.5)	22.8 (1.9)	22.65 (0.65)
Min.	4	12	12	15	5	4
Max.	30	12	27	40	40	40
Missing values	0	55	5	3	5	69

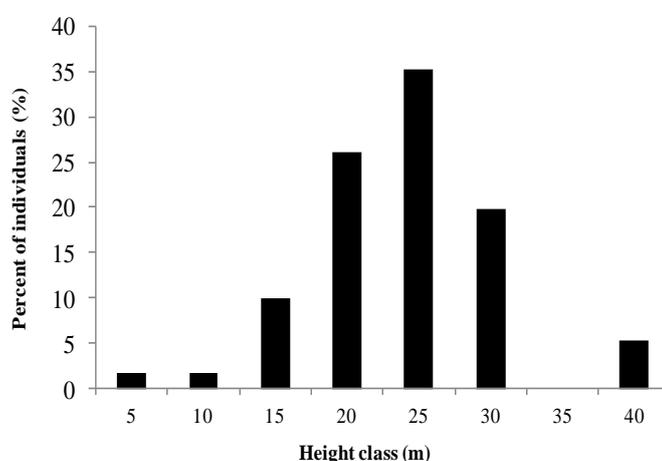


Figure 2.10 Percent of *Pittosporum kirkii* host species in differing height classes across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island).).

Host size

Host size varied across the five populations. The mean host diameter ranged from 37.5 cm at Mount Hobson to 196.7 ± 22.9 cm at the Waipoua Forest population, with a combined average diameter of 151.41 ± 10.47 cm (Table 2.4). Across all populations 70 percent of hosts surveyed were 50 – 199 cm in diameter (Figure 2.11). All populations had a significantly different size range, with Erua Forest and the Waitakere Ranges being the most pronounced. This was due to the presence of a single tree fern host at Erua Forest (minimum values at each population) and emergent, or large canopy trees (maximum values) (Table 2.4). Similar to host height, at Waipoua Forest 29 percent of hosts were giant kauri that were 200 – 522 cm in diameter (Table 2.4). Statistical analysis did not reveal

significant correlation between the diameter (DBH) of host to the number of *P. kirkii* individuals.

Table 2.4 *Pittosporum kirkii* host species diameter at breast height mean, minimum and maximum values across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island). Standard error of mean in parentheses. N.B: missing values row equates to individuals that were rupestral and terrestrial, or fallen.

	Erua Forest	Mount Hobson	Mount Taranaki	Waipoua Forest	Waitakere Ranges	Combined
<i>n</i>	44	1	23	28	18	114
Mean	134.5 (18.8)	37.5	150.5 (11.8)	196.7 (22.9)	131.07 (24)	151.41 (10.47)
Min.	9	37.5	46	65	12.4	9
Max.	400	37.5	334.8	522	400	522
Missing values	0	55	5	3	5	59

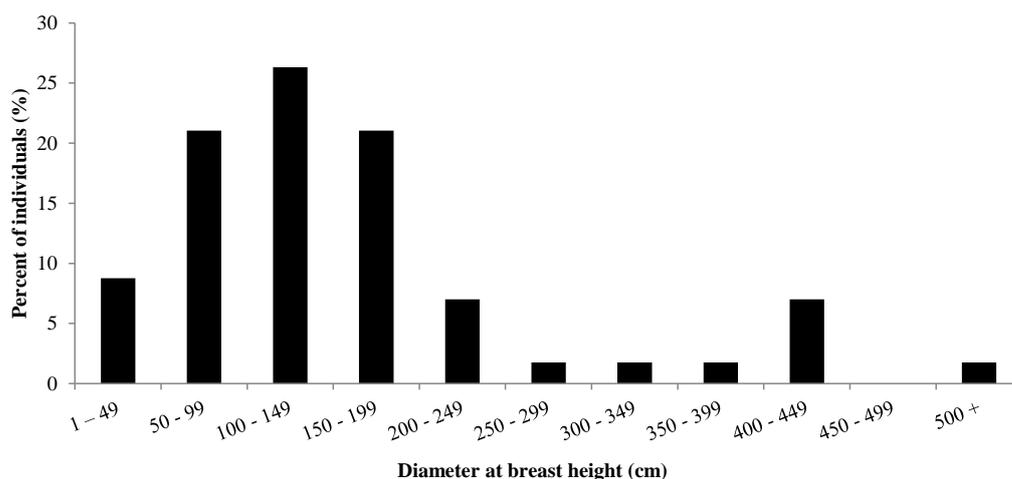


Figure 2.11 Percent of *Pittosporum kirkii* host species in differing diameter (cm DBH) size classes across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island).

Host Bark

Six bark types were represented on host species recorded across the five populations (Figure 2.12). The fibrous bark type represents the single tree fern (wheki) host at Erua Forest and the Waitakere Ranges populations. The most common bark type, flaky ($n = 70$) is the bark type of the most common host; rimu. Smooth bark types were commonly found on hosts; tāwari and kāmahi. Other bark types were recorded across all host species. Across the five populations the

six bark types and number of *P. kirkii* individuals did not reveal a statistically significant relationship.

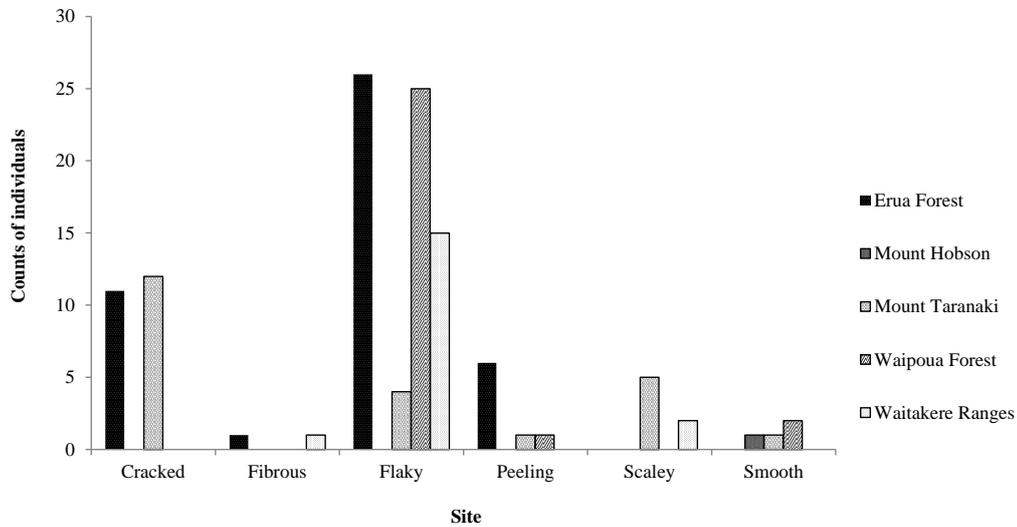


Figure 2.12 Number of *Pittosporum kirkii* epiphytic individuals per host by bark type across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island). N.B: rupestral and terrestrial individuals are inapplicable.

2.4.7 Growing substrate

Substrate preferences

Pittosporum kirkii individuals ($n = 181$) were recorded growing in six substrate types at the four North Island populations and single offshore island populations (Figure 2.13). No substrate data was available from the supplementary data sets. No individuals were directly attached or, growing on the bark of host species (except for a single individual on a tree fern trunk), or rock faces.

Individuals growing epiphytically were very frequently associated with nest epiphytes at all four mainland populations, with Erua Forest displaying the highest proportion of the population growing amongst nest epiphytes; 98 percent (Figure 2.13). These nest epiphyte species include *Astelia solandri*, *Collospermum hastatum* and *C. microspermum*.

On the offshore island population of Mount Hobson (Great Barrier Island), 82 percent of individuals ($n = 46$) were growing terrestrially in ground detritus (encompasses kauri detritus). Rupestral individuals were found growing mostly on

moss clumps covering andesitic rocky outcrops ($n = 8$), with only one individual growing amongst the nest epiphyte, *A. solandri* (Figure 2.13).

Individuals at the Waitakere Ranges population were found on the largest range of substrate types. Nest epiphytes were the most common, hosting 65 percent of individuals ($n = 15$), followed by 13 percent on fallen and decomposing hosts ($n = 3$) and nine percent on kiekie and associated detritus ($n = 2$) (Figure 2.14). Lastly, a further nine percent ($n = 2$) were growing terrestrially in ground detritus (Figure 2.13).

The least common substrate was the fibrous trunk of tree fern, *Dicksonia squarrosa*, (Figure 2.13); one *P. kirkii* individual at Erua Forest was directly attached to the tree fern trunk (Figure 2.14).

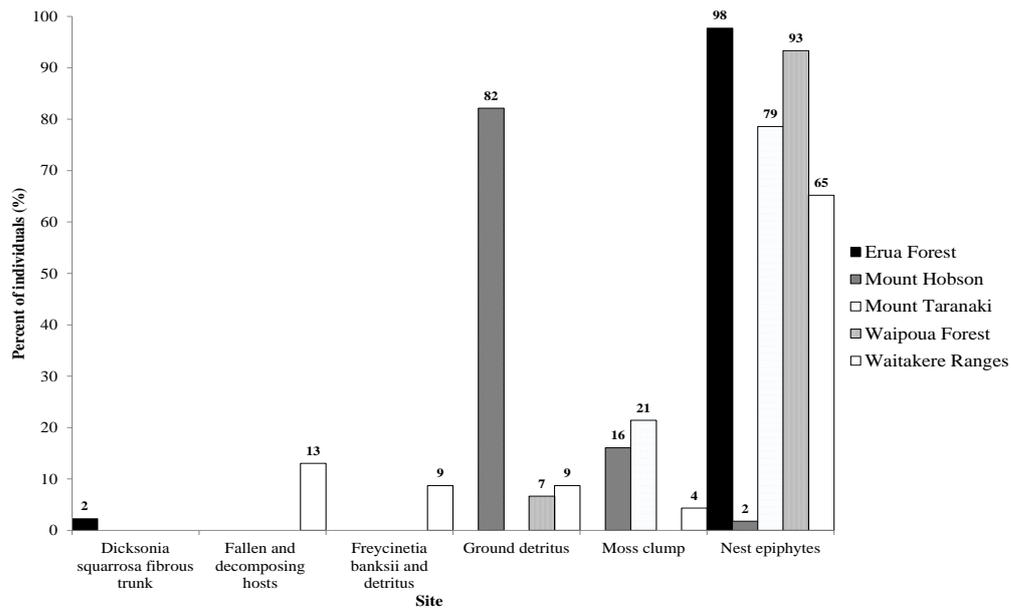


Figure 2.13 Percent of *Pittosporum kirkii* individuals on each growing substrate across four North Island populations.



Figure 2.14 *Pittosporum kirkii* individuals growing directly attached to a fibrous tree fern trunk (wheki) at Erua Forest (A) (Photo: C.L Bryan), and amongst detritus held in the tufted stems of kiekie at the Waitakere Ranges (B) (Photo: S. Edwards).

Establishment site

As an epiphyte *Pittosporum kirkii* frequently grows in nest epiphytes, which are mostly attached to primary or secondary ramifications on hosts. These include branch-trunk fork and branch-branch ramifications (see Figure 2.1). However, they are not restricted to these areas, as individuals were also found in inner to mid branch locations, but never in outer branch locations. The main trunk was rarely a location of attachment, except for two tree fern hosts. Terrestrial and rupestral individuals were almost always found in open, well-lit forest habitats.

2.4.8 Population characteristics

In the four North Island populations and single offshore island population of Mount Hobson, Great Barrier Island a range of population structures (life stages) were recorded (Figure 2.15; Table 2.5). Three populations exhibited regeneration; Erua Forest, Mount Hobson and Waitakere Ranges, although regeneration was more prevalent on Mount Hobson (Figure 2.15; Table 2.5). Regenerating populations exhibited varying levels of regeneration, with Mount Hobson having the most significant recruitment with 20 percent ($n = 11$) of the population classed

as seedlings and 32 percent were in the juvenile size class ($n = 18$). Forty eight percent ($n = 27$) of the population were adults. This was followed by Erua Forest where five percent ($n = 2$) of the population were seedlings, 32 percent were juveniles ($n = 14$), and 64 percent were adults ($n = 28$), and lastly the Waitakere Ranges where four percent ($n = 1$) were seedlings, 26 percent ($n = 6$) were juveniles and 70 percent ($n = 16$) were adults (Figure 2.15; Table 2.5). No juvenile individuals were present at Waipoua Forest although seedlings (7 percent) were present. Mount Taranaki had no seedlings, but saplings made up 43 percent of the population (Figure 2.15; Table 2.5).

Table 2.5 Counts of individuals in each life stage across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island).

	Erua Forest	Mount Hobson	Mount Taranaki	Waipoua Forest	Waitakere Ranges
Adult	28	25	16	28	16
Juvenile	15	20	12	0	6
Seedling	1	11	0	2	1
Total	44	56	28	30	23

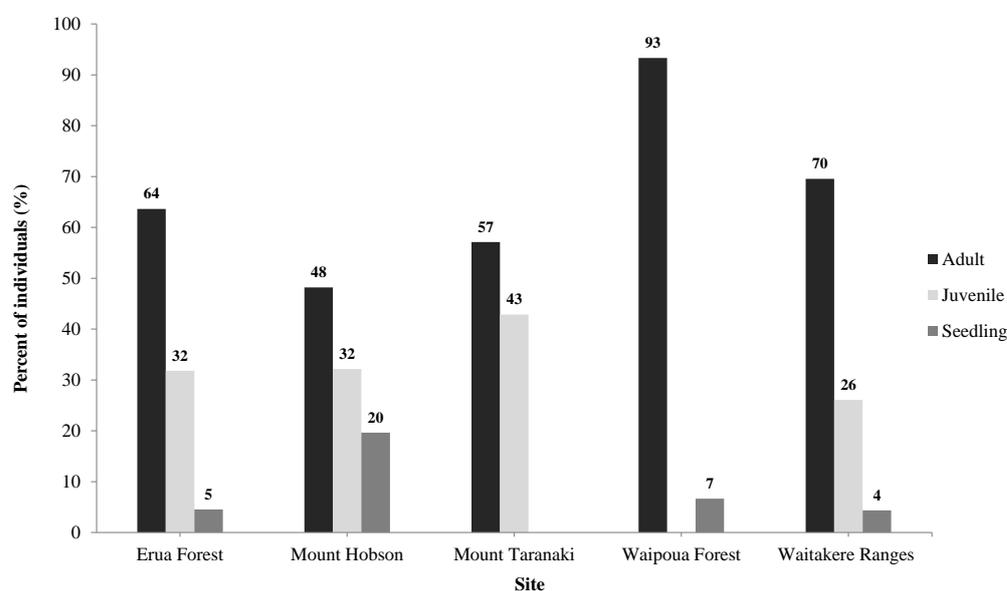


Figure 2.15 Percent of *Pittosporum kirkii* individuals in each life stage (population structure of each surveyed site) across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island).

Size

The mean, minimum and maximum values of *P. kirkii* height and width across four North Island and offshore island populations are presented in Table 2.6. Erua Forest and Waipoua Forest yielded the largest maximum length and width (3 and 5 m; 5 and 3 m, respectively) and mean values, hence contained largest sized individuals of the five populations. The Mount Hobson population (Figure 2.4), was the smallest population, ranging from 0.17 to 2.4 m in height, and 0.1 to 2 m in width.

Table 2.6 *Pittosporum kirkii* height and width (m); mean, minimum and maximum values across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island). Standard error of means are shown in parentheses.

		Erua Forest	Mount Hobson	Mount Taranaki	Waitakere Ranges	Waipoua Forest
Height (m)	Min	0.3	0.17	0.4	0.074	0.3
	Max	3	2.4	2.5	2.5	5
	Mean	1.36 (0.91)	1.03 (0.56)	1.05 (0.62)	1.05 (0.78)	1.82 (0.91)
Width (m)	Min	0.1	0.1	0.2	0.074	0.1
	Max	5	2	3	2	3
	Mean	1.22 (0.17)	0.62 (0.06)	0.79 (0.07)	1.07 (0.13)	1.47 (0.14)
	<i>n</i>	43	56	28	23	30

Dieback and herbivory

Population dieback was not significantly correlated with population size, or the size of *P. kirkii* individuals. Dieback was minimal across the 181 individuals recorded in the five populations (Figure 2.16). The Waitakere Ranges population exhibited the highest level of dieback with 26 percent of individuals so classified, followed by Erua Forest where 11 percent showed light to moderate dieback ($n = 5$), then Waipoua Forest where only three individuals (ten percent of the population) showed light dieback. The number of individual's exhibiting dieback in the Mount Taranaki and Mount Hobson populations were negligible (Figure 2.16). No evidence of possum herbivory was detected in the field survey.

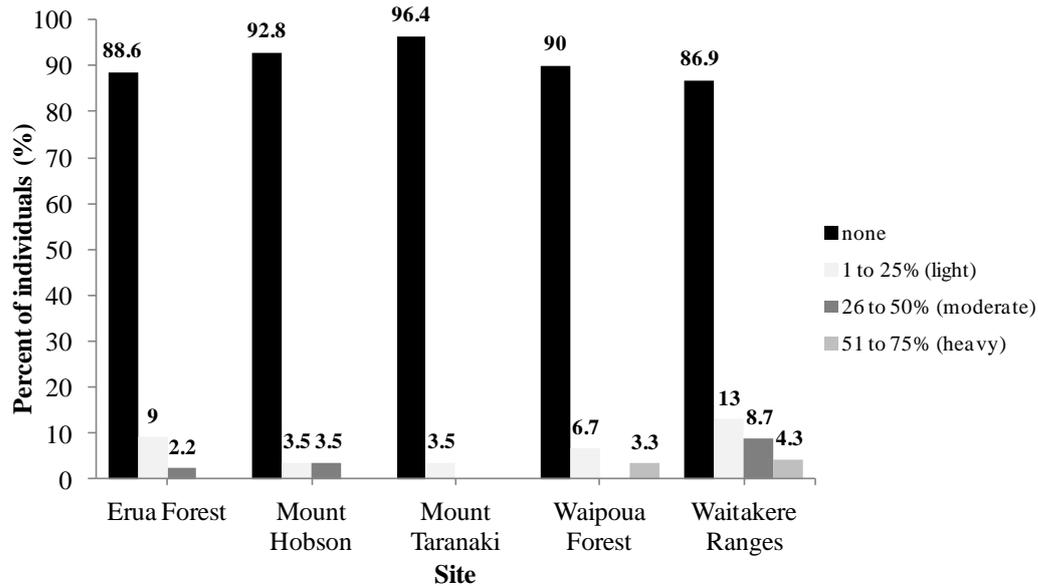


Figure 2.16 Percent of *Pittosporum kirkii* individuals exhibiting different degrees of plant dieback across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island).

Life span

No published data were available on the life span of *P. kirkii*. Dendrochronological analysis has not been carried out on wild or nursery individuals, possibly owing to the relative inaccessibility of the epiphytic lifestyle and also threatened conservation status of the species. Records of persistent individuals located in the Waitakere Ranges, from which herbarium specimens have been harvested, indicated the oldest individual to be at least 30 – 40 years old. Additionally, nursery records suggest individuals can live up to 80 years (G. Davidson, pers. comm. Oratia Nursery 2011). This is in line with congener, *Pittosporum cornifolium*, which shares similar lifestyle preferences where ages of over 50 years have been documented (Clarkson et al. *In press*).

2.4.9 Phenology

Field data from the present research ($n = 43$), and supplementary data from herbaria records, and observations from field botanists ($n = 102$) were compiled to produce a phenology calendar (Figure 2.17).

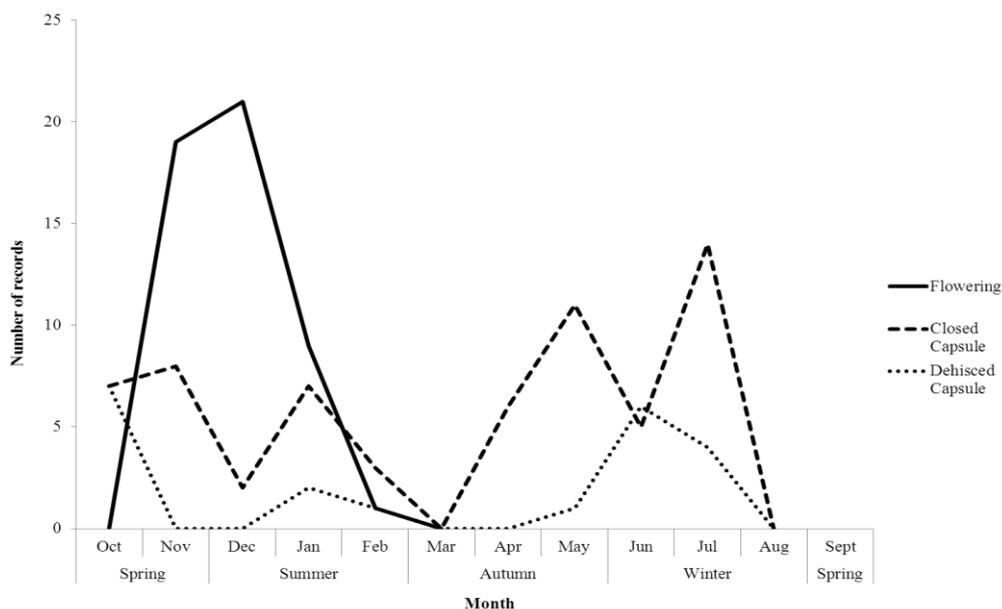


Figure 2.17 Phenology calendar of *Pittosporum kirkii* produced from field data and supplementary data sources.

Although the total number of records was 145, these were uneven and lacking for some months of the year. There were no records available for March, August and September, and limited records for February and April. Records for dehisced capsules were sporadic.

Pittosporum kirkii has a short and abrupt annual flowering season, which spans from October to February and peaks in November and December (late spring-early summer) (Figure 2.17). There were no significant differences in flowering periods between mainland and offshore (Great and Little Barrier Islands) populations. However, noteworthy morphological variability is evident in flowers between mainland and offshore populations (Great Barrier Islands) (see Figure 1.3 & Figure 2.23). Observations from nursery individuals (Oratia Nursery) indicated that there was a difference in flower longevity between the sexes, with male flowers being longer-lived than female flowers which rapidly shed their perianth upon pollination.

Closed capsules were found on 63 female individuals across the entire year, and there appears to be a peak in capsule dehiscence in late autumn-winter and also in October. Consequently, a female individual can frequently possess green (closed) capsules from the current flowering year, yellow dehiscent capsules from

previous year(s) and various brown dehisced capsules (with or without seeds) from several years of flower cycles and capsule development.

2.4.10 Sex ratio

All five populations' sex ratios were strongly male skewed (Figure 2.18). The combined sex ratio of the four mainland populations and the single offshore island population was 18 female: 72 male: 9 unknown. There were no records indicating that male *P. kirkii* produce infrequent capsules, which has been reported for other members of the *Pittosporum* genus in New Zealand (Godley 1979; Clarkson 2011).

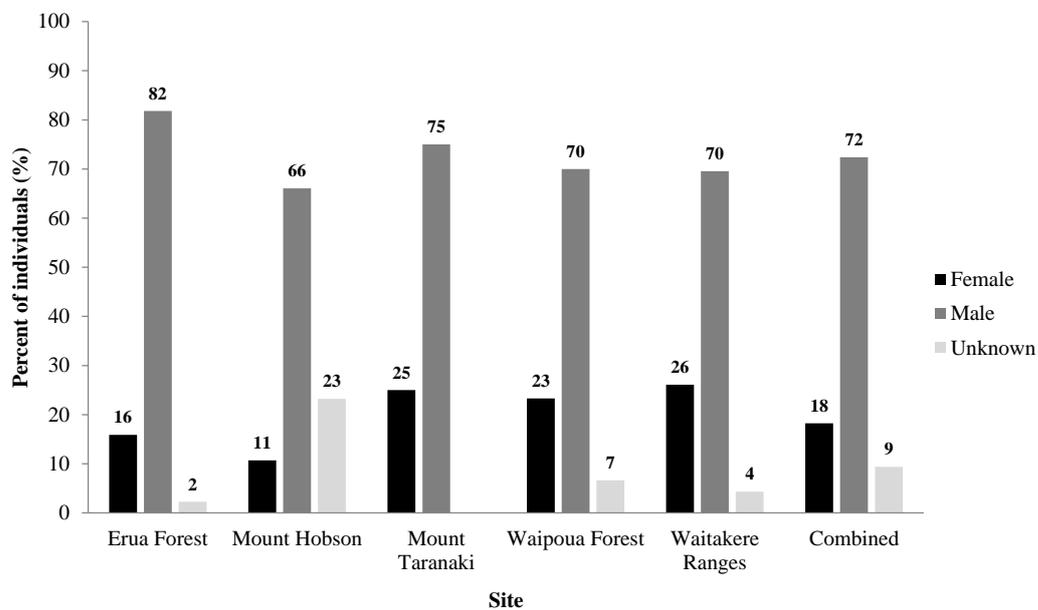


Figure 2.18 Sex ratios of *Pittosporum kirkii* across four North Island populations and one offshore island population (Mount Hobson, Great Barrier Island). Combined sex ratio data is shown. The unknown category was seedlings or individuals that were unable to be sexed.

2.4.11 Anatomical analysis

Leaves

A transverse representative section of the leaf cross section through the mid rib is presented below (Figure 2.19). The thick cuticle on the abaxial surface covers a single epidermis layer, followed by two to three layers of square hypodermis cells, which function as water storage cells and are formerly known as aqueous tissue (*cf.* Oliver 1930). The palisade layer consists of two to three layers of short oblong

cells; beneath this is the spongy mesophyll which, makes up the bulk of the leaf structure. Within the spongy mesophyll, or spongy parenchyma, are loosely packed round to oblong shaped chlorenchyma cells. The vascular bundle is made up of xylem tissue and a relatively large phloem, surrounded by three to four secretory ducts amongst the lower bundle sheath (Figure 2.19; Table 2.7). These specialised secretory ducts named schizogenous ducts are lined and divided with epithelium tissue composed of secretory cells (Evert et al. 2006). The adaxial epidermis and cuticle are thinner than those on the abaxial. The presence of substomatal chambers was not detected.

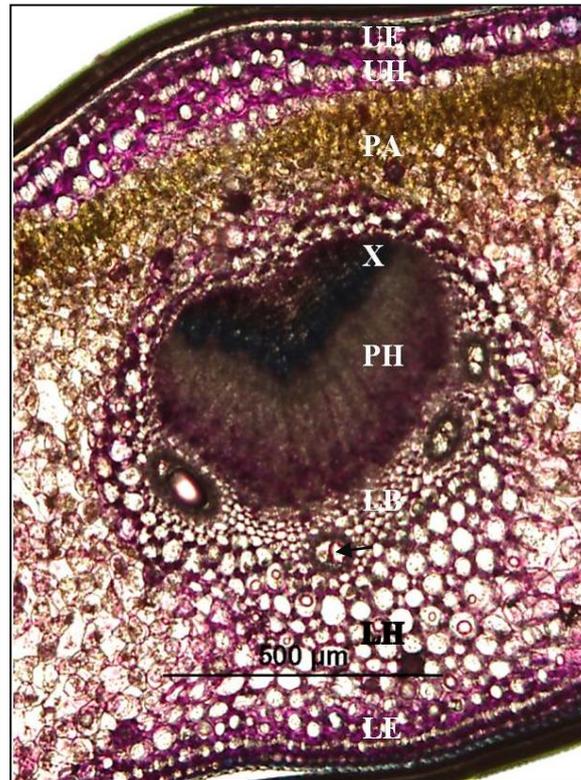


Figure 2.19 Transverse hand section through the mid rib of a *Pittosporum kirkii* leaf stained with toluidine blue. Scale shown (μm). The arrow shows an epithelium divide in a secretory duct.

Table 2.7 Measurements of mean lamina tissue depths of a transverse hand section through the mid rib of *Pittosporum kirkii* ($n = 4$) leaves. Letters refer to tissue types in Figure 2.19.

Tissue type	<i>P. kirkii</i>
Upper cuticle	16.67
Upper epidermis (UE)	44.91
Upper hypodermis (UH)	104.86
Palisade cells (PA)	131.60
Upper bundle sheath cells	43.05
Xylem (X)	93.12
Phloem (PH)	159.89
Lower bundle sheath cells (LB)	102.80
Spongy mesophyll (spongy parenchyma)	426.50
Lower hypodermis (LH)	156.42
Lower epidermis (LE)	41.23
Lower cuticle	11.88
Total	1332.94 μm

Young *P. kirkii* seedlings have multicellular, capitate, glandular trichomes on both the lamina adaxial and abaxial (Figure 2.20). These trichomes are caducous in nature and are not present on the mature leaves of seedlings, or on adult individuals (this authors' observation). Multicellular, glandular trichomes are a characteristic feature of the genus *Pittosporum*, and have been reported on endemic congener *Pittosporum crassifolium* (Cockayne 1921; Haas 1977; Abraham 1986).

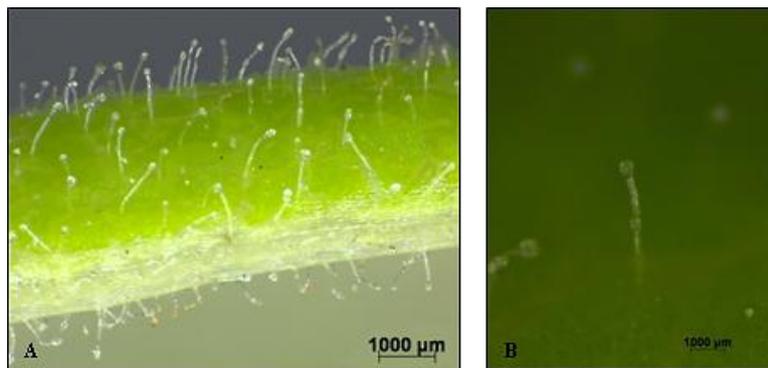


Figure 2.20 Multicellular capitate glandular trichomes on the leaves of young *Pittosporum kirkii* seedlings. A: side view of a young leaf showing numerous trichomes on the adaxial (darker green) and abaxial (paler green). B: a single glandular trichome on the adaxial (Photos: K.J Myron).

The root and stem

A representative transverse section of the root and stem as a cross section divided into a quarter of the complete section is presented below (Figure 2.21). Cross sections reveal the periderm in both root and stem sections. However, it is only in the root section that the phellem (cork), phellogen (cork cambium) and phelloderm cell layers are clearly distinct and visible. The stem cross section reveals a ring of axial secretory ducts between the cortex and primary phloem. It is unclear whether these secretory ducts lack epithelium tissue. However, an epithelium divide present in leaf secretory ducts (Figure 2.21) and absence in stem secretory ducts, suggests lysigenous formation of the stem secretory ducts (Evert et al. 2006).

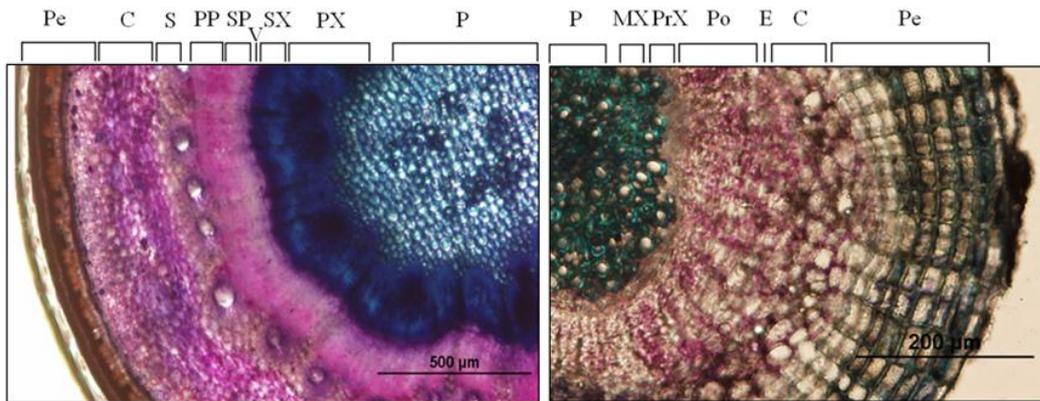


Figure 2.21 *Pittosporum kirkii* stem (left) and root (right) transverse hand sections, stained with toluidine blue. Scale shown (micrometre). P: pith; PX: primary xylem; SX: secondary xylem; V: vascular cambium; SP: secondary phloem; PP: primary phloem; S: ring of secretory ducts; C: cortex; Pe: periderm; MX: meta xylem; PrX: proto xylem; Po: phloem; E: endodermis (with the casparian strip).

2.4.12 Leaf and capsule morphology

Pittosporum kirkii had an overall mean leaf length of 82.6 ± 1.8 mm and width of 21.6 ± 0.6 mm, which ranged from 40.5 – 111.3 mm in length and 11 – 31.3 millimetres in width (Figure 2.22). A scatter graph of leaf length and width data sets showed a clumped distribution including all five populations, with an overlap in leaf length of Great Barrier Island and North Island individuals (Figure 2.22). However, leaf width was distinct on offshore island individuals which had narrower leaves, 18.23 ± 0.8 mm, in comparison to wider leaved North Island individuals 23.3 ± 0.6 mm. There was also some discernible difference in leaf length between Waipoua Forest individuals, 73.3 – 103 mm, and Erua Forest individuals, 40.5 – 90 mm. A statistically significant relationship was found between leaf length and latitude which reflects the reduction in length with increasing latitude ($P = 0.002$). No significant relationship was found between leaf width and latitude, or between leaf size and altitude.

Capsule size (Appendix three) had an overall mean length of 28.6 ± 1.0 mm and width of 13.7 ± 0.6 mm, and shows a clumped distribution across populations. Capsule size varied between offshore island and North Island individuals, with offshore island individuals being smaller in length (17 – 31.5 mm) and width (6 – 14 mm), and North Island individuals being larger in length (25 – 35 mm) and width (11 – 20 mm). Furthermore, observations of viscid fluid inside the capsule

exhibited colour variation between Great Barrier Island (white) and North Island (yellow) individuals. No statistically significant relationships were found between capsule size and latitude, or between capsule size and altitude.

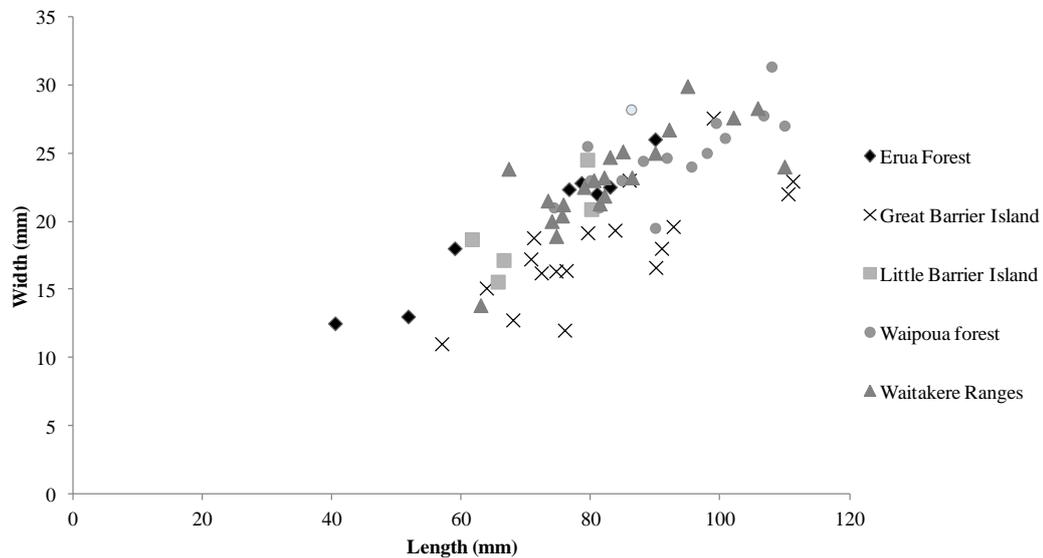


Figure 2.22 Length and width (mm) comparison of *Pittosporum kirkii* individual leaves. Combined from herbarium records and field surveys across five populations: Erua Forest ($n = 8$), Great Barrier Island ($n = 18$), Little Barrier Island ($n = 5$), Waipoua Forest ($n = 16$), Waitakere Ranges ($n = 21$).

2.4.13 General morphology

Great Barrier Island individuals differ from mainland individuals by several characteristics: a small shrubby habit (with multiple stems from the base); an almost entirely terrestrial/rupestral lifestyle; a corolla and calyx with creamy yellow-white colouring at the base that changes to purple to dark-pink at the mid corolla and calyx tip; smaller capsules with a white viscid fluid; and generally narrower leaves (this authors' observation) (Figure 2.23). Based on these noteworthy differences it is suggested that genetic assessment is warranted to establish if Great Barrier Island (and perhaps Little Barrier Island) is host to a unique *P. kirkii* variant.



Figure 2.23 *Pittosporum kirkii* individuals on Mount Hobson, Great Barrier Island: A: umbel flowers, yellow corolla tube with pink/purple petals (Photo: R. E. Thomson). B: small shrubby habit (Photo: S. Edwards). C: small (3 x 1.1 cm) dehiscent capsule with white viscid fluid (Photo: S. Edwards).

2.5 Discussion

2.5.1 Distribution

Pittosporum kirkii distribution is restricted both by altitude and latitude, being limited to the upper North Island in upper lowland to lower montane bioclimatic zones (primarily above 471 ± 0.11 m a.s.l). However, analysis of the predicted environmental distribution highlights discrepancies between observed and potential distributions. This is supported by the observed absences of *P. kirkii* in areas where environmental variables are favourable for potential distribution. These include a large area west and south-west of Taupo, east coast of Northland and half of the East Cape (e.g. Urewera National Park). Similar to congener *P. cornifolium*, the Taupo Volcanic Zone is predicted as favourable for potential distribution (Clarkson 2011), but shows the species is absent from higher altitude areas. This is probably due to the large scale disturbance created by the 186 AD Taupo eruption, which changed the ecological landscape significantly (Rogers & McGlone 1989; Newnham et al. 1999).

Smaller, but notable areas of favourable environmental conditions where the species is unrecorded include high altitude and high rainfall areas on Mahia peninsular, and across the Ruahine and Ikawhenua ranges. Further south these areas include higher altitude humid forest in the Wairarapa (Aorangi Range), and

in the South Island, across the Wakamarama and Burnett Ranges in Tasman, and Richmond-Gordon range in Marlborough. In these areas, mixed beech/podocarp with northern rata forests have remained intact due to the challenges of forest removal for logging (DoC 2011b, a). It is in the latter areas that searches should be undertaken to determine *P. kirkii* potential observed presence.

The abrupt observed and predicted distribution cessation of *P. kirkii* in Northland may be due to the combined effects of high temperatures and low rainfall. On the East Coast, absences are due to high vapour pressure deficits and low rainfall which, coupled with the destruction of native forest, has limited the epiphyte flora as found elsewhere in New Zealand (McGlone 1989; Clarkson & Clarkson 1991). In the lower North Island and majority of the South Island, a gap in distribution matches with extensive modification of the ecological landscape, due to the Pliocene and Pleistocene glaciations (2 – 2.5 myo) (Mildenhall 1980; Winkworth et al. 2005). During these glacial maxima it has been argued that many plants were restricted to ice-free regions and failed to recolonise previously inhabited areas after the ice retreated, thus causing the current disjunct distribution patterns of many of New Zealand's flora (Cockayne 1921; Wardle 1963; McGlone 1985). Accordingly, it is possible *P. kirkii* could have also been limited to retreated northern ice-free areas, along with preferred host kauri, in higher altitude areas and has been unable to recolonise current environmentally favourable regions. The absence from the lower North Island and majority of the South Island is primarily due to low temperatures, solar radiation and rainfall. Oliver's (1930) initial study on epiphytes in New Zealand supports this, stating that temperature and rainfall are the most important environmental variables impacting upon epiphyte distribution.

Since completing the predicted environmental distribution, a reliable record for *P. kirkii* on Mount Karioi near Raglan has been obtained. This suggests that other areas where there are currently no records of *P. kirkii* are likely to harbour this species.

2.5.2 Habitat

Pittosporum kirkii habitat is restricted primarily to old-growth upper lowland and lower montane forested ecosystems, where individuals commonly adopt an epiphytic lifestyle. It is also occasionally terrestrial in podzolized kauri detritus in semi-shaded and open kauri forests, and rupestral in exposed locations. Cheeseman et al. (1914) recognised this, finding that *P. kirkii* frequently inhabits these three distinct lifestyles, but also stated that individuals were commonly and equally found exhibiting a rupestral lifestyle. In this manner, *P. kirkii* lifestyle preferences grade from epiphytism, to terrestrialism and lithophytism and consequently, under Benzing's (1990) life history classification scheme it is a facultative epiphyte (Benzing 1990; Benzing et al. 2004). This is exemplified on possum-free Great Barrier Island, where populations flourish in both terrestrial and rupestral lifestyles across the Mount Hobson landscape, amongst regenerating and old-growth kauri-podocarp montane ecosystems.

It is hypothesised that as competition for sunlight in the damp, dark understory of temperate forests persisted, epiphytism evolved autochthonously amongst New Zealand's four typical epiphytic shrubs (Oliver 1930). This theory is supported by the adaptation of *P. kirkii* to high light conditions, and hence its ability to grow abundantly on rhyolitic outcrops found on Mount Hobson, and survive on fallen hosts in high light tree fall gaps in the Waitakere Ranges. However, individuals also tolerate to a limited extent, semi-shaded conditions in open, comparatively dry habitat, as confirmed by *P. kirkii* presence in the understory of kauri forests. Examples of this habitat can be found at Waipoua Forest and in areas of remnant kauri in the Waitakere Ranges. It is in these forests that *P. kirkii* were frequently epiphytic, with terrestrial individuals restricted to directly beneath or in the close vicinity of large, old kauri.

Within the montane ecosystems of Erua Forest all individuals were found growing epiphytically upon large (thus, old) remnant rimu, mataī and northern rata, which are at varied stages of collapse due to anthropogenic destruction 650–560 years ago (Horrocks & Ogden 1998). This is gradually causing the composition of the forest to change to greater dominance by kāmahi, reducing the habitat suitability

for *P. kirkii* as it becomes restricted to larger, older and senescing hosts. Similarly, on Mount Taranaki large canopy and emergent trees in old-growth forest are the preferred hosts for *P. kirkii*. It is these large and often remnant, canopy and emergent trees that act as an ecological refuge, hosting conspecific *P. kirkii* individuals in over 51 percent of instances. The latter habitat preference is similar to fellow epiphytic shrubs, *Griselinia lucida* and *Pittosporum cornifolium* (Bryan et al. 2011; Clarkson et al. *In press*).

Consequently, the specific habitat preferences of *P. kirkii*, coupled with the impacts of possum herbivory (Forester & Townsend 2004), has perhaps rendered the species sparsely distributed and thus, naturally uncommon, or in decline, across a narrow range of ecosystems.

2.5.3 Host species

Eighteen host species were recorded across upper lowland and lower montane old-growth forested ecosystems; however, it was the large canopy and emergent trees that were the most frequent, and preferred hosts of *P. kirkii*: rimu, northern rata, miro and kauri. As previously mentioned, larger, older hosts frequently support more than one *P. kirkii* individual, and this is probably correlated to area: as larger, older hosts have greater surface area available for successful epiphyte interception, and colonisation over longer periods of time (Yeaton & Gladstone 1982; Benzing 1990; Zotz 2007). This apparent correlation between host preference and larger older hosts, probably occurs because as these hosts grow there is an increase in the size, and number of ramifications of branches (Sillett & Pelt 2007; Kersten et al. 2008). This in turn increases the availability of suitable microhabitats and favourable microclimatic conditions, as larger epiphyte mats and nest epiphytes can abundantly persist in, and around large ramifications (Affeld et al. 2009) (Figure 2.24). Hence, the architecture of hosts is important, as shown by the primary trunk-branch (fork) ramification and inner branch areas of the crown being the preferred establishment sites for *P. kirkii* (Figure 2.24). In these areas, large amounts of humus accumulate and the development of thick epiphyte mats occurs, allowing for favourable micro-environmental conditions for *P. kirkii* and diverse epiphyte communities (Affeld et al. 2008) (e.g. Figure 2.24).

Evidently, each preferred host has distinct but, specific characteristics that create favourable conditions for *P. kirkii* to establish. One such characteristic which has been reported by several authors as significant to host preference, is bark type (Callaway et al. 2002; Mehltreter et al. 2005; Wyse & Burns 2011). The bark of a host has multiple facets which exert influence upon epiphyte colonisation, persistence and diversity, these include: bark rugosity, stability, excretion of allelopathic compounds, and water/humidity holding capacity (Talley et al. 1996a; Callaway et al. 2002; Malizia 2003; López-Villalobos et al. 2008; Valencia-Díaz et al. 2010). Kauri, a preferred host, was historically recorded as a poor host of vascular epiphytes due to its continuously flaking bark (Oliver 1930). However, this has been recently challenged for the lower reaches of trees by Wyse and Burns (2011) who concluded, that of the large forest trees, mature kauri support the largest abundance and diversity of vascular epiphyte species. Furthermore, it was been found that smooth/defoliating barked trees are poor hosts, due to their lack of crevices for humus and moisture accumulation, thus restricting epiphytic colonisation and persistence (Oliver 1930; Akinsoji 1990; Hietz & Hietz-Seifert 1995b). In parallel, cracked/fissured bark types support a greater epiphyte diversity and abundance due to the larger number of crevices available for humus accumulation, propagule establishment, and anchorage of roots (Benzing 1990; Talley et al. 1996b; Malizia 2003). This is exemplified by *P. kirkii* primarily growing in nest epiphytes found upon fissured/cracked barked, such as the preferred host: rimu (Figure 2.24). Additionally, as preferred hosts such as rimu increase in size they often exhibit increased fissuring, which continuously favours epiphyte growth (e.g. epiphyte mats) (Tewari et al. 1985 ; Hofstede et al. 2001; Bryan 2011).



Figure 2.24 Epiphyte mats surrounding the inner-mid areas on branches of a large northern rata/rimu at Mount Taranaki (Photo: S. Edwards). Nest epiphyte community in the primary trunk-branch fork ramification. *Pittosporum kirkii* individual indicated.

2.5.4 Assemblages of co-occurring epiphytes

At the five populations surveyed, 61 different vascular epiphyte species were recorded in association with *Pittosporum kirkii*. The most common of these associates were *Astelia solandri*, *Hymenophyllum* species, *Asplenium polyodon*, *Collosporum microspermum* and conspecific *P. kirkii* individuals. The distributional pattern of these associated species reveals unique patterns of community composition, and microhabitat partitioning on *P. kirkii* hosts.

The vertical distribution (zonation) of associated epiphyte species reveals microhabitat preferences, which relates to the resource partitioning of hosts (Nieder et al. 2000). The vertical zonation of a host is generally shown by the segregation of epiphyte species into distinct microhabitats, which they have adapted to survive in (Johansson 1974; Reyes-García et al. 2008). This zonation is primarily influenced by increasing or decreasing microclimatic gradients, particularly of irradiance, temperature, humidity and wind (ter Steege & Cornelissen 1989; Callaway et al. 2002; Parra et al. 2009). It is also related to, and influenced by, host architecture, humus deposits and tree fall events (Bøgh 1992; Nieder et al. 1999; Nieder et al. 2000).

On *P. kirkii* hosts vertical zonation is shown by the most common associated species, which were more or less abundant across specific zones or microhabitats (see Johansson 1974). This represents eco-physiological adaptations of these epiphytes to changing microclimatic gradients, resulting in their microhabitat specialisation (or partitioning) (Hietz & Hietz-Seifert 1995a; Nieder et al. 2000; Krömer et al. 2007). Consequently, microhabitat specialisation has been found to be prominent in multi-layered forests like those in New Zealand (Gentry & Dodson 1987; Hofstede et al. 2001). This is exemplified by *Hymenophyllum* species predominantly occurring in understory microhabitats while *P. kirkii* primarily occurs in the canopy amongst nest epiphytes. Oliver (1930) lists species restricted to these different areas as either, ‘shade epiphytes’ due to their climatic constraints for high humidity and low irradiance, or ‘sun epiphytes’ which possess xeromorphic features to inhabit the often xeric canopy environment (Oliver 1930; Benzing 1978) (see, Chapter one:

Figure 1.2). Benzing (1981), suggests that this partitioning of preferred microhabitats allows populations of associated vascular epiphytes to exist in perpetuity on a single host with sufficient longevity to minimise competition. Many authors have attributed this to the slow growth of vascular epiphytes (Lüttge 1989; Benzing 1990; Hietz et al. 2002; Schmidt & Zotz 2002).

The distributional patterns of nest epiphytes, and consequently of *P. kirkii*, overlaps in certain zones, but has the highest abundance in the trunk-branch ramification and inner-crown. This demonstrates niche separation and potential competitive interactions (Hietz & Hietz-Seifert 1995a; Jácome et al. 2004). Certainly, several studies have highlighted the diversity and abundance of epiphytes to be highest towards the inner-crown of a host, due to increased stability and humus accumulation afforded in these zones (ter Steege & Cornelissen 1989; Freiberg 1996a; Hofstede et al. 2001; Arévalo & Betancur 2006; Krömer et al. 2007). Consequently, the trunk-branch ramification is also a microhabitat preferred by associated endemic epiphytic shrubs, perched amongst nest species which have colonised epiphyte mats. Of these shrubs, *Pittosporum cornifolium*, *Griselinia lucida*, and *Brachyglottis kirkii* var. *kirkii* were found in association, 25, 29, and 15 percent of the time, respectively. These percentages are

relatively low compared to other epiphytic species such as nest species. The infrequent association of *P. kirkii* with these three shrubs is most likely due to different niche preferences. *Pittosporum cornifolium* and *G. lucida* primarily inhabit lowland old-growth forest and coastal rocky habitats (Bryan et al. 2011; Clarkson et al. *In press*), while *Brachyglottis kirkii* var. *kirkii* also inhabits lowland forest systems and is found further south, specifically across the Ruahine Ranges, where *P. kirkii* is unrecorded (Newhook 1942-3; de Lange 2010). Where habitats overlap interspecific competition may be occurring.

Lastly, tree fall gaps may relate to the distributional overlap of *P. kirkii* and its common nest epiphyte associates. Tree fall events create canopy gaps, which shift the microclimatic conditions and allow for the colonisation of ‘sun epiphytes’ with high irradiance demands further down the trunk of a host, or on the forest floor (ter Steege & Cornelissen 1989). This is illustrated by terrestrial individuals in cut-over and regenerating forest in the Waitakere Ranges and highlights the facultative nature of *P. kirkii*. Therefore, *P. kirkii* demonstrates microclimatic preferences by primarily being restricted to higher light environments in the inner-crown amongst nest epiphytes, or if conditions allow in the understory or on the forest floor.

2.5.5 Growing substrate

The *Asteliaceae* family in New Zealand contain three epiphytic species, which were the most frequent growing substrate of epiphytic *Pittosporum kirkii*, these were; *Astelia solandri*, *Collospermum hastatum* and *C. microspermum*. Commonly referred to as nest epiphytes, these species frequently perch on large ramifications, collecting and accumulating leaf litter debris and dead organic matter through their long narrow leaves, creating moisture rich, albeit low nutrient, arboreal soil (Oliver 1930; Martin 1961; Dawson & Sneddon 1969; Dickinson et al. 1993; Matelson et al. 1993; Affeld et al. 2008) (see, Figure 2.24). Frequently found hanging from the base of these nests is a number of pendulous orchids, such as *Winika cunninghamii*; drooping ferns such as *Asplenium polyodon*; and shrubs such as, *P. kirkii*. This key association has been found by several authors and likely reflects the facilitative succession of vascular epiphytes generally on large

canopy and emergent hosts that *P. kirkii* inhabits (Johansson 1974; Wallace 1981; Yeaton & Gladstone 1982; Dickinson et al. 1993; Nadkarni 2000; Hofstede et al. 2001). This is characterised by the initial establishment of desiccation-tolerant pioneering species such as lichens, which co-occur and ameliorate the bark surface allowing for the growth of epiphyte mats (Johansson 1974; Wallace 1981; Nadkarni 2000). As these thick epiphyte mats develop in humus rich trunk-branch forks, they spread outwards as the host grows, to the inner and mid branches; hence, larger older trees host larger, thicker epiphyte mats (Freiberg & Freiberg 2000; Sillett & Bailey 2003; Krömer et al. 2007; Reyes-García et al. 2008). By functioning in this manner, epiphyte mats have increasingly greater area to retain water and nutrients, capture propagules and provide anchorage for vascular epiphyte seedlings (Nadkarni 1984a; Zotz & Vollrath 2003). Subsequently, epiphyte mats function by ameliorating the microclimatic conditions of the ramosphere (Freiberg 1996b, 2001), thus, creating favourable microhabitats for the growth of detritus collecting nest epiphytes (e.g. *CollospERMUM* species), which in turn ameliorate conditions for shrub epiphytes to colonise in deep humus at the base of these nests.

Another common distinct growing substrate was podzolised kauri soils (detritus) to which terrestrial individuals were entirely confined. Kauri are often present on ridges in yellow-brown clays and loam soils, which are strongly leached and characterised by low fertility (Gibbs et al. 1968). Large kauri exacerbate these soil conditions, by possessing highly acidic leaf litter which accumulate and decompose over extremely long periods of time, due to the longevity of kauri (Jongkind & Buurman 2007; Stewart & Beveridge 2010). Consequently, kauri detritus creates low soil fertility, which can persist for many years even after deforestation events, as poignantly seen by terrestrial individuals persisting on ridges once abundant with kauri in the Waitakere Ranges (Esler 1983; Jongkind & Buurman 2007). Coupled with the latter, is the characteristic open canopy of large old-growth kauri forests. This unique architecture of kauri, creates dry and well-lit microclimatic conditions throughout the canopy and understory, as first recognised by founding botanists upon drought-prone ridges abundant with kauri in Waipoua Forest (Cockayne 1908; Oliver 1930). Hence, the terrestrial environment under large kauri draws parallels with the drought-prone, low

nutrient canopy environment where *P. kirkii* commonly resides. As a result, the unique soil and microclimatic conditions created by kauri exerts influence on the surrounding forest composition, as only a limited set of plant species can colonise and thrive in exposed climatic conditions with highly acidic low nutrient, kauri detritus. Of these species, other typical shrub epiphytes are often found growing terrestrially, including *P. cornifolium* (Clarkson 2011) and *Brachyglottis kirkii* var. *kirkii* (Cockayne 1921).

Another common substrate preference, entirely restricted to Great Barrier Island, was rhyolitic rocky outcrops, at Mount Hobson and Windy Canyon. With the exception of one individual, found in association with *Astelia solandri*, all other individuals were found growing directly on rock and moss clumps. The fine texture and structure of jagged rhyolitic outcrops is perforated with crevices. This allows for the build-up of detritus similar to nest epiphytes and hence, allows for the penetration of *P. kirkii* roots in exposed locations. Many other native plants (e.g. *Kunzea sinclairii* and *Olearia allomii*) are well-adapted to a rupestral lifestyle, possessing similar xeromorphic features to enable survival on a range of rock types (Wardle 1991; Cameron et al. 2002; de Lange & Norton 2004).

The vertical trunk of hosts is believed to be an obstacle to the establishment of vascular epiphytes, primarily due to constant stem-flow and the lack of crevices for colonisation (Benzing 1990). Despite this, the fibrous root mantle of tree ferns was a substrate type for *P. kirkii* and for congener *P. cornifolium*, albeit less commonly preferred (Clarkson 2011). Oliver (1930) initially recognised the specialised growing substrate that a tree ferns root mantle provides to epiphytes, finding that some epiphytic fern species are nearly entirely restricted to them (e.g. *Tmesipteris tannensis*). The root mantle of tree ferns is easily penetrated by the roots of epiphytes, such as *P. kirkii*, and provides relatively high water retention (Cockayne 1921; Oliver 1930; Benzing 2004; Mehltreter et al. 2005). These characteristics differ between tree fern species, for example, tree ferns with persistent skirts are known to be poor epiphyte hosts, and these skirts have been hypothesised to have evolved to prevent epiphyte colonisation (Page & Brownsey 1986; Dawson & Lucas 1993).

To conclude, it appears that *P. kirkii* can tolerate, and has adapted to climatic extremes, being found on a range of substrate types across upper lowland and lower montane old-growth forests, which are themselves subject to extreme variations in environmental conditions. Perched high in the canopy amongst nest epiphytes, periods of drought are assured by high wind and irradiance coupled with the limited capacity of nest epiphytes to retain water (and nutrients) over longer periods of time (Lüttge 1989; Zotz & Hietz 2001; Dawson & Lucas 2005; Moore 2008). These conditions have likely led to the evolution of xeromorphic features in *P. kirkii* (e.g. thick, coriaceous leaves), which have allowed individuals to persist in drought-prone, exposed microhabitats. It is perhaps competition with other epiphytic shrubs, which share similar microhabitats that has resulted in the current narrow distribution and habitat range of *P. kirkii*.

2.5.6 Population characteristics

Dieback, regenerative failures and possum herbivory across the five populations surveyed was not clearly evident or detected by this research. However, the results were not entirely conclusive, due to the relative inaccessibility of the epiphytic lifestyle and research time constraints. The ability to view seedlings from the ground (via binoculars) has limitation, and the capacity to differentiate juvenile individuals is difficult because size does not necessarily correlate to life stage. This was particularly problematic in very tall forests, such as Waipoua Forest.

On Mount Hobson all three life stages and lifestyles were prevalent, with numerous seedlings and reproductive females present. Whereas, all North Island populations had uneven individual life stages, especially Mount Taranaki and Waipoua Forest populations which had limited or no seedlings or juveniles present. A disproportionate seedling to juvenile ratio at Waipoua Forest is because seedlings were clearly visible on kauri snags, which had likely been lethally effected by kauri die back disease (*Phytophthora* taxon *Agathis*) (Kauri Management Dieback Team 2009). However, at Erua Forest and the Waitakere Ranges there appears to be a sufficient number of reproductive females present to maintain regeneration. This may reflect an adequate level of possum control,

reducing herbivory of *P. kirkii* (A. Hawcroft, pers. comm., Department of Conservation 2011).

Every population exhibited, to differing degrees, a clumped distribution pattern across all lifestyle types and life stages. This was seen for terrestrial individuals in each life stage at Waipoua Forest and the Waitakere Ranges; across all populations for epiphytic individuals; and at the rupestral population restricted to Mount Hobson. A clumped spatial pattern encompassing individuals at each life stage, has been found to reflect dispersal limitations, proximity to conspecifics (intraspecific competition) and the structure and composition of a forest (Hietz & Hietz-Seifert 1995c; Zotz et al. 1999; Nieder et al. 2000; Vandunne 2002; Köster et al. 2009).

The epiphytic population of Erua Forest exemplified a clumped distribution, as upon a single emergent rimu up to five *P. kirkii* individuals were recorded. Emergent and large canopy trees likely act as ecological refugia, as previously discussed. Large hosts have greater surface area to capture propagules that are dispersed by birds, hydrochory and gravity, to the multiple microhabitats and tiers of the canopy. Resultantly, a clumped spatial distribution is assured, as only a limited number of preferred hosts and favourable microhabitats are available at any point in time (Hietz & Hietz-Seifert 1995c; Zotz et al. 1999; Nieder et al. 2000). A similar clumped spatial distribution is exhibited by terrestrial individuals growing directly beneath, or in the close vicinity of large kauri. At the Waitakere Ranges and Waipoua Forest, the favourable environmental conditions created by large kauri, which held multiple epiphytic *P. kirkii*, coupled with incidences of hydrochory and gravity, has likely allowed for abundant terrestrial *P. kirkii*. As a result, remnant kauri in the regenerating Waitakere Ranges forest population, likely act as refugia and a possible seed source on regenerating emergent and large canopy species (*cf.* Akinsoji 1990). Mount Hobson rhyolitic outcrops present a similar spatial pattern, with the majority of individuals densely distributed across a number of exposed vertical rock faces. Rupestral individuals on possum-free Mount Hobson were generally smaller, but the population was more abundant than all North Island populations. It has been suggested that by maintaining a small size, vascular epiphytes have greater physiological plasticity to fluctuations

in environmental conditions, as exemplified in the exposed microhabitats *P. kirkii* commonly inhabits (Zotz et al. 2001; Schmidt & Zotz 2002).

As previously mentioned, interspecific competition between vascular epiphytes is reduced, or avoided via partitioning of preferred microhabitats of each epiphyte species. However, the clumped spatial distribution shown by *P. kirkii* individuals, demonstrates that intraspecific relations are likely occurring. Intraspecific relationships occur in epiphyte populations as the result of either the mobility of propagules and dispersers (e.g. birds) or the preference of substrate requirements (Hietz & Hietz-Seifert 1995c). *Pittosporum kirkii* populations may therefore parallel patterns demonstrated in tropical bromeliad communities (Hietz & Hietz-Seifert 1995c; Zotz & Hietz 2001).

2.5.7 Phenology

Pittosporum kirkii flowers annually in late spring-summer, extending from November to February with peak flowering occurring in November-December, after which flowering gradually ceases in February. The flowering season reported in this research is similar to that reported by Allan (1961) and Cooper (1956); November-January, and with slight variance to that reported by de Lange (2006); October-December. Differential flower longevity between male and female flowers likely reflects differences in reproductive investment in both sexes (Primack 1985). Furthermore, flowering records do not suggest different flower peaks across the geographical distribution of *P. kirkii*, including island populations such as Great Barrier Island. Within the New Zealand *Pittosporum* genus there are thirteen species which have a similar flowering season, flowering between November and January (e.g. *Pittosporum rigidum*, *P. dallii* and *P. divaricatum*). The majority of these species are found in similar bioclimatic zones as *P. kirkii*, across upper lowland and lower montane zones, and a few are also found in association with kauri (e.g. *Pittosporum cornifolium*, *P. ellipticum*, *P. pimeleoides* subsp. *pimeleoides* and *P. virgatum*) (Cooper 1956; Allan 1961; NZPCN 2012).

The period of published capsule development is varied, with de Lange (2006) reporting fruiting from January- May and Alan (1961) from November-January, with peak dehiscence occurring in the autumn-winter months. Capsules can persist on a female individual for several seasons with individuals often displaying several different years of capsule development at any one time. Richards (1956) suggested that capsules can take up to three years to mature and dehisce. There were no records indicating that male *P. kirkii* produce infrequent capsules, which has been reported for other members of the *Pittosporum* genus in New Zealand (Godley 1979; Clarkson & Clarkson 1994; Townsend 1999; Clarkson 2011).

Targeted data collection would enhance the understanding of phenology patterns, in particular on capsule dehiscence. Specifically, data is required to better understand development in March, August and September, where no records were available and also for February and April as records were limited.

2.5.8 Sex ratio

The combined phenotypic gender ratio of *Pittosporum kirkii* populations were strongly male-biased (skewed); 18 female: 72 male: 9 unknown individuals. Research has shown that dioecious species with male-bias are related to differential allocation of resources between sexes, in low resourced and perturbed environments (Allen & Antos 1988; Sakai & Weller 1991; Shea et al. 1993). An example of this includes intraspecific competition for niche space between fecund female individuals, which invest greater resources into reproduction than faster growing males, which only invest in producing flowers (Lloyd 1973; Ågren et al. 1986). This differential allocation of resources of males and females likely causes male-biased sex ratios in populations. This can result in contrasting growth and survival rates: slower growth and higher mortality in female individuals, and different growth patterns: males are larger in size and out-compete females for favourable habitat (Lloyd & Webb 1977; Allen & Antos 1988, 1993). A study by Barradas & Correia (1999) also supported the latter, finding that males are more competitive in resource limited habitats; which draws parallels with the drought-prone and generally low nutrient canopy microhabitats of epiphytic *P. kirkii*.

The current male-biased sex ratios in *P. kirkii* populations may potentially limit regeneration and increase the possibility of inbreeding depression due to the relatively low proportions of females producing seed and contributing to the genetic diversity of subsequent generations (Ackerly et al. 1990; Delph & Wolf 2005).

2.5.9 Anatomical analysis

The leaf, root and stem anatomies of *P. kirkii* displayed xeromorphic characteristics similar to other shrub epiphytes endemic to New Zealand (Oliver 1930). In the root and stem anatomies the xeromorphic features that are evident include, highly developed peridermal layers and a wide casparian strip surrounding the endodermis. These features may prevent and reduce excess water loss in times of desiccation stress (Ginzburg 1966). The leaf anatomy displayed similar features associated with xeromorphy. These include a thick coriaceous lamina with a thick cuticle and water storage tissue (hypodermal tissue). Oliver (1930) describes the water storage tissue and xeromorphic features of the four endemic epiphytic shrubs, however, oddly ignored *P. kirkii* in his detailed transverse sections. Another xeromorphic feature restricted to the leaves of young *P. kirkii* seedlings is the presence of multicellular capitate glandular trichomes which are caducous in nature. It is known that a function of trichomes is to reduce water loss and to increase water absorption which is vital in drought-prone canopy habitats (Benzing 1990).

Overall, these xeromorphic features have been reported in other *Pittosporum* species (Wilkinson 1992), and have been heralded as an evolutionary adaption for plants to survive in drought prone habitats (e.g. the canopy environment) (Seddon 1974; Waldhoff & Parolin 2010).

2.5.10 Leaf and capsule morphology

The mean leaf length of 82.6 ± 1.8 mm of *Pittosporum kirkii* places it in the notophyll leaf size category as described by Dawson (1986b). Dawson (1986b) suggests that species in this category have adapted to survive in cold conditions

and thus, are able to persist through glaciation events, which is demonstrated by the current distributional range of *P. kirkii*, in terms of both latitudinal and altitude (discussed previously). Although, a correlation with altitude was not found between leaf size and capsule size, there was evidence that leaf size displayed clinal traits with increasing latitude. This was statistically supported, as leaf length decreased with increasing latitude, as shown also for *Pittosporum obcordatum* (Clarkson & Clarkson 1994). Clinal patterns of physical traits increasing or decreasing monotonically along an environmental gradient are known to be common across plant species (Jonas & Geber 1999). An example this is a latitudinal gradient which encompasses a number of complex environmental variables which change with latitude these include; temperature, solar radiation and rainfall (Li et al. 1998). Thus, as latitude decreases the environmental variables associated with latitude impact upon leaf size. Certainly, native *Myrsine* species, show a latitudinal trend of decreasing leaf size with increasing latitude, while other *Pittosporum* species are noted to have smaller leaves at higher altitudes (Dawson 1986b).

Lastly, although no statistically significant variation was found between Mount Hobson (Great Barrier Island) and North Island population's, notable observed differences on Mount Hobson of smaller capsules and narrower leaf size, require further investigation.

2.5.11 Conservation implications

Aside from Great Barrier Island where *Pittosporum kirkii* is abundant, the species appears to have always been a sporadically occurring local species of kauri dominated and mature-old growth forests in upper lowland and lower montane ecosystems. Consequently, *P. kirkii* may not be in decline as currently listed (de Lange et al. 2009). The current lack of ecological knowledge, coupled with its strict habitat and host preference, may mean the species could be classified as naturally uncommon. In fact, Rogers and Walker (2002) found that a large number of New Zealand *Pittosporum* species are naturally uncommon due to specific and narrow habitat requirements. However, while the current distribution of *P. kirkii* suggests that it is ecologically sparse, it is also likely to be vulnerable

to possum herbivory, and some populations were probably lost or reduced by destructive logging of kauri, and of large canopy, and emergent trees (McGlone 1989; Brandon et al. 2004; Forester & Townsend 2004). The palatability of *P. kirkii* to possums is unconfirmed as only anecdotal evidence has been recorded. However, the limited North Island populations in contrast to the abundant population on possum-free Great Barrier Island, suggests that *P. kirkii* is threatened by possum herbivory. This could be due to a number of reasons including, inadequate possum control at mainland populations and/or slow recovery rates after recent possum control. Overall, as the data quality available on the possible threats is poor, uncertainty remains about the current declining threat status of *P. kirkii* (Townsend et al. 2008; de Lange et al. 2009).

Informed conservation management is critical to the survival and regeneration of *P. kirkii* populations. This was highlighted in the Waitakere Ranges where a tramping track provided high light penetration that facilitated the growth of a *P. kirkii* individual in an unusually low epiphytic position. Unfortunately, when the track was re-directed to protect this plant from human disturbance, the subsequent understory growth reduced light availability and the plant died (S. Jones, pers. comm. Auckland Botanical Society 2011). Thus, it is suggested that the application of ecological knowledge in conservation management would be beneficial for the effective protection of this species.

Education would be a useful tool for increasing the appreciation of *P. kirkii*, but also to address the current information gap through enabling people to identify, assess and report the locations and condition of *P. kirkii* individuals; potentially leading to a better understanding of its natural range and threat status. On-going public education about kauri die back disease (*Phytophthora* taxon *Agathis*) is also vital to protect terrestrial, and epiphytic *P. kirkii* communities that exist in the unique conditions that large kauri create. This has two-fold importance, firstly to protect the current hosts, habitat and seed source of many *P. kirkii* individuals, and secondly, to ensure the seed source of future kauri hosts and habitat.

There are myriad factors that are potentially causing the decline of *P. kirkii*. These include; the inherent slow growth rate that is a feature of vascular epiphytes in

general (Benzing 1990; Schmidt & Zotz 2002), the potential limitation of seed dispersal due to limited bird dispersers (see, Kelly et al. 2010), skewed sex ratios of populations due to intraspecific competition with conspecifics (e.g. Hietz & Hietz-Seifert 1995c), unavailability and loss of suitable hosts and microhabitats, and possum browse; particularly of succulent new growth (including seedlings) and flowers. However, the data quality available on these potential threats is either poor or anecdotal as is particularly the case for possum browse. Hence, it is recommended that a scientific possum palatability trial be undertaken (Mallinson & Hickling 1993) to investigate if possum browse is detrimentally effecting populations.

This species also should be considered for inclusion in suitable restoration plantings and reintroduction projects, given its sparse distribution and absence from predicted locations. Certainly, this has been recognised in a few restoration programmes which have included *P. kirkii* in their restoration planting plans. These include Matakohe/Limestone Island restoration plan (Ritchie 2000) and the Waitakere Ranges threatened species management plan (Waitakere Threatened Species Management Policy 2009).

Chapter Three: Water relations of *Pittosporum kirkii* and *P. cornifolium* under desiccation stress

3.1 Introduction

Vascular epiphytes in New Zealand's temperate forests constitute a significant proportion (25–50%) of all plant species present, with their biomass often exceeding that of the foliage of their host tree (Dawson 1986a; Gentry & Dodson 1987; Hofstede et al. 2001). Perched in the canopy, vascular epiphytes are divorced from terrestrial soil and are exposed to the desiccating effects of high irradiance and wind and limited by the irregular supply of water and nutrients in the ramosphere (Benzing 1987, 1990; Freiberg 2001; Larcher 2003; Moore 2008). Epiphytes exhibit a range of morphological adaptations and physiological responses that are critical to survival in these often harsh conditions, and are typical of plants classed as xerophytes (Lüttge 1989; Moore 2008). Several authors have listed a number of xeromorphic adaptations, these include: thick waxy cuticles, thick hypothermal layers, multiple layers of palisade cells, sunken stomata, mucilage and trichomes (Seddon 1974; Richards 1983; Benzing 1990; Kirkham 2005). However, the bulk of literature on the physiological responses and water relations of epiphytes under desiccation stress primarily emanates from research undertaken on tropical epiphyte families, particularly the Bromeliaceae (Griffiths & Smith 1983; Griffiths et al. 1989; Nowak & Martin 1997; Graham & Andrade 2004; Bader et al. 2009) and Orchidaceae (Sinclair 1983a, b; Zotz & Tyree 1996).

Numerous classification schemes have been produced to categorise and align the physiological responses of plants under desiccation stress with Shantz (1927) being one of the first to mention epiphytes, aligning them under a drought resistant category. Classifications have since advanced with Ludlow (1989) broadly classifying terrestrial and epiphyte species into three main stress strategies according to their morphological features and physiological responses; desiccation escape, desiccation postponement and desiccation tolerance. Each stress strategy involves a trade-off between the plants potential growth rate and the ability to survive drought (Ludlow 1989; Lambers et al. 2008; Bader et al. 2009). It has

been recognised that plants are not restricted solely to one distinct stress strategy; instead they can display phenotypic and developmental plasticity along a spectrum of stress strategies at each life stage (Fisher & Ludlow 1984; Ludlow 1989). Hence, the developmental stage of an epiphyte affects which part of the drought response spectrum they are aligned with. This is widely reported for seedlings which are less desiccation tolerant and demonstrate greater plasticity in physiological responses than adults (Donovan & Ehleringer 1991; Zotz & Tyree 1996; Zotz 1997a, 2000; Schmidt et al. 2001; Zotz et al. 2001).

3.1.1 Stress strategies for xerophytes

Desiccation escape strategy

Plants that escape drought (Table 3.1) display a set of responses which often allow dormancy during extreme desiccation conditions, this is exemplified by species that produce dormant seeds in seasonally arid environments (Benzing 1990). A key feature of plants that escape or evade drought is developmental plasticity, of which desert ephemerals are a prime example (Ludlow 1989; Larcher 2003). Highly sensitive to drought and with rapid transpiration, desert ephemerals such as the annual grass species *Avena barbata*, germinate and flower rapidly only when there is sufficient moisture to do so (Shantz 1927; Ludlow 1989; Sherrard & Maherali 2006). This has been hypothesised to be an evolutionary growth advantage; as plants have a short, fecund life cycle; reaching maturity and setting seed before soil moisture dissipates and harsh drought conditions return (Sherrard & Maherali 2006; Donovan et al. 2007). Developmental plasticity responses are not limited to this example, with some plants in this strategy also displaying morphological and physiological characteristics to moderately tolerate and escape desiccation conditions, such as osmotic adjustment (Ludlow 1989). Vascular epiphytes do not typically adopt this strategy (Benzing 1990), likely because the epiphytic lifestyle does not provide long term substrate stability (Bryan 2011) to store dormant seeds over significant periods of time.

Desiccation postponement strategy

Desiccation postponement was historically categorised as desiccation avoidance (Table 3.1), but this term has become redundant as drought avoiders belong to the escape strategy: avoiding drought through seed dormancy and developmental plasticity (Ludlow 1989; Benzing 1990). Ludlow (1989) recognised the distinct difference between the two stress strategies, finding that plants are able to postpone the detrimental effects of desiccation through a number of physiological and morphological responses. However, plants with this strategy are strongly sensitive to dehydration, and so to postpone the effects of desiccation they maintain high water potential and turgor for as long as possible (Ludlow 1989; Larcher 2003). To do this, postponers undertake two key responses, these include either maximising water uptake and/or reducing water loss (Ludlow 1989) this is achieved through a multitude of adaptations and features (Ludlow 1989; Benzing 1990). Desiccation-postponement adaptations include, rapid stomata responses; high root-to-shoot ratios; small, coriaceous, fleshy, and waxy leaves, dense indumenta and sunken stomata (Turner & Burch 1983; Akinsoji 1990; Kozlowski & Pallardy 2002).

Vascular epiphytes which exhibit this strategy include tropical orchids and bromeliad species, which characteristically utilise physiological adaptations of crassulacean acid metabolism, highly elastic cell walls and low stomatal conductance to postpone the effects of desiccation (Stiles & Martin 1996; Zotz & Tyree 1996; Nowak & Martin 1997; Zotz & Andrade 1998; Graham & Andrade 2004).

Desiccation tolerance strategy

The last stress strategy utilised by xerophytes is desiccation tolerance (Table 3.1). The well-known, extreme example of this strategy is that of resurrection plants or poikilohydric plants (Larcher 2003; Lambers et al. 2008). These plants enter and show remarkable recovery from anhydrobiosis; regaining full turgor from under two percent relative water content only a few days after re-watering (Bewley 1979; Gaff 1981; Ingram & Bartels 1996). However, resurrection plants only form a small, albeit notable group of desiccation tolerators. The majority of plants in this strategy belong to two main groups; those that tolerate desiccation stress at a low

water potential with high relative water content and those that tolerate with both a low water potential and low relative water content (Kozłowski & Pallardy 2002).

Cell wall elastic adjustment and osmotic adjustment are two physiological responses which have been noted to be prominent in desiccation tolerant plants at low water potentials (Turner & Begg 1981; Turner 1986). Osmotic adjustment involves an increase in solute concentration within the cytoplasm and vacuole, lowering the osmotic potential and maintaining turgor despite a decreasing water potential (Hsiao et al. 1976). Turgor can also be maintained by an increase in cell elasticity, expressed as the bulk modulus of elasticity (ϵ) (Lambers et al. 2008). An increase in cell wall elasticity (decrease in ϵ) increases the turgor potential for a given relative water content. An increase in elasticity results in prolonged turgor maintenance under desiccation stress by allowing more tightening of the cell wall as cells shrivel due to water loss (Kozłowski & Pallardy 2008; Lambers et al. 2008). These responses maintain turgor through different mechanisms which physiologically acclimate plants to desiccation conditions over a period of time. They cannot occur concurrently to the same degree, as increases in cell wall elasticity alongside osmotic adjustments would cause cells to rupture due to the accumulation of solutes (Lambers et al. 2008). Instead, desiccation tolerant plants either maintain turgor and reduce water loss at high relative water content through osmotic adjustment or, endure higher water loss through adjustments of cell wall elasticity at low relative water content by having greater capacity to store and release water (Lambers et al. 2008) (see, Table 3.1).

A high number of tropical epiphytes such as cacti (Andrade & Nobel 1997), bromeliads (Stiles & Martin 1996; Bader et al. 2009) and ferns (Sinclair 1984; Zhang et al. 2009) are categorised as desiccation tolerant. This has prompted authors to hypothesise that this stress strategy predominates throughout the epiphyte lifestyle; as it has often been associated with the slow growth rates of epiphytes and their ability to survive the environmental constraints faced in drought-prone canopy habitats (Lüttge 1989; Benzing 1990; Martin et al. 2004).

Table 3.1 Desiccation strategies of xeromorphic plants with key responses and examples. A plant can have multiple morphological and physiological characteristics aligning with multiple strategies; forming a continuum of responses as reported by Ludlow (1980). Adapted from Shantz (1927); Fisher & Ludlow (1984); Levitt (1980); Ludlow (1989); Kozłowski & Pallardy (2002, 2008); Lambers et al. (2008); Turner (1989) and Henson (1989). **WP** = water potential; **RWC** = relative water content.

Plant strategies	Morphological and physiological responses	Examples
Escape or evade	<ul style="list-style-type: none"> • Rapid life cycle and developmental plasticity 	Primarily desert annuals
Postpone (historically, avoid)	<ul style="list-style-type: none"> • Low WP prevented, or postponed / maintain a high WP • Improved water uptake, or reduced water loss 	Desert succulents and vascular epiphytes
Resist or tolerate	<ul style="list-style-type: none"> • Tolerance at low WP: turgor maintained by various physiological and morphological adaptations • Low WP endured with low RWC • Low WP maintained with high RWC 	Some crop plants, e.g. wheat and cotton, vascular epiphytes and resurrection plants

3.1.2 Water relations of *Pittosporum kirkii* and *P. cornifolium*

Limited research has been conducted on vascular epiphytes in New Zealand with respect to their water relations and physiological responses to the desiccation which typifies their habitat. Studies have instead been focused on morphological descriptions (e.g. thick cuticle) (Oliver 1930) and casual observations (e.g. “not bothered by drought”) (Smith 2004). It has been hypothesised that epiphytes predominantly use physiological responses and morphological features typical of the desiccation tolerance strategy (Benzing 1990; Martin et al. 2004). However, a recent investigation by Bryan (2011) has revealed that the New Zealand endemic hemi-epiphyte, *Griselinia lucida*, adopts both desiccation tolerance and desiccation postponement strategies.

The present research focuses on the water stress strategies of shrub epiphyte, *Pittosporum kirkii*. This species is an epiphyte of upper lowland and lower montane forests and one of two *Pittosporum* epiphytes in New Zealand; the other being *P. cornifolium*. *Pittosporum cornifolium* was included in this study to investigate how these related *Pittosporum* species respond to desiccation stress

and to identify any differences related to the different bioclimatic zones they typically inhabit. These two species were also chosen for this research as there is a paucity of information on the water relations of these shrubs and specifically on how they respond to the periodically drought-prone, arid conditions of their canopy microhabitat.

The leaf morphologies of *P. kirkii* and *P. cornifolium* are distinctively different. *Pittosporum kirkii* possess dark green leaves approximately 1300 µm thick (see, Chapter two) at the midrib, are very thick, and coriaceous. Features such as these are often characterised as xeromorphic adaptations to withstand drought conditions and postpone its effects (Oliver 1930; Dawson 1986a; Benzing 1990; Martin et al. 2004). In contrast, *P. cornifolium* has relatively smaller, thinner leaves, 500 µm thick, that are less coriaceous and generally lighter green in colour (Clarkson 2011). Both *Pittosporum* species have been found to have relatively thick upper cuticles above hypodermal water storage tissue (see, section 2.4.11; Clarkson 2011); features which have been also suggested to reduce desiccation stress (Oliver 1930).

Ecologically, both epiphytic shrubs share similar microhabitats as previously stated. However, they commonly established in distinctively separate bioclimatic zones which are subject to different environmental extremes (Moore 2008). *Pittosporum kirkii* is primarily found in upper lowland and lower montane ecosystems, which are often subject to a combination of extreme environmental factors; drought, low temperatures, and high wind velocities and rainfall (Grubb & Whitmore 1966; Webb 1968). As a result, *Pittosporum kirkii* likely possesses an array of both morphological adaptations and physiological responses to survive in such environmental extremes. In contrast, *P. cornifolium* predominately inhabits lowland and coastal ecosystems (Clarkson 2011), which may generally be drier with higher salinity, but with less extreme fluctuations in temperature, wind and water availability.

As a result of these distinctively different morphological features and the occupation of environmentally dissimilar bioclimatic zones by *P. kirkii* and *P. cornifolium* it was hypothesised that:

1. The thick, coriaceous and fleshy leaves of *Pittosporum kirkii* are able to postpone desiccation by reducing photosynthetic function and facilitating rapid recovery from drought. This is likely achieved through the rapid closure of stomata and reliance on stored water that prevents or delays the onset of more negative leaf water potentials.
2. *Pittosporum cornifolium*, inhabiting a less environmentally extreme bioclimatic zone, with thinner, less coriaceous leaves; will have less ability to store water than *P. kirkii*. Under desiccation stress it will exhibit responses associated with the desiccation tolerance stress strategy through osmotic maintenance of turgor and high photosynthetic rates under lower leaf water potentials.

This chapter presents a drought experiment, investigating the water relations of *Pittosporum kirkii* and congener, *P. cornifolium*. It discusses and compares the morphological features, physiological responses and desiccation stress strategy that each *Pittosporum* species may be aligned with during their seedling developmental stage.

3.2 Materials and Methods

3.2.1 Plants and glasshouse conditions

Seedlings of both *Pittosporum* species were sourced from Oratia Nursery (Auckland) in March 2011. The seed source was from the Waitakere Ranges. *Pittosporum kirkii* seedlings were three years old. They were root bound when received and short in height; on average, 18.3 ± 0.8 centimetres tall. The *Pittosporum cornifolium* seedlings were two years in age and an average of 25.2 ± 0.4 centimetres in height when received. Both species were re-potted with standard potting mix (“Just” brand, Daltons Ltd., NZ with Osmocote® controlled release fertiliser) within one week of arrival in 1.5 litre plastic pots. Leaf thickness was measured at the midrib in the middle of the leaf with an electronic calliper, which was modified to allow for readings that were accurate to 0.01 mm at a single point. A total of 78 mature leaves were randomly chosen from separate

plants of each species and across the three treatments (see experimental design, below). Measurements of leaf tissue thicknesses were made using optical microscopy; the detailed methodology is described in Chapter two. The numbers of leaves were counted each week for every plant. The experiment was conducted over the spring months of September and October in a climate controlled glasshouse. The temperature (°C), photosynthetically active radiation (nm) and relative humidity (%) were recorded and are presented (Table 3.2).

Table 3.2 Mean, minimum and maximum temperature (T), relative humidity (RH), and photosynthetic photon flux density (PPFD) in glasshouse over the duration of the experiment. Standard error of means are shown in parentheses.

	PAR ($\mu\text{mol m}^{-2}\text{s}^{-1}$)	Temperature (°C)	RH (%)
Mean	93.9 (± 1.3)	20.8 (± 0.03)	53.1 (± 0.12)
Minimum	-0.184	9.72	27.26
Maximum	931	30.16	105.9

3.2.2 Experimental design

A randomised block design was used to position 117 seedlings into nine rows (Martin & Ogden 2005). Each seedling was randomly chosen and positioned into a row, with each row having an equal number of each species in each treatment. A randomly selected subset of 27 plants (three plants of each species of each treatment) was chosen to measure leaf number and pot weight twice a week. Pots were weighed using a Denver XL-6100 balance.

Seedlings were drought hardened for one week. This was done to acclimatise plants to the glasshouse environment and to provide conditioning similar to that of *in situ* seedlings that must acclimate to drought early in a natural canopy habitat (Lüttge 1989; Bader et al. 2009). Drought hardening of seedlings is likely to provide an advantage to *in situ* epiphytes by initiating the development of mechanisms to morphologically and physiologically respond to periodically dry conditions (Kozłowski & Pallardy 2008; Bader et al. 2009). In the first week, pre-dawn water potentials and pot weights were measured twice. This was undertaken to create a baseline for the experiment by determining soil volumetric water content and thus to estimate the weight (and volume) of water required to water

each plant back to their initial pot capacity volume. The goal of this was to enable the creation of three stress treatment categories; control, moderate and severe. The control treatment was watered twice a week to ensure the pot weight remained the same as the initial mean weight. The moderate treatment was similarly watered twice a week with a reduced volume of water to create 'moderate' stress at water potentials between -0.3 and -0.4 MPa for both species; measured pre-dawn. The severe treatment stress was created by not watering for the duration of the experiment.

The length of the experiment was 42 days. Once 25 % of individuals across both species in the severe treatment reached severe predawn wilting point (Ealson & Richards 2009; Yadollahi et al. 2011) the experiment was concluded and plants were re-watered.

3.2.3 Plant harvest and relative growth rates

The harvesting of plants to calculate relative growth rates occurred at the beginning and end of the experiment. At the start, plants were selected randomly from each species ($n = 14$). At the end, selected plants were chosen randomly from each species and each treatment ($n_{\text{end}} = 18$). A greater number of plants were available for harvest at the end for comparison between stress treatments. Harvesting occurred in the glasshouse so as to maintain constant environmental conditions between the harvest of each individual. The leaves, roots and stems of each individual were separated and immediately weighed using a Mettler AE260 balance to record the fresh weight. Following this the leaf area of each plant were measured using a Li-Cor Li-3100 area meter. All three parts of the plant were then immediately placed into a standard herbarium oven (36 °C) to dry for five days. Leaf counts and mean leaf area per leaf from each species in each stress treatment were used to calculate total plant leaf area for non-harvested plants. Relative growth rates were calculated with the dry weight of leaves, roots and stems from each species and each treatment using an excel programme developed by Hunt et al. (2002).

3.2.4 Leaf water relations

Leaf water potentials (ψ_{leaf}) were measured in a pressure chamber (Model 1505D PMS Instrument Co.), following the Boyer (1995) and Scholander et al. (1965) methodology. The creator of the pressure chamber, Scholander et al. (1965), found that it can be utilised to directly measure xylem pressure (generally negative) in the xylem. Xylem pressure was measured at pre-dawn (ψ_{pd}) and midday (ψ_{md}) once a week on randomly selected individuals: three from each stress treatment, from each species. It was also measured after re-watering at week seven. Before being placed in the pressure chamber, leaves and petioles were rapidly excised at a slight angle to the plant and placed in a small humidified plastic bag to prevent transpiration and discrepancies in xylem pressure measurements. Pre-dawn measurements were taken before significant evapotranspiration demand, and were assumed to be the equivalent of average soil water potential. Pre-dawn measurements were used to indicate when plants in each treatment were approaching the desired stress level (van Oostrom 1985). Conservative methods were used to ensure only five percent of leaves were taken for pressure chamber measurements over the duration of the experiment, as otherwise it may have biased the results by detrimentally effecting the leaf area and growth rates of the plants.

3.2.1 Osmotic potentials

Osmotic (symplasmic) potentials of each species in each treatment were measured using a vapour pressure osmometer (Vapro 5600, Wescor, Logan, Utah). Six leaves from each treatment from each species ($n_{\text{total}} = 36$), were taken from the harvested individuals at the end of the experiment. The leaves were immediately frozen in liquid nitrogen, wrapped in aluminium foil and placed in a freezer (-20 °C) until required for sap extraction and osmotic potential measurements. Initial trails using a hydraulic press were unsuccessful in extracting sap from both *Pittosporum* species in each stress treatment. This was attributed to the highly viscous nature of *Pittosporum* cell sap; a feature of the genus as a whole (Gowda 1951; Haas 1977). Therefore, a different method was applied, where a leaf from each stress treatment were taken from the deep freeze, frozen again in liquid nitrogen, broken up into a centrifuge vial and spun in a Beckman Coulter E

Centrifuge for five minutes (e.g. Dey et al. 1997). After this treatment, the highly viscous sap was extracted with a pipette. The osmolality of this sap was determined by an osmometer and these measurements were expressed as MPa by converting them with the van 't Hoff equation (see, Nobel 2009).

3.2.2 Stomatal conductance and photosynthesis

Stomatal conductance (g_s) and photosynthesis (A) were measured once a week at midday, and at week seven after re-watering took place. Plants were measured at their block positions in the glasshouse using a portable photosynthesis system with an artificial light source (LI-6400XT, Li-COR, Inc., Lincoln, Nebraska). The system was acclimatised to glasshouse conditions for half an hour before measurements were taken. Three plants from each stress treatment ($n = 21$) were randomly chosen and the photosynthesis and stomatal conductance of the youngest fully expanded leaf was measured on each plant at midday. The cuvette temperature and photosynthetically active radiation (PAR) were matched to glasshouse conditions.

3.2.3 Cuticular conductance

At the start of the experiment cuticular conductance (g_c) was measured following Sack et al. (2003). Cuticular conductance was determined by recording the weight loss of three leaves from each species until loss (in grams) was negligible. Leaf weight was measured every 15 minutes for five hours then every hour for three hours. The equation used to calculate cuticular conductance for each *Pittosporum* species was:

$$g_c = \mathbf{T}/\mathbf{D}_1$$

Total cuticular conductance, g_c , ($\text{mol.m}^2.\text{s}^{-1}$), was determined by the rate of transpired water lost per area over time (\mathbf{T}); divided by the differences in water vapour concentration between the air and leaf (\mathbf{D}_1); which was calculated from recording relative humidity (%) and air temperature ($^{\circ}\text{C}$) measured with a hygro-thermometer (Extech EasyView™20).

3.2.4 ^{13}C measurements

Foliar delta carbon-13 analysis ($\delta^{13}\text{C}$) of *P. cornifolium* and *P. kirkii* individuals in the control, moderate and severe stress treatments were undertaken to determine and compare water use efficiency (Lambers et al. 2008) under different degrees of desiccation stress. The first fully expanded leaves were taken at the end of the final harvest ($n_{\text{total}} = 24$) and dried in a standard herbarium oven (36 °C) for seven days. The leaves of each plant were then finely ground for $\delta^{13}\text{C}$ isotope composition (‰) by the Waikato Stable Isotope Unit at the University of Waikato. A less negative leaf $\delta^{13}\text{C}$ is known to equate to higher water use efficiency because with decreasing stomatal conductance (increasing drought stress) more $^{13}\text{CO}_2$ accumulates in plant biomass (Farquhar et al. 1989; Lambers et al. 2008).

Mature leaves collected from *in situ* epiphytic ($n = 15$), terrestrial ($n = 14$) and rupestral ($n = 3$) *Pittosporum kirkii* individuals were also analysed using the above method. This was done to compare water use efficiency across all three distinct lifestyles.

3.2.5 Statistical analysis

Analysis of Variance with Tukey's Honestly Significant Difference test were undertaken to analyse physiological data. The conditions of normality were assessed with the Shapiro-Wilk test. When sample sizes were over 30 the assumptions of homogeneity were ignored as data sets met the central limit theorem (Rosenblatt 1956). Hence, data sets with less than 30 samples were analysed using non-parametric Kruskal-Wallis ANOVA. Linear regression was utilised to investigate correlations between variables. The null hypothesis was rejected and statistically significant results were reported when the p-value was significant (<0.05).

3.3 Results

3.3.1 Leaf growth

The absolute growth in leaf area (cm^2) of treatments for both species was variable (Figure 3.1) and did not show statistically significant differences between any of

the groups. The moderate and severe stress treatments for *Pittosporum cornifolium* showed negative growth; indicating leaf loss in both drought treatments. The moderate stress treatment for *P. kirkii* displayed higher growth than the control, and both the control and moderate treatments showed higher growth than the severe treatment. The change in absolute leaf thickness across stress treatments indicated a trend of decreasing thickness with increasing stress (Figure 3.2). It also showed the general difference in leaf thickness between both *Pittosporum* species. In both species, the control and moderate treatments were similar, with the severe stress treatments being significantly thinner at the midrib than the controls; *P. kirkii* $P = 0.05$, *P. cornifolium*, $P = 0.03$.

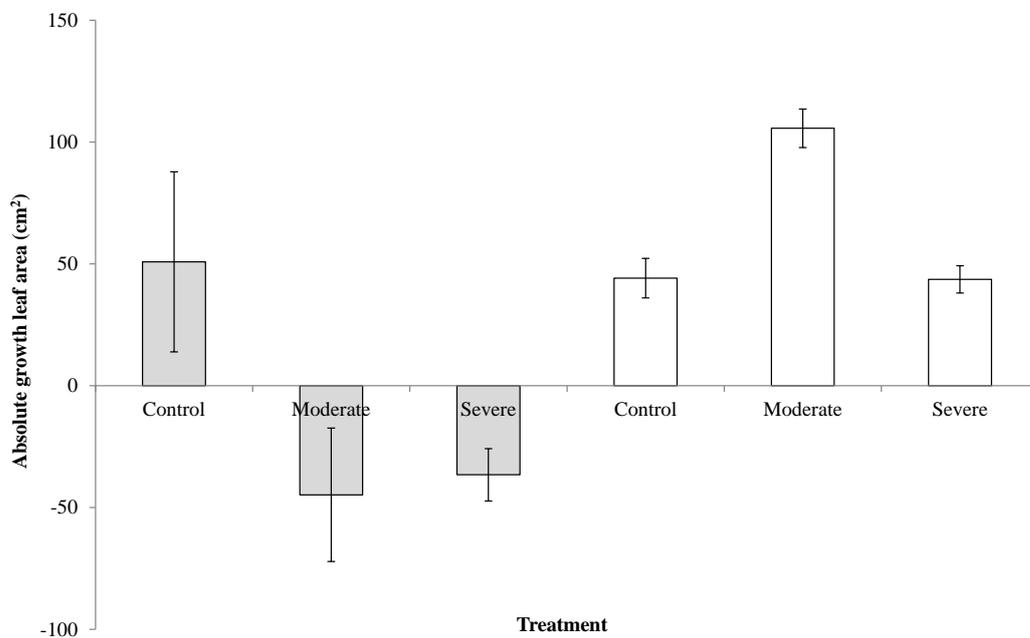


Figure 3.1 Absolute growth (cm²) in leaf area over the duration of the experiment for *Pittosporum cornifolium* (closed bars) and *Pittosporum kirkii* (open bars) in each treatment group. Standard error of means are shown.

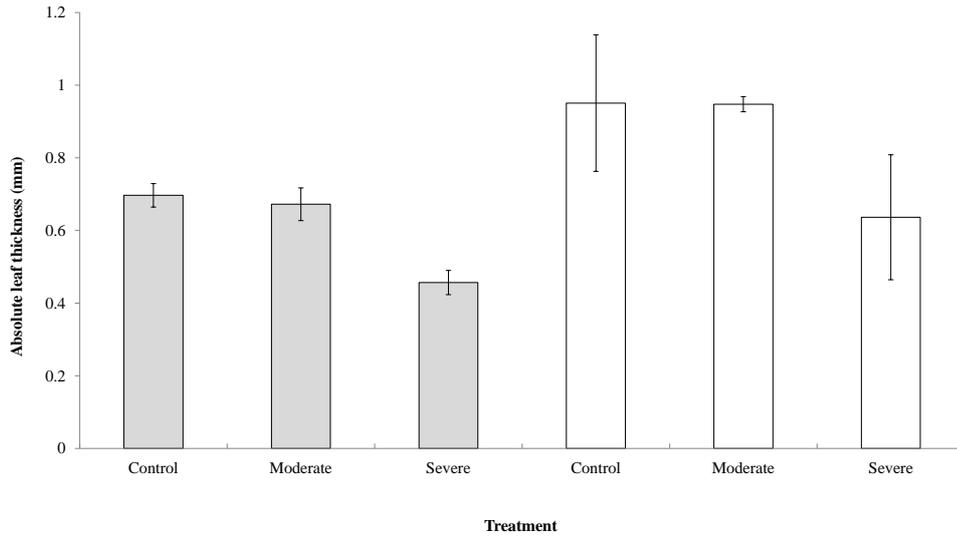


Figure 3.2 Absolute leaf thickness (mm) over the duration of the experiment for *Pittosporum cornifolium* (closed bars) and *Pittosporum kirkii* (open bars) in each treatment group. Standard error of means are shown.

3.3.2 Relative growth rates

The relative growth rates of the leaves, shoots and roots of each species are shown in Figure 3.3. The weight of each plant part decreased with increasing desiccation stress. However, due to a large standard error this trend was not significant.

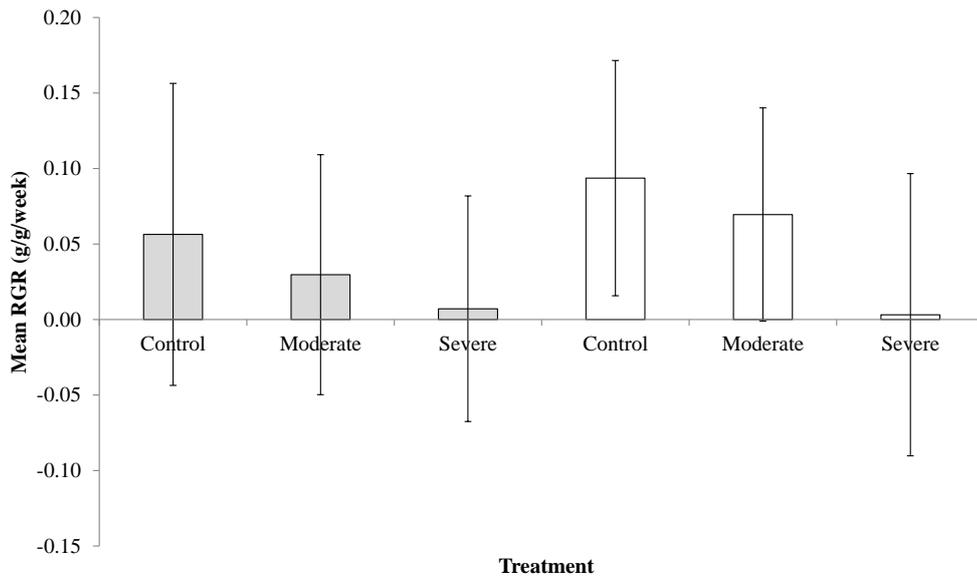


Figure 3.3 Relative growth rates (g) for *Pittosporum cornifolium* (closed bars) and *Pittosporum kirkii* (open bars) in each treatment group. Standard error of means are shown.

3.3.3 Time course of water potential, stomatal conductance and photosynthesis

The time course of midday water potential (ψ_{vmd}), stomatal conductance (g_s), and photosynthesis (A) for the control and severe treatments is shown in Figure 3.4. Overall both species displayed similar reduced function but at different rates over the course of the experiment. Midday water potential and stomatal conductance declined rapidly at week two for *Pittosporum cornifolium*, while *P. kirkii* showed a more gradual descent. The stomatal conductance and photosynthesis of both species reached almost zero at week six and showed a rapid recovery in all measured functions after re-watering, with photosynthesis being the fastest function to fully recover to pre-stress levels. There are slight fluctuations in the response of each control treatment, but these are not pronounced. High standard errors for certain weeks reflects variation amongst the individual plants, this is particularly evident for week seven (re-watered week) of the control treatment for photosynthesis.

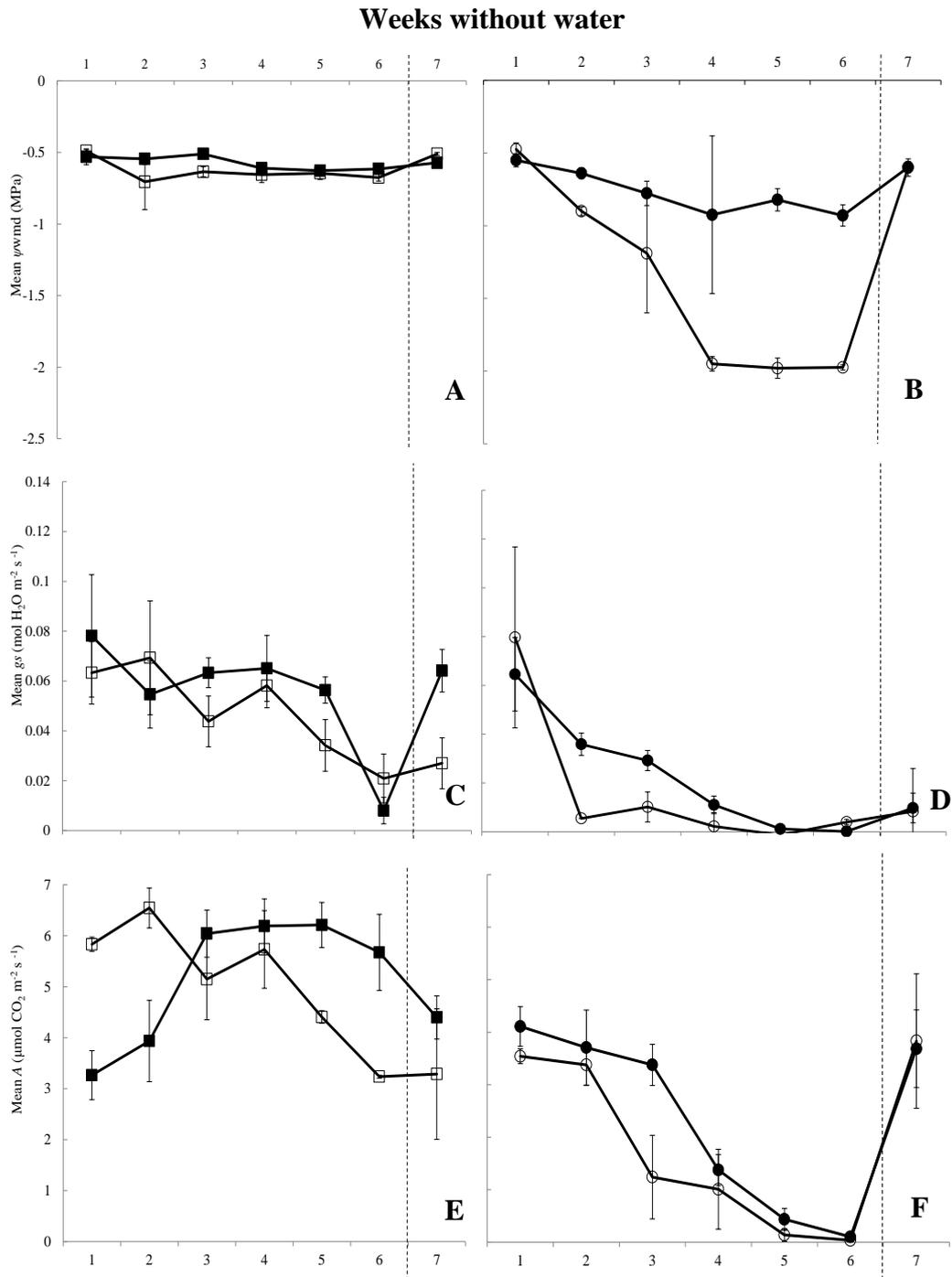


Figure 3.4 Time course of midday water potential (ψ_{wmd}), stomatal conductance (g_s), and photosynthesis (A) for *Pittosporum cornifolium* (open symbols) and *Pittosporum kirkii* (closed symbols) in the control (A, C, E) and severe stress (B, D, F) groups. The dashed line represents the final week of treatments and week seven (re-watered) to highlight the recovery of both species. Standard error of means are shown.

3.3.4 Leaf and plant characteristics

Table 3.3 shows selected leaf characteristics and traits for *Pittosporum kirkii* and *P. cornifolium*. The mean area per leaf, fresh weight per unit area, specific leaf area and cuticular conductance (g_c) were significantly higher for *Pittosporum kirkii* than for *P. cornifolium* ($P = 0.003$). While mean leaf thickness was significantly higher for *P. kirkii* ($P = 0.01$).

The variable size of both species at the start of the experiment is shown in Table 3.4. *Pittosporum kirkii* has a smaller mean height, with lower number of leaves and leaf area than *Pittosporum cornifolium*.

Table 3.3 Mean leaf area per leaf, thickness, specific leaf area (SLA) and cuticular conductance (g_c) ($\text{mol m}^{-2}\text{s}^{-1}$) per leaf for *Pittosporum cornifolium* and *Pittosporum kirkii*. Standard error of the means are presented in parentheses.

Species	Leaf area (cm^2)	Leaf thickness (mm)	Fresh weight (g) per cm^2	SLA (cm^2g^{-1})	g_c ($\text{mol.m}^2.\text{s}^{-1}$)
<i>Pittosporum cornifolium</i>	7.27 (± 0.42)	0.7 (± 0.3)	0.04 (± 0.0009)	81.61 (± 2.19)	0.004 (± 0.0006)
<i>Pittosporum kirkii</i>	6.51 (± 0.39)	0.95 (± 0.19)	0.06 (± 0.0011)	66.12 (± 2.42)	0.0094 (± 0.0015)

Table 3.4 Mean height, number and area of leaves per whole *Pittosporum cornifolium* ($n = 12$) and *Pittosporum kirkii* ($n = 10$) individuals pre harvest. Standard error of the means are presented in parentheses.

Species	Height (cm)	Mean number of leaves	Mean leaf area (cm^2)
<i>Pittosporum cornifolium</i>	54.56 (± 3.31)	40.33 (± 5.70)	293.06 (± 37.75)
<i>Pittosporum kirkii</i>	22.20 (± 1.82)	18.70 (± 1.41)	121.74 (± 11.36)

3.3.5 Soil moisture

The mean volumetric water capacity (θ) for the control treatments of both species was kept between 36 – 46% and -0.008 – -0.24 MPa. In the moderately stressed treatments mean predawn water potential (ψ^{wpd}) was kept below -0.30 MPa for *Pittosporum kirkii* and -0.34 MPa for *P. cornifolium*. In the severely stressed treatments withholding water for 42 days resulted in ψ^{wpd} of *P. kirkii* dropping to -0.80 MPa while, ψ^{wpd} of *P. cornifolium* dropped to a minimum of -1.70 MPa (Figure 3.5). The reduction in predawn water potential, which is assumed to be equivalent to mean soil water content, influences plant functions such as stomatal conductance and photosynthesis. Hence, these functions have been graphed (below) against decreasing mean soil water content rather than time since water was withheld.

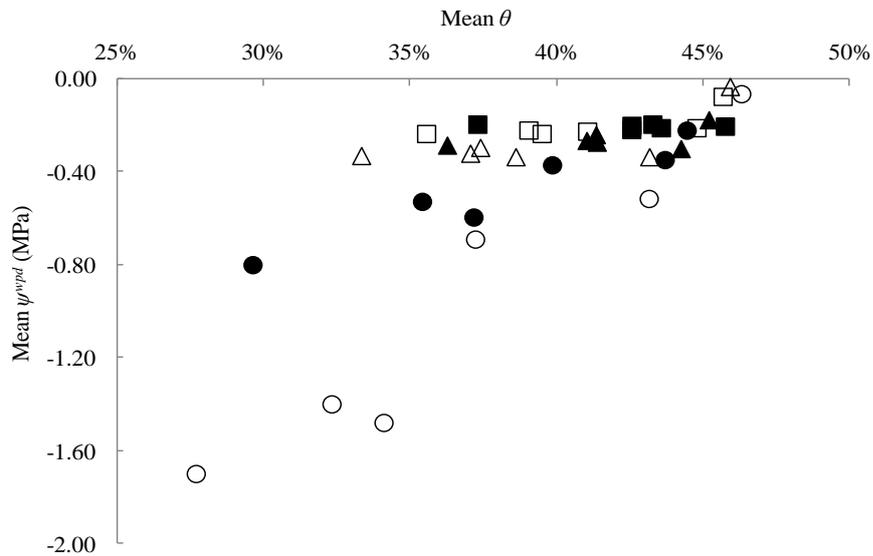


Figure 3.5 Mean volumetric soil moisture (θ) (percent) against mean predawn water potential (ψ_{wpd}) for *Pittosporum cornifolium* (open symbols) and *Pittosporum kirkii* (closed symbols) in the three treatments: control (squares), moderate stress (triangles) and severe stress (circles).

3.3.6 Stomatal conductance

Measurements of mean midday stomatal conductance (g_s) show a different relationship for both *Pittosporum* species. *Pittosporum kirkii* shows a relatively rapid reduction in mean midday stomatal conductance with decreasing mean pre-dawn predawn water potential (ψ_{wpd}). In contrast the mean midday stomatal conductance of *Pittosporum cornifolium* reduces over a much greater range of pre-dawn water potentials. These relationships are presented in Figure 3.6, and show a greater slope for *P. kirkii*, but a slightly weaker fit ($R^2 = 0.76$) than for *P. cornifolium* ($R^2 = 0.82$). This graph also shows that mean midday stomatal conductance for *P. kirkii* reaches zero at a higher (less negative) mean pre-dawn predawn water potential than *P. cornifolium*.

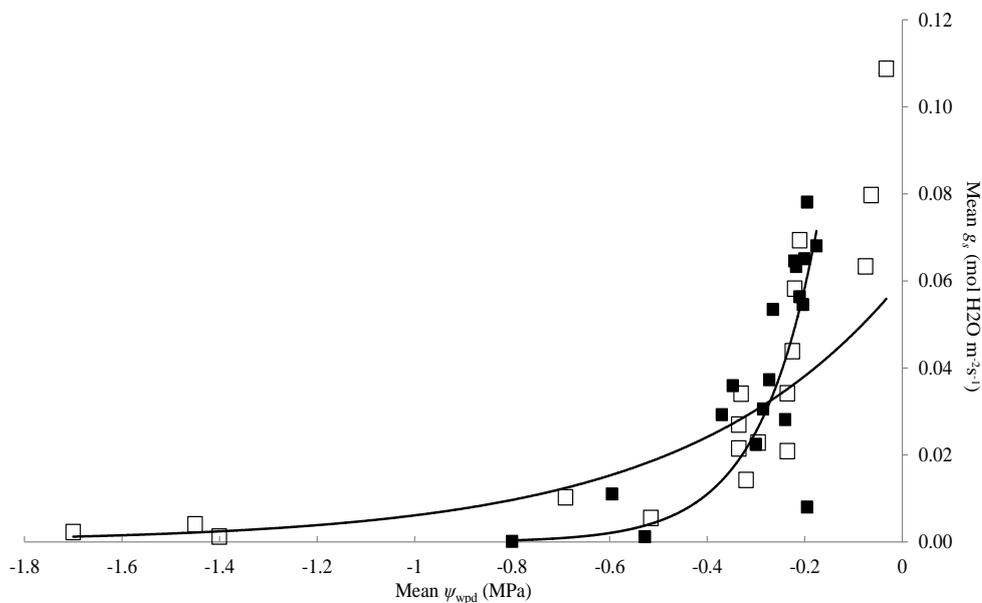


Figure 3.6 Mean midday stomatal conductance (g_s) against mean predawn water potential (ψ_{wpd}) for *Pittosporum cornifolium* (open symbols) ($R^2 = 0.82$) and *Pittosporum kirkii* (closed symbols) ($R^2 = 0.76$) under increasing desiccation stress (control, moderate stress and severe stress data sets combined). Exponential trend lines are presented.

3.3.7 Plant photosynthesis

Mean midday photosynthesis (A) plotted against mean midday stomatal conductance (g_s) showed a near linear trend. This indicated that A and g_s are related as mean midday photosynthesis decreased with declining midday stomatal conductance for both *Pittosporum kirkii* ($R^2 = 0.40$) and *P. cornifolium* ($R^2 = 0.55$) (Figure 3.7).

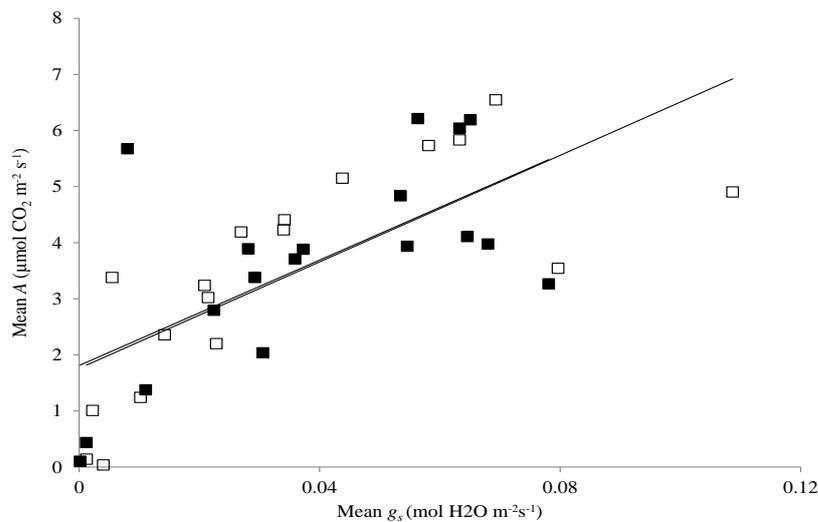


Figure 3.7 Mean midday photosynthesis (A) against mean midday stomatal conductance (g_s) for *Pittosporum cornifolium* (open symbols) ($R^2 = 0.55$) and *Pittosporum kirkii* (closed symbols) ($R^2 = 0.40$) under increasing desiccation stress (control, moderate stress and severe stress data sets combined). Linear trend lines are presented.

Plotting mean midday photosynthesis (A) against mean pre-dawn water potential (ψ_{wpd}) shows a similar relationship for both species to that found in Figure 3.6 for stomatal conductance. The rate of mean midday photosynthesis of *P. kirkii* has a more distinct decline with reducing pre-dawn water potential than *P. cornifolium* and reaches zero at a less negative mean pre-dawn water potential (Figure 3.8). *Pittosporum cornifolium* reaches a more negative mean pre-dawn water potential before ceasing photosynthetic activity.

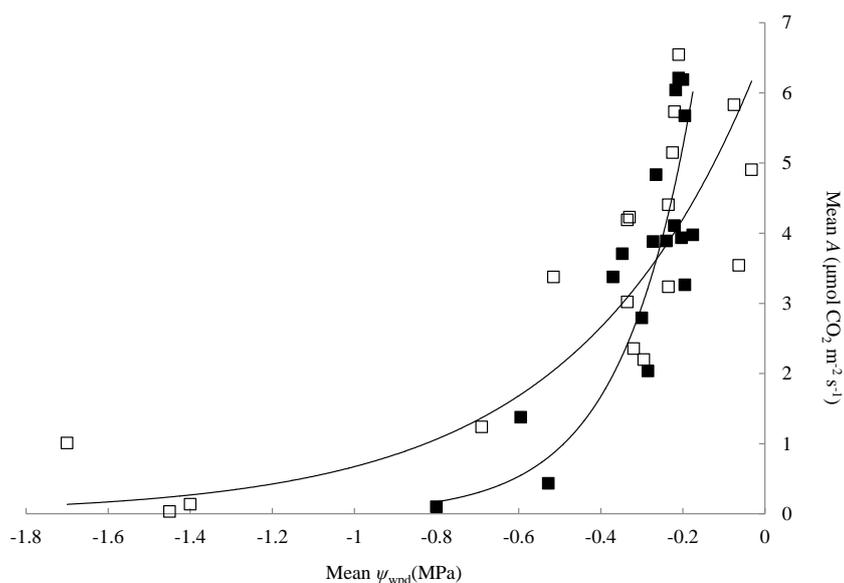


Figure 3.8 Mean midday photosynthesis (A) against mean predawn water potential (ψ_{wpd}) for *Pittosporum cornifolium* (open symbols) ($R^2 = 0.70$) and *Pittosporum kirkii* (closed symbols) ($R^2 = 0.83$) under increasing desiccation stress (control, moderate stress and severe stress data sets combined). Exponential trend lines are presented.

3.3.8 Osmotic potential

Measurement of foliar symplasmic osmotic potentials (MPa) clearly showed reductions in osmotic concentrations with increasing desiccation stress for both *Pittosporum* species. The greatest reduction occurred in *P. cornifolium* leaves which decreased from a mean of $-1.22 (\pm 0.005)$ for the control to a mean of $-2.41 (\pm 0.10)$ for the severe treatments; this difference was statistically significant ($P = 0.002$). *Pittosporum kirkii* also displayed statistically significant reductions in mean osmotic concentrations from the control (-1.03 ± 0.01) to the severe (-1.83 ± 0.003) treatments ($P = 0.03$) (Table 3.5).

Table 3.5 Mean osmotic potential (MPa) of *Pittosporum cornifolium* ($n=18$) and *Pittosporum kirkii* leaves ($n = 18$) for each treatment; control, moderate stress and severe stress. Standard errors are presented in parentheses.

	Control		Moderate stress		Severe stress	
	<i>Pittosporum cornifolium</i>	<i>Pittosporum kirkii</i>	<i>Pittosporum cornifolium</i>	<i>Pittosporum kirkii</i>	<i>Pittosporum cornifolium</i>	<i>Pittosporum kirkii</i>
Mean	-1.22 (± 0.005)	-1.03 (± 0.01)	-1.31 (± 0.004)	-1.42 (± 0.12)	-2.41 (± 0.10)	-1.83 (± 0.003)
Max.	-1.21	-1.01	-1.23	-1.24	-2.23	-1.82
Min.	-1.23	-1.07	-1.37	-1.88	-2.57	-1.83

3.3.9 Delta ¹³C measurements

Foliar delta carbon-13 analysis ($\delta^{13}\text{C}$) of *P. cornifolium* and *P. kirkii* leaves in the control, moderate stress, and severe stress treatments (Table 3.6) showed no significant differences, and ranged from -24.61‰ (*P. kirkii*) to -27.07‰ (*P. cornifolium*). Additionally, $\delta^{13}\text{C}$ analysis of *P. kirkii* individuals inhabiting three distinct lifestyles (epiphytic, terrestrial and rupestral) also showed no significant differences (Table 3.7).

Table 3.6 Mean $\delta^{13}\text{C}$ values (‰) of each stress treatment ($n = 24$). Standard error of the mean is presented in parentheses.

	Control	Moderate	Severe
<i>Pittosporum cornifolium</i>	-26.66 (± 0.827)	-27.07 (± 0.265)	-26.82 (± 0.436)
<i>Pittosporum kirkii</i>	-24.81 (± 0.175)	-25.49 (± 0.268)	-25.74 (± 0.267)

Table 3.7 Mean $\delta^{13}\text{C}$ values (‰) for *in situ* epiphytic ($n = 15$), terrestrial ($n = 14$) and rupestral ($n = 3$) *Pittosporum kirkii* individuals. Standard error of the mean is presented in parentheses.

Epiphytic	Terrestrial	Rupestral
-27.68 (± 2.1)	-28.54 (± 1.4)	-29.43 (± 2.8)

3.3.10 Leaf anatomy

The depths of tissue layers within *Pittosporum kirkii* leaves were significantly higher than those of *Pittosporum cornifolium* for all but one tissue type (lower bundle sheath cells). The most notable differences were in the abaxial and adaxial cuticle, epidermis and hypodermis with *P. kirkii* having tissue layers up to 87 % thicker than *P. cornifolium*. The bundle sheath cells and xylem cells had the most similar measurements for each species. The phloem tissue and the lower bundle sheath cells were the thickest for *P. cornifolium*, and the lower hypodermis and phloem were the thickest for *P. kirkii* (Table 3.8).

Table 3.8 Measurements of mean lamina tissue depths (μm) of a transverse hand section through the mid rib of *Pittosporum cornifolium* ($n = 8$) (Clarkson 2011) and *Pittosporum kirkii* ($n = 4$) leaves (see, Chapter two) and the difference between each tissue type (%).

Tissue type	<i>P. cornifolium</i> (μm)	<i>P. kirkii</i> (μm)	Difference (%)
Upper cuticle	6	17	65
Upper epidermis	27	45	40
Upper hypodermis	22	105	79
Palisade cells	60	132	54
Upper bundle sheath cells	41	43	5
Xylem	84	93	10
Phloem	113	160	29
Lower bundle sheath cells	106	103	-3
Lower hypodermis	20	156	87
Lower epidermis	18	41	56
Lower cuticle	4	12	67
Total	501	1333	62

3.4 Discussion and conclusions

The morphological features, physiological functions and response of leaf water relations under desiccation stress amongst New Zealand's vascular epiphyte species has been notably under-studied. This drought experiment attempts to amend this knowledge gap by investigating the morphological and physiological responses of *Pittosporum kirkii* and congener, *Pittosporum cornifolium* seedlings under three levels of desiccation stress.

Over the duration of six weeks, both *Pittosporum* species exhibited morphological and physiological changes in response to increasing desiccation stress. Overall, the two species displayed similar reductions in function with increasing desiccation but at different rates. These changes are described below in the context of the hypotheses proposed.

Hypothesis one predicted that *Pittosporum kirkii* would exhibit a desiccation postponement stress strategy; this hypothesis was supported by the water relations results. Under decreasing soil water content (increased stress) *P. kirkii* seedlings

rapidly responded by reducing stomatal conductance and rates of photosynthesis. This response maintained relatively high leaf water potentials, thus postponing the desiccation effects of reduced soil water content.

Hypothesis two predicted that *Pittosporum cornifolium* would exhibit a desiccation tolerance stress strategy; this hypothesis was also supported by the water relations results. *P. cornifolium* maintained relatively high photosynthesis rates and stomatal conductance under decreasing soil water content which resulted in reduced leaf water potentials.

Further support for each hypothesis is provided in discussion of the experiment results below.

Leaf growth rates indicated that the plants were negatively affected by the drought treatments. Growth rates were different between each treatment, with comparisons between the control and severe stress treatment being the most discernible. Both *Pittosporum* species exhibited lower absolute leaf growth in the severe treatment than in the control. *Pittosporum cornifolium* displayed the greatest differences in absolute leaf growth between control, moderate and severe treatments. In the moderate and severe stress treatments leaf growth was negative due to leaf shedding. Leaf shedding is reported to be a response that plants exhibit to tolerate short term desiccation, likely resulting in reduced transpiration and maintenance of a more favourable water potential (Seddon 1974; Lambers et al. 2008). *Pittosporum kirkii* showed unexpectedly high growth in the moderate treatment, which may be related to the conditions of harvest; it is known that leaf weight can be sensitive to the time of day that harvests take place and also how they are treated prior to post-harvest measurements (Garnier et al. 2001).

Relative growth rates of both species showed a similar trend to absolute growth rates with decreased growth as desiccation stress increased. However, differences between treatments were not significant because of high standard errors, the result of variation in size and form between individual plants, the limited sample size available for destructive harvest, and the method for estimating the standard error of the relative growth rate (Hunt et al. 2002).

Reduced leaf thickness was exhibited in both species with increasing desiccation stress. This is speculated to occur because as leaf water potential drops water is lost from the leaves, reducing leaf thickness as they desiccate.

The ability of *P. kirkii* to postpone the effects of desiccation and survive in xeric canopy conditions can be linked to distinctive xeromorphic features that are not as pronounced in *P. cornifolium*. Important anatomical features include the substantial upper cuticle, upper and lower hypodermis which are 65, 79 and 87 percent thicker than *P. cornifolium* respectively (Table 3.8). These features may have contributed to reduce water loss and protection of inner leaf tissues from dehydration under desiccation conditions (Guerfel et al. 2009), which postpones more negative leaf water potentials and allows for continual survival.

Morphological features contributing to stress responses include variations in plant size and leaf characteristics. *Pittosporum kirkii* has less leaves which are smaller in area, more coriaceous, thicker, and darker green in colour than *P. cornifolium*. These features are aligned with the drought postponer strategy as they have each been suggested to be important in storing water for use in drought conditions (Benzing 1990; Kozłowski & Pallardy 2002). In contrast, *P. cornifolium* has more leaves with greater area that are readily lost to maintain function and tolerate desiccation at lower leaf water potentials. The morphological features displayed by both *Pittosporum* species are in line with their observed physiological responses and contribute to the interpretation of desiccation stress strategies.

The significant differences in leaf symplasmic osmotic potential between control and severe treatments illustrate that both *Pittosporum* species adjust leaf solute concentrations to maintain leaf turgor with increasing desiccation stress. There were differences in osmotic adjustment between species with *P. kirkii* (-1.03 to -1.83MPa) adjusting considerably less than *P. cornifolium* (-1.22 to -2.41 MPa) under increasing desiccation stress. This reflects the greater reliance on morphological adaptations by *P. kirkii* to postpone the effects of desiccation and greater physiological adjustments by *P. cornifolium* to tolerate drought conditions. It also reconfirms the alignment of *P. cornifolium* as a desiccation tolerator as

osmotic adjustment is prominent in desiccation tolerant plants (Turner & Begg 1981; Turner 1986).

The higher osmotic adjustment of *P. cornifolium* under increasing stress lowers osmotic potential of the symplast which maintains turgor and functioning of photosynthesis. As *P. kirkii* postpones the effects of drought through the use of morphological adaptations first, further osmotic adjustment may not be exhibited until protracted drought stress occurs (longer than this experiment).

The osmotic potentials of both *Pittosporum* species under stress are contradictory with tropical epiphyte species, particularly of bromeliads and orchids. Tropical epiphytes have been found to maintain high osmotic potentials of around -1.0 MPa even after substantial drought stress (Sinclair 1983a; Benzing 1990; Martin et al. 2004). A recent study also found the endemic hemi-epiphyte, *G. lucida* to exhibit similar values as tropical epiphyte species after desiccation stress (Bryan 2011). This highlights the significance of osmotic adjustment both *Pittosporum* species to maintain turgor and survive drought conditions.

Cell elasticity was not measured in this experiment, however, the significant osmotic adjustment results indicate that elastic adjustment is unlikely as both physiological adjustments cannot act concurrently Lambers et al. (2008). However, cell elasticity may be important for adult *P. kirkii* as this feature is often associated with thick hypodermis tissue layers (Table 3.8; Figure 2.19). In times of desiccation stress hypodermal cells can maintain high cell wall elasticity by preferentially losing water and relocating it to photosynthetic cells (Nowak & Martin 1997; Martin et al. 2004). Hence, adult *P. kirkii* may exhibit increasing drought tolerance through increased elastic adjustments, which maintains leaf turgor in periods of desiccation stress (Lambers et al. 2008). Further research on comparisons between developmental stages is required to confirm this hypothesis.

Foliar delta carbon-13 analysis of *P. kirkii* and *P. cornifolium* showed similar water use efficiencies, which did not alter for either species with increasing desiccation stress. This is possibly because photosynthesis and stomatal conductance were reduced rapidly over the short duration of the experiment;

hence the much of the leaf carbon available for analysis is likely to have been fixed pre-treatment. Thus, these carbon-13 results may not accurately reflect water use efficiency under stress. Longer term observations, or extraction of recently fixed photosynthate would be required to detect significant differences (Farquhar et al. 1989).

Similarly, water use efficiency was found to be comparable across all *in situ* lifestyles of *P. kirkii*; epiphytic, terrestrial and rupestral. These results suggest that the three habitat types of *P. kirkii* have similar water availability constraints (as suggested in chapter two) and support the theory that water availability is a major limiting factor to epiphytes (Benzing 1990). Hence, the tolerance of intermittent water availability is a major determinant of the habitats they occupy.

After re-watering, the midday leaf water potentials and rates of photosynthesis in the severely stressed treatments for both species recovered rapidly to reach levels of the control treatment. *Pittosporum cornifolium* showed rapid recovery from much lower leaf water potentials than *P. kirkii*, which reiterates its alignment as a desiccation tolerator. The wilted leaves of severely stressed plants of both species showed full recovery within three days of re-watering. This rapid recovery of function to utilise available water reflects the nature of extreme habitats, as these *Pittosporum* species must both cope with fluctuations in environmental variables and respond quickly to irregular rainfall in drought prone epiphytic, rupestral and terrestrial habitats. Recent research supports this, reporting that the hemi-epiphyte *Griselinia lucida* postponed the effects of drought and rapidly responded to re-watering with increased photosynthetic function (Bryan 2011).

In summary, the water relations, growth, anatomy, morphology, osmotic potentials and recovery of *Pittosporum kirkii* and *P. cornifolium* provide evidence in support of the presented hypotheses.

Pittosporum kirkii most strongly aligns with a desiccation postponement stress strategy which involves morphological features and physiological responses that delay the detrimental effects of drought. This strategy relates to both the distribution and habitats of *P. kirkii*. The upper lowland/lower montane forests

where it occurs are associated with severe environmental fluctuations (chapter two), as are the epiphytic, rupestral and terrestrial habitats within this distribution (Benzing 1987, 1990; Freiberg 2001; Moore 2008). Therefore, it is important that *P. kirkii* can survive short term drought and recover quickly when conditions improve.

Pittosporum cornifolium most strongly aligns with desiccation tolerance stress strategy. The delayed closure of stomata at low soil moisture contents enables *P. cornifolium* to continue to photosynthesise during drought. However, this is not viable as a long term response as continual water loss through open stomata cause tissue dehydration, which is certainly lethal over prolonged periods of droughts (Ludlow 1989). A similar result has been found for tropical epiphytic fern species which enabled tolerance of the most xeric of canopy locations (Hietz & Briones 1998). This strategy relates to the lowland and coastal environment that *P. cornifolium* inhabits (chapter two) which has more regular rainfall and less environmental extremes than the habitats of *P. kirkii*.

These stress strategies have been aligned with each *Pittosporum* species during seedling life stage. It should be considered that these juvenile forms are likely to have relatively high tissue sensitivity because they lose water faster than adults in periods of desiccation stress due to high area/volume ratio (Benzing 1990; Winkler et al. 2005). Accordingly, the stress strategies of these two species may change with maturity. Also, responses to desiccation stress are best classified along a continuum between different stress strategies (Ludlow 1989) and thus, individuals of these two species may exhibit varying degrees of desiccation tolerance or postponement.

Chapter Four: Biological Flora of New Zealand. *Pittosporum kirkii*, Kirk's kōhūhū, thick-leaved kohukohu

4.1 Abstract

Information on the biology and ecology of *Pittosporum kirkii* Hook.f. ex Kirk (Pittosporaceae R. Br.) available through published and unpublished sources is assembled and reviewed. *P. kirkii* is commonly an epiphytic shrub, which is occasionally terrestrial, and rarely rupestral. Coriaceous, thick, fleshy leaves distinctively sets this species apart from any other member of the *Pittosporum* genus in New Zealand. *P. kirkii* has an abrupt distribution with strong habitat preferences restricting it to the upper North Island, in upper lowland and lower montane old-growth forest ecosystems. It appears that low elevation, low solar radiation, low mean daily temperatures, low mean annual rainfall and high vapour pressure deficits are the main environmental factors restricting distribution. *P. kirkii* is currently listed as a threatened plant and classified as declining but data poor because of a lack of autecological information. Palatability to possums and forest clearance have been suggested as the main agents of decline, but evidence is anecdotal and circumstantial. Overall the current threat listing for *P. kirkii* is uncertain. Further research on this species would be invaluable to fill a current knowledge gap on *P. kirkii* threats, sexual expression, dispersal and pollination.

Key words: Biological flora; *Pittosporum kirkii*; epiphyte; morphology; taxonomy; distribution; associations; conservation; restoration; New Zealand

4.2 Morphological description

Pittosporum kirkii Hook.f. ex Kirk is a glabrous evergreen perennial shrub that reaches up to 5 m in height and possesses distinctive coriaceous, fleshy, thick leaves (Kirk 1871; Cooper 1956; Myron 2012). It is commonly epiphytic; however, it can be observed occasionally growing terrestrially, and is very rarely rupestral. Sprawling in architecture, the trunk reaches up to 10 cm in diameter, (Dawson & Lucas 2011) and holds densely arranged, light green-brown branches, with flexible stout reddish to purple branchlets (Cooper 1956; Allan 1961; Dawson 1986a). Leaves are green on the abaxial, paler green on the adaxial, and are alternate, crowded or sub-verticillate towards the tips of branchlets. Leaves are coriaceous and thick with slightly revolute margins (Cooper 1956; Allan 1961; Dawson 1986a), are 4–10–(12) cm long, 0.7–3.2 cm broad, with a prominent costa on the adaxial and flattened on the adaxial (Cooper 1956). Around 18 secondary veins are on either side of the midrib, displaying an anastomosing pattern and are obscure (Cheeseman et al. 1914; Cooper 1956; Dawson 1986a). Leaves are shaped linear-obovate, obovate-oblong, to oblong-elliptic, obtuse to acute at the apex, and are cuneately narrowed to a purple-reddish distinctive 0.1–0.2 mm broad petiole which is 0.3–1.6 mm in length. (Cheeseman 1906; Cooper 1956; Allan 1961). Leaf length increases with increasing latitude and multicellular, glandular, caducous trichomes are present on the leaves of young seedlings (Myron 2012).

Umbel inflorescences are terminal with 1–10 flowers supported by 5–10 mm glabrous pedicles (Cheeseman 1906; Cooper 1956; Allan 1961). Once in fruit, the flower pedicles contract and are subtended by a whorl of leaves and numerous caduceus, glabrous bud scales, which are 1–2 mm long (Cooper 1956). The calyx holds sepals which are 6–10 mm long and 1.5–4 mm broad (Cooper 1956; Narayana & Radhakrishnaiah 1982). Sepals are basally connate and imbricate, yellow to white in colour; lanceolate-ovate to lanceolate-oblong, acute to acuminate in shape and glabrous to pilose in texture (Cheeseman 1906; Cooper 1956; Allan 1961). The corolla holds imbricate petals, 1.5–2.9 mm long and 2.5–3.5 mm broad (Cooper 1956; Allan 1961). Petals are frequently coloured yellow to creamy-yellow, but can also be red to dark pink with a yellow suffused corolla

tube (Myron 2012). Petals are oblanceolate and acuminate in shape, and are sharply reflexed, similar to congener *Pittosporum cornifolium* (Cooper 1956; Allan 1961). Stamens are 6–7 mm long, with 2.5–3 mm long elliptic-oblong anthers. The gynoecia encase a 3–4 mm long and approximately 1.5 mm broad tomentulose ovary (Cooper 1956). The stout style is around 3 mm long, with a capitate stigma. The gynoecia is reduced on male flowers while the androecia are reduced on female flowers (*cf.* Cheeseman et al. 1914). At anthesis the gynoecia is equal to, or slightly longer than the androecia (Cooper 1956). Hence, flowers are typically unisexual in function and perfect in structure. Capsules are 2.8–4.2 cm long, and 0.6–2.8 cm wide, coriaceous and glabrate (Cheeseman 1906; Cooper 1956). They are compressed and elliptic-obovate to ellipsoid in shape with an elliptic outline (Cooper 1956; Allan 1961). A gradual progression in capsule colour from green to yellow marks the initiation of loculicidal dehiscence (Figure 4.1). Capsules are predominantly bi-valved, and are occasionally tri-valved (Figure 4.1); both types have been observed found on an single female individual (Myron 2012). Capsule pericarps are coriaceous, approximately 1.5 mm thick; light yellow-orange in colour, and turn dark orange-brown with capsule maturation. The irregularly shaped black seeds (up to 40 per capsule), are supported by thick strap-like funicles up to 4 mm long, extending from basal placenta (Cooper 1956), and are held in place by aureolin-yellow coloured viscid fluid (Figure 4.1). The latter is a characteristic feature in the family Pittosporaceae and genus *Pittosporum* (Cooper 1956).



Figure 4.1 *Pittosporum kirkii* capsule morphology: progression of capsule development. A: clusters of green un-ripe capsules, Mount Taranaki (Photo: W.M Clarkson). B: ripening yellow bi-valve capsule, Waitakere Ranges (Photo: C.L Bryan). C: ripe dehiscent tri-valve capsule, highlighting the irregular shaped black seeds immersed in yellow viscid fluid Mount Taranaki (Photo: W.M Clarkson).

4.3 Anatomical description

Leaf, stem and root transverse cross-sections reveal anatomical features typical of xerophytic dicotyledons. Thick peridermal layers and a wide casparian strip surrounding the endodermis can be seen in stem and root cross sections. These features may reduce or prevent excess water loss in times of desiccation stress (Ginzburg 1966). In the stem a ring of axial secretory ducts are present between the cortex and primary phloem, however it is unclear whether these secretory ducts lack epithelium tissue (Myron 2012).

The leaf anatomy displayed similar features indicative of, and associated with xeromorphy (Seddon 1974). These include a thick coriaceous lamina with a thick cuticle on the abaxial surface, covering a single epidermal layer. Beneath this, two to three layers of square hypodermal cells are present which function as water storage cells, formerly known as aqueous tissue (*cf.* Oliver 1930). The palisade layer consists of two to three layers of short oblong cells; beneath this is the spongy mesophyll which makes up the bulk of the leaf structure. Within the spongy mesophyll, or spongy parenchyma, are loosely packed round to oblong shaped chlorenchyma cells. The vascular bundle is made up of xylem tissue and a relatively large phloem surrounded by three to four secretory ducts, amongst the lower bundle sheath cells. These specialised secretory ducts, named schizogenous ducts, are lined and divided with epithelium tissue composed of secretory cells (Evert et al. 2006). They are a feature of the genus *Pittosporum* (Jay 1969). The adaxial epidermis and cuticle are thinner than those on the abaxial. The presence of sub-stomatal chambers was not detected.

4.3.1 Floral anatomy

The floral anatomy of *Pittosporum kirkii* was previously described by Narayana & Radhakrishnaiah (1982) (Figure 4.2). Inflorescences are pedicellate, complete and pentamerous, except for the gynoecia (Figure 4.2: 16). The calyx is pentamerous and basally connate. The calyx tube displays quincuncial aestivation, has five sepal traces which trifurcate and produce three lateral traces conjoint with the median (Figure 4.2: 15–19). The corolla is pentamerous, up to 1 mm in height, basally connate and sympetalous (Figure 4.2: 14). The corolla tube displays

imbricate aestivation (Figure 4.2: 15–20), has one petal trace which is independent on an alternisepalous plane. The androecia consist of five free stamens on antisepalous radii, with one trace (Figure 4.2: 15–19). The gynoecia consist of a solid style vascularised by dorsal and ventral bundles (Figure 4.2: 20), and a bilobed stigma. The gynoecia are bicarpellate, syncarpous and chambered at the base, and unilocular above (Figure 4.2: 16–19). The ovary is superior. After the divergence of the five sepal and petal traces in the thalamus (Figure 4.2: 11), the main stele branches, and converges to form a series of branches, of which two pairs centralise and form the ventral bundles. The remaining branches form a ring of bundles which supply nutrients to the ovary wall (Figure 4.2: 12–16). Within the ovule, the ventral bundles pair with adjacent carpels and then fuse to form common ventral bundles, which produce ovular traces into the wall of the ovary (Figure 4.2: 16–18). Occurring at the same time as ventral bundle organisation, the dorsal bundles divide at the ovary apex, which causes separation from the stamens. They then immediately position amongst the ovary wall, alongside ovary wall bundles (Figure 4.2: 15–16). The dorsal and ventral bundles function by vascularising the style (Figure 4.2: 20). The external base of the ovary is glandular, disc shaped and lacks vasculature tissue (Figure 4.2: 15). Placentation is parietal. The overall vascular system has a corresponding system of resin canals, which is characteristic of the genus *Pittosporum*.

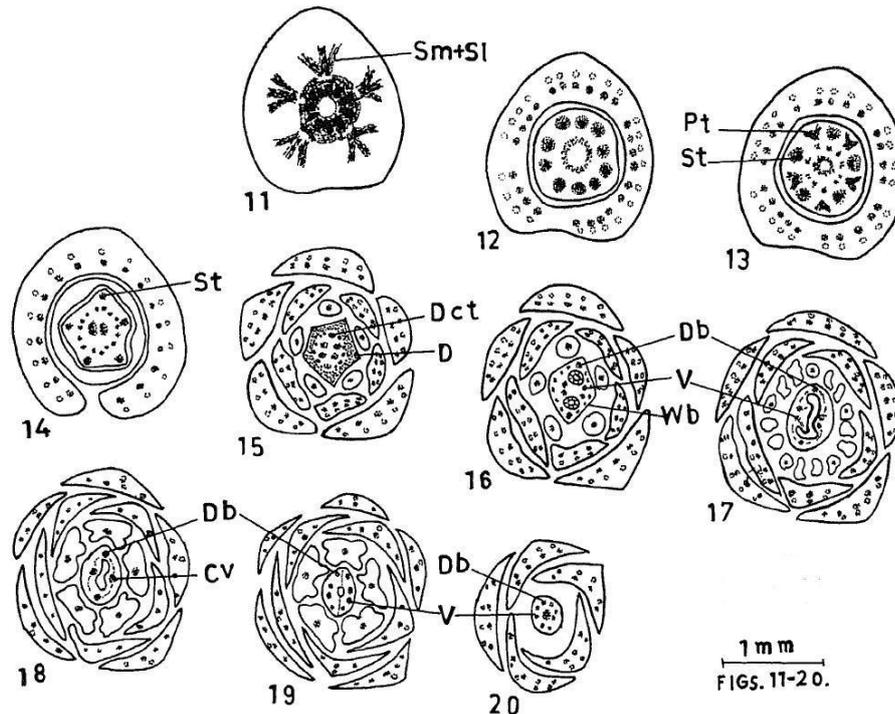


Figure 4.2 Serial transverse sections (11-20) of *Pittosporum kirkii* flower buds, showing the origin and distribution of traces of floral parts: Cv, common ventral bundle; D, Disc; Db, dorsal bundle; Dct, dorsal carpellary; Pt, petal trace; Sl, sepal trace; Sm, sepal midrib; Sm + Sl, septal midrib trace and sepal lateral trace; St, staminal trace; V, ventral bundle; Wb, wall bundle (Narayana & Radhakrishnaiah 1982).

4.4 Taxonomy and relationships

4.4.1 The genus *Pittosporum*

The genus *Pittosporum* Banks ex. Garthen is widespread throughout the tropic and temperate regions of the world and is notably absent from the Americas (Allan 1961; Crisp et al. 1989). *Pittosporum* is the largest, most primitive and only genus in Pittosporaceae that is widespread outside of Australia (Haas 1977); other Pittosporaceae genera are largely endemic to Australia, with monotypic *Hymenosporum* also occurring in New Guinea (Haas 1977; Plunkett et al. 2004). There are between 160 to 200 species in the genus *Pittosporum* (Cooper 1956; Haas 1977), however, this number is constantly being revised and updated as evident by the recent integration of *Citriobatus* into *Pittosporum* (Chandler et al. 2007).

Pittosporum species are usually small evergreen shrubs, or trees which generally reach up to 10 metres and occasionally 30 metres in height (Cooper 1956; van Balgooy 1966). Leaves are alternate, sometimes crowded and whorled towards the branch tips (Cooper 1956). Flowers are perfect, or functionally unisexual with a hypogynous and tetracyclic floral plan (Narayana & Radhakrishnaiah 1982). Flower structure consists of 5 sepals, petals and stamens, with usually 2–5 fused carpels within a unicellular, single, superoid, sessile or stipulate ovary with 2–5 parietal placentae (Cooper 1956; Hegnauer 1969; Stevens 2001). *Pittosporum* seeds are encased in coriaceous or woody capsules, which remain fused at the base upon dehiscence (Bennett 1988). Capsules are usually two or three valved (occasionally up to five) (Allan 1961), with valve number being dependent on carpel number (Haas 1977). The seeds are immersed in an aromatic, resinous, viscid fluid (Cooper 1956; Allan 1961), and it is after this distinctive feature that *Pittosporum* was named; ‘pitta’ meaning resin, and ‘spora’ meaning seeds (Gowda 1951; Haas 1977).

Pittosporum taxa were historically classified on specific morphological features, these have included: inflorescence types; presence, absence or colour of hairs on shoots; leaf size, shape and anatomy; arrangement and number of sepals; petal number; number and shape of capsules; arrangement and size of funicles; and finally, variation in the thickness and length of the placenta (Gowda 1951; Cooper 1956; Wilkinson 1992). The predominant focus and argument on valve number to split the genus permeates early literature, with the genus being grouped into either bivalve or trivalve clades (Gowda 1951; Haas 1977). However, continual difficulty resulting from phenotypic plasticity, hybridism and introgression, hinders the sole use of morphological characters to unequivocally divide taxa in the *Pittosporum* genera. Hence, the evolution of molecular tools has been important in classifying *Pittosporum* taxa (Hathaway 2001; Gemmill et al. 2002). This is evident by recent systematic work on *Pittosporum* which has not matched with the historical utilisation of morphological characteristics (Gemmill et al. 2002), particularly with bivalve and trivalve characters. Consequently, the numbers of *Pittosporum* species are continually debated, revised and updated as a result of work by taxonomists and molecular work.

4.4.2 The genus *Pittosporum* in New Zealand

In New Zealand there is an imbalance of *Pittosporum* species diversity between the North and South Island. Of the 21 endemic species present (de Lange et al. 2010), nine are endemic to the North Island, while, two are endemic to the South Island (Eagle 1982, 2006). Two species are common throughout; *Pittosporum eugenioides* and *Pittosporum tenuifolium*. In New Zealand the number of *Pittosporum* species recognised has varied from 12 to 26 over time (Kirk 1871; Cooper 1956; Allan 1961; de Lange et al. 2010) with 21 currently recognised (de Lange et al. 2010). This is due to historical and on-going difficulties in differentiating species because of similar morphological characteristics. Historic relationships among New Zealand *Pittosporum* were inferred using bi-valve and tri-valve capsule structure (Gowda 1951). However, recent molecular data does not support these groupings (Hathaway 2001; Chandler et al. 2007), which also placed Australia as the centre of diversity and origin of the *Pittosporum* genus (Chandler et al. 2007). That research estimated the number of colonisation events to New Zealand was at least two, which formed two separate clades (Chandler et al. 2007). The main monophyletic clade contains all endemic *Pittosporum* to New Zealand, within this clade *Pittosporum dalli* and sister taxa *Pittosporum kirkii* diverged from all other New Zealand taxa approximately 13.5 million years ago (Dr. Chrissen Gemmill, pers comm. The University of Waikato, 2011). The second separate clade contains *Pittosporum pimeleoides* subspecies and *Pittosporum cornifolium* which are believed to have more recently colonised from New Caledonia (Hathaway 2001).

4.4.3 *Pittosporum kirkii* nomenclature

Pittosporum kirkii Hook.f. ex Kirk type locality is Great Barrier Island (Kirk 1869; Cheeseman et al. 1914). A validly published description does not exist for *P. kirkii*. Instead the initial brief description titled “*Pittosporum* n. sp.?” by Thomas Kirk was published in his paper on Great Barrier Island in 1868 (Kirk 1868). This description along with herbaria specimens* were sent to Dr. J. D Hooker at Kew Gardens in 1868 (Kew Gardens n.d.) where he likely applied the specific epithet

* Kew herbarium sheets: K000591690, K000591691, K000591693 and K000591693

kirkii after T. Kirk in an unpublished manuscript. The new name was likely sent back to T. Kirk and he accredited it to J.D Hooker in his paper on the Thames Gold-fields (Kirk 1869) (Dr. A. S. George, pers. comm. Murdoch University 2011). Hence the authority is Hook.f ex. Kirk, as it is after T. Kirk's original description that *Pittosporum kirkii* was named. However, further investigation is warranted on the etymology of *P. kirkii*, as no specific evidence of correspondence between T. Kirk and J. D Hooker could be found regarding *P. kirkii*.

Kirk's (1869) description reads: "*Pittosporum Kirk, Hook. f., n. sp., A handsome, laxly-branched shrub, 8–15 feet high, without flower or fruit, but differing widely in habit and foliage from any described N. Z. species of this genus, was observed at an altitude of 1600–1700 feet [with] broad purple petioles, excessively coriaceous...*" (Pp. 92). *Pittosporum kirkii* was the last endemic epiphytic shrub to be officially found and described (Kirk 1869, 1871).

An illustration in Cheeseman et al. (1914) (Figure 4.3) was the first to highlight the male and female reproductive structures (dioecy) of *P. kirkii*. Cheeseman et al. (1914) states that "...it is frequently epiphytic on the trunks and branches of the rata (*Metrosideros robusta*) and other large forest-trees, but it is often rupestral as well, and may also be seen forming part of the ordinary undergrowth of the forest [however] its relationships are somewhat obscure" (Pp. 80).

Vernacular names used include, Kirk's *Pittosporum* (Cooper 1956) and Kirk's Matipo (Martin 1961). More commonly used are the combined Māori-English names; Kirk's kōhūhū and thick-leaved kohukohu (Andersen 1926; de Lange 2006). Kōhūhū translates to shrub and kohukohu refers to a tree having a resinous smell (Taylor 1848). General terms such as perchers and perching *Pittosporum* are also in use (Cockayne 1910).

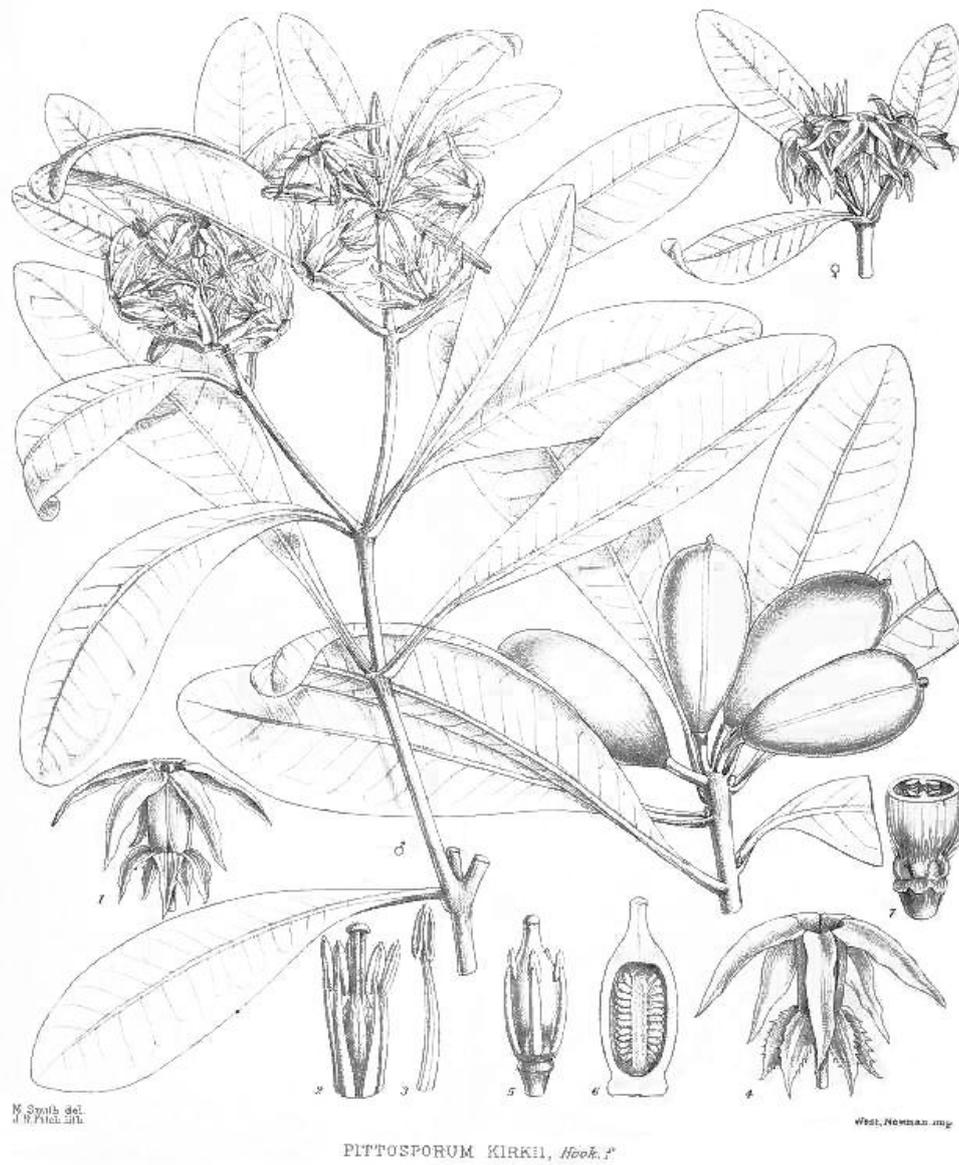


Figure 4.3 *Pittosporum kirkii* morphological characteristics. Illustration modified from Cheeseman et al. (1914). 1: male flower; 2: stamens and rudimentary pistil; 3: single stamen; 4: female flower; 5: pistil with rudimentary stamens; 6: longitudinal section of a pistil; 7: cross-section of pistil (all enlarged).

4.5 Chemistry

Phytochemical research on *P. kirkii* has not been undertaken. Nevertheless, phytochemical investigations have been undertaken within the family Pittosporaceae and the genus, *Pittosporum*.

Within the family Pittosporaceae a range of secondary compounds have been identified. The dominant compounds include; caffeic acid, coumarin, flavones, furano-coumarin, phenolic, saponins, sinapic acids, triterpenes (Hegnauer 1969), flavinols, kampferol and quercetin (Jay 1969).

Organic compounds identified within the genus *Pittosporum* include several classes of terpenes; monoterpenes, limonene, α -pinene (*P. tenuifolium*), and olefinic natural compound, myrcene (Brooker et al. 1981; Nemethy & Calvin 1982). In addition, linoleic acid has been extracted from the fruit, and/or seeds of *Pittosporum resiniferum* and *Pittosporum undulatum* (Stuhlfauth et al. 1985; Rao et al. 1990). Within the New Zealand *Pittosporum*, two flavonoids; kampferol and quercetin have been identified in *P. crassifolium*, *P. dallii*, *P. eugenioides* and *P. tenuifolium* (Jay 1969). Other secondary compounds found include, flavonoid isorhamnetin in *P. eugenioides* and flavone apigenin in *P. tenuifolium* (Jay 1969). Additionally, phytosterols have been extracted from the bark of *P. colensoi* and *P. eugenioides* (Cambie & Parnell 1969), and polyacetylenes extracted from the roots, monoenes and linoleic acid from seeds of *P. crassifolium*. Saponin and tannin are common throughout the genus *Pittosporum* and have been extracted from the leaves of several New Zealand taxa, including *P. cornifolium*, *P. crassifolium*, *P. eugenioides* and *P. huttonianum* (Greshoff 1909; Cambie 1976; Brooker et al. 1989).

4.6 Cytology

Pittosporum kirkii has a chromosome count of $2n = 24$. This count is the same in all members of the genus *Pittosporum* in New Zealand (Dawson 1995, 2008) and outside of New Zealand (Gros 1965, as cited in Jay 1969).

4.7 Additional uses and cultivation

Additional uses of *P. kirkii* have not been explicitly researched. Nevertheless, uses of other New Zealand members of the genus are known. The ornamental value of many well-known species, including *Pittosporum tenuifolium* and *P. eugenioides* was recognised by early colonists in the late 1700's with successful attempts at growing specimens in Great Britain (Brooker et al. 1989; Haase 1990). Essential oils and a resinous gum were obtained from the latter species by early Māori for anointing purposes and eaten to improve foul breath and health (Calder & Carter 1945; Brooker & Cooper 1962; Cooper & Cambie 1991). While early settlers utilised the by-products of the bark of *P. tenuifolium* for the purpose of tanning leather (Cooper & Cambie 1991).

Pittosporum kirkii is cultivated in New Zealand and available at specialist native plant nurseries. Smith (2004) recommends its use as a low maintenance pot plant due to its ability to grow in limited nutrient, drought prone and confined habitats. It can be grown from fresh seed or semi hardwood cuttings (but is slow to strike) (de Lange 2006).

4.8 Reproductive biology

4.8.1 Flowering and fruiting

Pittosporum kirkii has an annual flowering season occurring in the spring-summer months of November to February (Cheeseman 1906; Cooper 1956; de Lange 2006; Myron 2012). Peak flowering occurs in November and December (Myron 2012; cf. Smith-Dodsworth 1991). Flowering duration is similar, with only slight deviations in known publications: November to January (Cooper 1956; Allan 1961) and October-December (de Lange 2006). Females can possess a solitary terminal flower or up to six flowers per terminal umbel (predominantly four– five), which typically develops up to six capsules (usually four and five). Capsules take one to three years to reach autumn maturity (Richards 1956; Myron 2012), and a single female individual can possess capsules from different years that co-occur with flowering. Male and bisexual individuals characteristically produce more flowers than females; typically having seven to eight flowers per umbel. There are

no reports of inconstant 'male' capsules being produced for *P. kirkii* (Myron 2012).

4.8.2 Sexual expression

Allan (1961) commented that knowledge of sexual expression in *Pittosporum* was fragmentary and that the degree of development towards complete dioeciousness was uncertain. Eagle (1982) repeated this view. *Pittosporum kirkii* individuals have been described as monoecious (Cooper 1956), dioecious and gynodioecious (de Lange 2006), but no population data was provided to substantiate these views. Dawson and Lucas (2011) classified *P. kirkii* as C = cosexual and B = bisexual or hermaphrodite but the congener *P. cornifolium* as dioecious specifically gynodioecious. Again, a comment was made specifically about the lack of information for the genus *Pittosporum*. Based on the survey of populations undertaken by Myron (2012) it is likely that individuals are functionally dioecious, specifically gynodioecious but more detailed study is required. Gynodioecy occurs in several other New Zealand members of the genus *Pittosporum*, and has been found to be the main breeding system of two percent of New Zealand's flowering plants (Godley 1979) with 35 (48.5%) of New Zealand tree genera dioecious or gynodioecious (Dawson & Lucas 2011). Male individuals in gynodioecious populations that produce seed are commonly called 'inconstant males', as they can grade from hermaphrodite to completely male (de Lange et al. 2011). However, the inconstant male trait apparent in other *Pittosporum* species (Godley 1979) has not been recorded for *P. kirkii*. Consequently, out-crossing is the likely main mode of fertilisation (Heine 1937).

4.8.3 Pollination

No records are available on specific pollinators. However, *P. kirkii* is likely entomophilous as flowers have unspecialised structures, are small in size, crowded and possess dull colours (Heine 1937; Webb et al. 1999; Clarkson 2011; Myron 2012). Consequently, it is unlikely that *P. kirkii* is monoecious as Cooper (1956) suggests, as monoecious individuals are typically anemophilous (Glover

2007). Hence, cross-pollination is ensured as flowers are typically unisexual in function (de Lange 2006), and crowded in architecture (Cooper 1956).

The crowding of small sized inflorescences has been suggested to increase the occurrence of pollination by various pollinators, predominantly by insects and to a smaller extent, by nectar feeding birds (Heine 1937). It is also suggested that crowded inflorescences increase the attractiveness and supply of nectar to pollinators (Heine 1937). Insects recorded on New Zealand *Pittosporum* include, noctuid moths; *Euxoa admirationis*, *Graphania mutans*, *G. ustistriga* and *Persectania averse* on the dark red flowers of *Pittosporum tenuifolium* and *P. ralphii* (Godley 1979). The yellow admiral butterfly, *Brassaris* species on *P. ralphii*, and beetle species; *Eriirhinus limbatus* and *Tigones caudate* on *P. tenuifolium* (Thomson 1927). Fly (*Diptera*) species; *Calliphora stygia* and *Syrphus novae-zelandiae*, members of families Tachinidae and Opomyzidae (Heine 1937), and members of the insect orders Coleoptera, Hymenoptera, and Hemiptera (Anderson 2003) have been recorded on *P. crassifolium*. Introduced flies have been recorded on *P. eugenioides* (Thomson 1927), and the introduced bee *Apis mellifera* on *P. crassifolium* (Heine 1937). It is likely that Diptera species are a dominant in the cross pollination of *Pittosporum kirkii* flowers. Certainly, observations of Diptera species have been noted on the leaves of *P. kirkii* individuals in full flower (yellow in colour) (Myron 2012).

Recent investigation has suggested nectar feeding birds play an role in pollination, principally in self-pollination (Castro & Robertson 1997; Anderson 2003), which was previously underestimated, or discredited as playing a significant role (Godley 1979; Kelly et al. 2010). Nectar feeding birds such as the bellbird (*Anthornis melanura*) and tui (*Prothemadera novaeseelandiae*) have been recorded taking nectar from *P. crassifolium* (Anderson 2003).

4.8.4 Dispersal

No records exist on the mode of dispersal for *P. kirkii*. The aromatic, viscid fluid immersing the black seeds is believed to attract birds and it has thus been suggested that seeds are either eaten or attached to bird feathers for dispersal

(Oliver 1930; Ridley 1930; Townsend 1999). Bird dispersal through both of these modes has been demonstrated in other New Zealand *Pittosporum*. Oliver (1930) recorded *Pittosporum cornifolium* seeds being stuck to bird feathers, while *P. cornifolium*, *P. eugenoides* and *P. tenuifolium* have been recorded as having seeds consumed and defecated by birds (Powlesland 1987; Burrows 1994b). Bellbird (*Anthornis melanura*), blackbird (*Turdus merula*), kereru (*Hemiphaga novaeseelandiae*), and the introduced silvereye (*Zosterops lateralis*) have been recorded as feeding from the latter two *Pittosporum* species (Burrows 1994b). Furthermore, the viscid *Pittosporum* seeds appear to have little nutritional value to birds (Burrows 1994b). Resultantly the seeds are likely to be a secondary source of food or, a source during winter when primary food sources are scarce. This is supported by capsule dehiscence occurring predominately in the autumn and winter months (see, Chapter 2). If it is dispersed by birds, there is no information about the viability of seeds once they have passed through digestive tracts.

To conclude, epizoochory (attachment via viscid fluid), endozoochory (by frugivorous ornithochory) and hydrochory (e.g. flooding of capsules) (Townsend 1999) have been listed as the main mechanisms for dispersal of *Pittosporum* seeds in New Zealand (Townsend 1999; Thorsen et al. 2009). Incidences of hydrochory, may explain why a number of *P. kirkii* individuals have been recorded growing terrestrially directly beneath female epiphytic individuals (Myron 2012; cf. Schneider & Sharitz 1988). Similarly, the threatened conservation status of *P. kirkii* may possibly be explained through the use of epizoochory. Epizoochory is more common in New Zealand than in similar temperate forests elsewhere, and species using this dispersal mechanism are over-represented amongst threatened species (Thorsen et al. 2009). *Pittosporum kirkii*, similar to other *Pittosporum* species, likely utilises all three of the latter mechanisms in the dispersal of its seed.

4.8.5 Seeding

Rates of seed germination vary in relation to the duration of seed storage; presence or absence of mucilage; and stratification. Freshly collected seeds sown without delay take eight months to a year to germinate (W.M. Clarkson, pers. comm. 2011). Subsequently, longer storage of seed is likely to decrease

germination rates as increased capsule leachate has been found to be an inhibitor in other *Pittosporum* species (Burrows 1996). Free draining soil and semi-shaded to open light conditions are vital for successful germination (W.M. Clarkson, pers. comm. 2011).

Stratification has been found to increase germination rates (W.M. Clarkson, pers. comm. 2011), as evident in , *P. eugenioides*, *P. obcordatum* and *P. tenuifolium* (Moore et al. 1994). Removal of mucilage maybe necessary for successful germination, as it appears to be an germination inhibitor (Burrows 1996). Mucilage removal occurs as seeds are passed through a bird's digestive track (*cf.* Burrows 1994b). No records for seed viability or germination rates exist, however Clarkson and Clarkson (1994) found that *P. obcordatum* female seeds were able to germinate successfully, while inconstant males failed.

4.8.6 Lifespan and population structure

No published data were available on the life span of *P. kirkii*. Herbarium collections from persistent individuals located in the Waitakere Ranges indicated the oldest individual to be at least 30–40 years old (Myron 2012). Additional nursery records suggest individuals can live up to 80 years (G. Davidson, pers. comm. Oratia Nursery 2011).

In the four North Island populations and the single offshore island population of Mount Hobson, Great Barrier Island surveyed by Myron (2012), a range of life stage structures (life stages) were displayed. Three populations exhibited regeneration; Erua Forest, Mount Hobson and Waitakere Ranges, albeit regeneration was more prevalent on Mount Hobson. Regenerating populations exhibited varying levels of regeneration, with Mount Hobson being the most ecologically balanced population, followed by Erua Forest, and lastly the Waitakere Ranges. Regeneration was limited at Waipoua Forest as no juvenile individuals were present and at Mount Taranaki as no seedlings were present.

4.9 Distribution

4.9.1 Geographical range

Pittosporum kirkii has a known restricted geographical range in the North Island, extending from Mangonui in Northland (ca. 35°01'S) to Raetihi and in the Matemateaonga Range south of Ohakune (ca. 39°38'S) (Figure 4.4). It is also notably abundant on the offshore islands of Great Barrier and Little Barrier (Myron 2012). There are no verified records (current or historic) for the South Island.

4.9.2 Environmental range

The distributional range of *Pittosporum kirkii* is restricted by both altitude and latitude. It is restricted to the upper North Island and limited primarily to old-growth forested ecosystems with a mean altitude of 471 (\pm 0.11) m above sea level, within the range of 50 – 1116 m above sea level (Myron 2012). A predicted environmental distribution map, produced through ArcView and ArcGIS™ extrapolation of selected environmental variables (Leathwick et al. 2003; Lehmann et al. 2003) fitted from current records ($n = 268$) highlighted discrepancies between observed and potential distributions. This showed that the most significant variables restricting *P. kirkii* distribution are low elevation (<50 m a.s.l.), low mean annual solar radiation (<1.4 kJ/m²/day), cold temperatures (mean daily temperature minimums of the coldest month <0.3 °C), low mean annual rainfall (<1172mm) and high (October) vapour pressure deficits (>0.15 kPa) (Myron 2012). This is supported by the observed absences of *P. kirkii* in areas where environmental variables are favourable for potential distribution. These areas include the east coast of Northland, the Raukumara Range and Urewera National Park. Similar to congener *P. cornifolium* (Clarkson et al. *In press*), *P. kirkii* is absent from the Taupo Volcanic Zone, where environmental conditions are predicted to be favourable (Figure 4.4) but the large scale ecological disturbance created by the 186 AD Taupo eruption is known to have significantly affected vegetation composition (Rogers & McGlone 1989; Newnham et al. 1999). Notable smaller areas with no recorded observations include high altitude (> 50 m above sea level) and high annual rainfall (>1172 mm)

areas of the Mahia peninsula, and across the Ruahine and Ikawhenua ranges. Further south other areas include high altitude, humid forest in the Wairarapa (Aorangi Range), across the Wakamarama and Burnett Ranges in Tasman, and the Richmond-Gordon range in Marlborough.

The abrupt observed and predicted distribution cessation of *Pittosporum kirkii* in Northland is probably due to the mean minimum daily temperature of the coldest month being too high (>8.2 °C), coupled with low mean total annual rainfall (<1172 mm). Along the east coast of the North Island absences may be due to high mean October vapour pressure deficits (>0.39 kPa) and low annual rainfall which, coupled with the destruction of native forest has resulted in a depauperate epiphyte flora (Clarkson & Clarkson 1991). In the South Island both actual and predicted distribution appears to be limited by a combination of relatively low elevation (< 50 m above sea level), annual (<1.4 MJ/m²) and daily solar radiation in June (<4.8 MJ/m²), mean annual temperature ($<12^{\circ}\text{C} \pm 0.09$) and annual rainfall (<1172 mm). Across the lower North Island and majority of the South Island, the gap in the distribution of *P. kirkii* correlates with extensive modification of the ecological landscape during the Pliocene and Pleistocene glaciations (2-2.5 myo) (Mildenhall 1980; Winkworth et al. 2005).

Listed as a sun epiphyte, *Pittosporum kirkii* is found in open, exposed and well-lit upper lowland and lower montane forested ecosystems, where it is also found in both rupestral and terrestrial lifestyles (Oliver 1930; Myron 2012). As an epiphyte, *P. kirkii* is exposed to the desiccating effects of high irradiance and wind, and limited availability and irregular supply of water and nutrients. These conditions are reflected in terrestrial *P. kirkii* populations, being found in low nutrient kauri detritus on exposed ridges where kauri often grow. Similar conditions are also present in the rupestral habitat, with many *P. kirkii* individuals densely populating exposed rhyolitic outcrops. To survive in these harsh habitats, *P. kirkii* exhibits and utilises a range of morphological and physiological features typical of xeromorphic plants. The coriaceous, thick and fleshy leaves are suggested to reduce water loss (Benzing 1990; Myron 2012). A desiccation experiment indicated that morphological adjustments may reduce the physiological effects of drought by rapidly reducing photosynthetic function (Myron 2012).

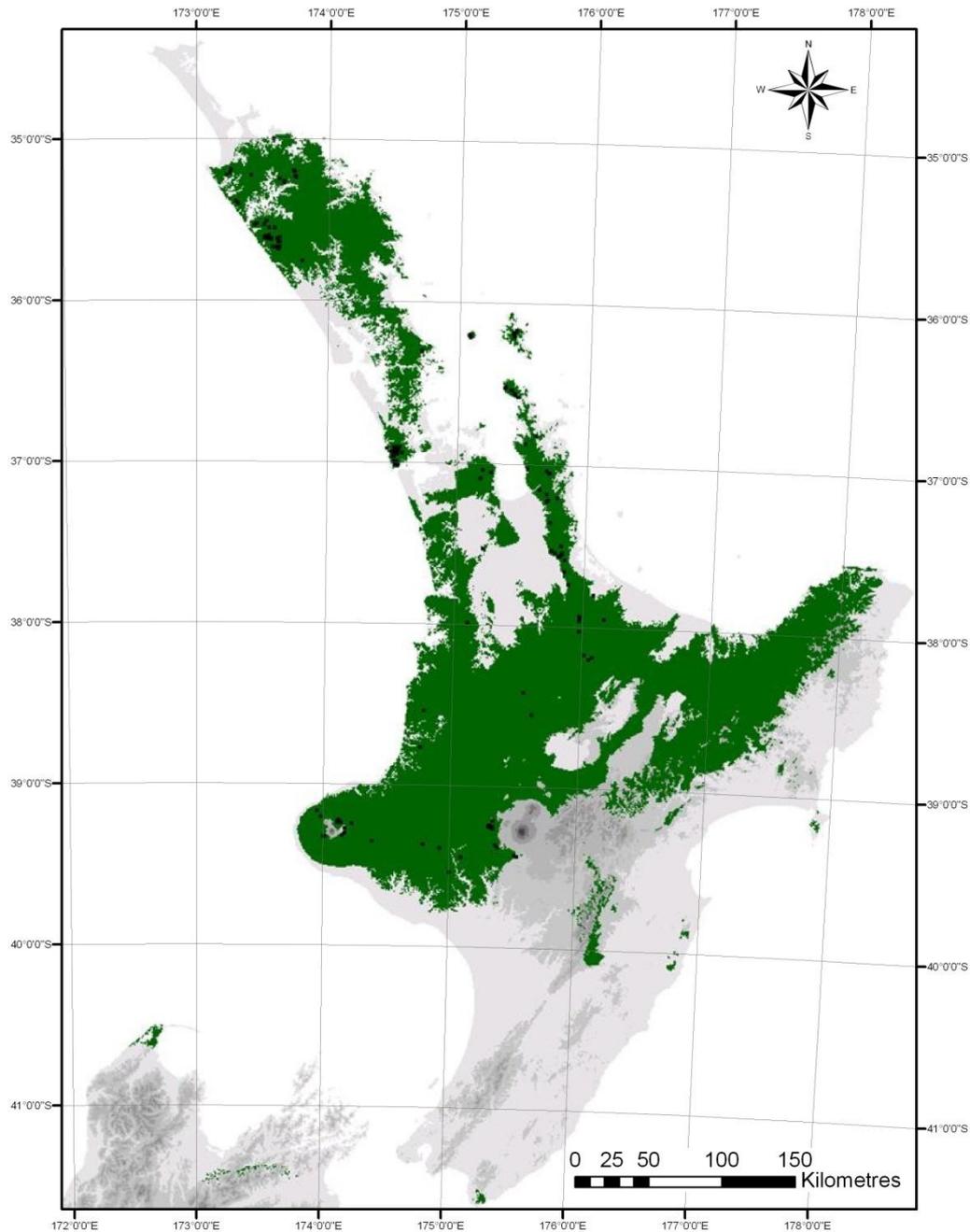


Figure 4.4 Observed (black points) and predicted/potential distribution (shaded green areas) map (environmental envelope) of *Pittosporum kirkii* produced from an ArcView and ArcGIS™ extrapolation of selected environmental variables at observed locations ($n = 268$). Environmental variables chosen were: elevation (m a.s.l), mean annual solar radiation ($\text{kJ/m}^2/\text{day}$); mean annual temperature ($^{\circ}\text{C}$); mean minimum daily solar radiation in June ($\text{MJ/m}^2/\text{day}$); mean minimum daily temperature of the coldest month ($^{\circ}\text{C}$); mean October vapour pressure deficits at 0900 hours (kPa); total annual rainfall (mm).

4.10 Plant communities and associations

Pittosporum kirkii has a restricted altitudinal and latitudinal range. Across its limited range it most frequently inhabits an epiphytic lifestyle, perched amongst nest epiphytes in the canopies of emergent or canopy trees. Terrestrial and rupestral lifestyles are less frequent, and those individuals found inhabiting these lifestyles are common only on offshore islands. The lifestyle statistics combined from ecological surveys ($n = 181$), herbaria and supplementary records ($n = 99$) found that 67% ($n = 186$), 28% ($n = 76$), and 5% ($n = 15$) were epiphytic, terrestrial and rupestral respectively. *Pittosporum kirkii* individuals were recorded across 18 different vegetation types (herbarium, supplementary, and field survey data sets, $n = 110$). Rimu forest, co-dominant with mataī ($n = 39$), kauri ($n = 32$), and rimu and general hardwood forest ($n = 27$) were the most common forest types.

Limited surveys have been undertaken on the plant communities and epiphytes found in association with *P. kirkii*. Plant communities and epiphytic associations assembled from the present and previous published and unpublished surveys is presented below, from north to south in three latitudinal zones.

35°01'° S–36° S - Northland from Mangonui to Waipoua Forest.

Pittosporum kirkii is found epiphytically and terrestrially in old-growth and cut-over *Agathis australis* - podocarp forest particularly upon plateau forest and ridges. Growing terrestrially, *Alseuosmia macrophylla*, *Astelia trinervia*, *Gahnia xanthocarpa*, and *Pseudowintera axillaris* are common understory associates (Myron 2012). Common epiphytic associates include: the nest epiphytes, *Astelia solandri* and *Collospermum* species; Orchidaceae, *Earina autumnalis*, *E. mucronata* and *Winika cunninghamii*; ferns and fern allies, *Asplenium flaccidum*, *A. oblongifolium*, *A. polyodon*, *Cardiomanes reniforme*, *Ctenopteris heterophylla*, *Huperzia varia*, *Hymenophyllum* species, *Microsorium novae-zealandiae*, *Microsorium pustulatum* subsp. *pustulatum* and *Loxogramme dictyopteris* and *Tmesipteris* species; *Metrosideros* species, *M. albiflora*, *M. fulgens*, *M. robusta*, and *M. perforata*; shrubs, *Brachyglottis kirkii* var. *kirkii*, *Griselinia lucida* and *Pittosporum cornifolium*.

36–37° S - northern Kaipara to the Coromandel Range

Pittosporum kirkii is found epiphytically on the summit of Mount Tamahunga (Omaha Forest) associated with *Collospermum* species, *Metrosideros robusta* and mixed podocarps (Young 2010). On Great Barrier Island, terrestrial and rupestral individuals are abundant across Mount Hobson. At lower altitudes on Mount Hobson, *P.kirkii* is terrestrial in association with *Dacrydium cupressinum*, *Halocarpus kirkii*, *Ixerba brexioides*, *Phyllocladus toatoa*, and regenerating *Agathis australis*. At higher altitudes, *P. kirkii* is found in association with *Lepidothamnus intermedius*, mature *Agathis australis* and podocarp species, and rupestral on rhyolytic outcrops with *Astelia solandri*, *Epacris sinclairii* and *Olearia allomii* (Moore 1973; Myron 2012). On Little Barrier Island *P. kirkii* is found in similar associations as Great Barrier Island, but also with *Griselinia littoralis*, *Collospermum microspermum*, *Hymenophyllum lyallii* and *Peraxilla tetrapetala* (Moore 1973). In Windy Canyon, Great Barrier Island, rupestral individuals are found in association with *Brachyglottis kirkii* var. *kirkii*, *Gleichenia dicarpa*, *Hebe macrocarpa* var. *latisepala* and *Kunzea sinclairii*. Epiphytic associates at the Waitakere Ranges include: nest epiphytes; ferns, *A. bulbiferum*, *A. flaccidum*, *A. oblongifolium*, *A. polyodon*, *Blechnum filiforme* and *M. pustulatum* subsp. *pustulatum*; shrubs, *B. kirkii* var. *kirkii*, *Coprosma* species, *Griselinia littoralis*, *G. lucida* and *P. cornifolium*; Orchidaceae, *E. autumnalis* and *W. cunninghamii*; Hymenophyllaceae, *C. reniforme* and *Hymenophyllum* species; vines/climbers, *Freycinetia banksii* and *Ripogonum scandens*; *Metrosideros* lianes, *M. fulgens*, and *M. perforata*. Terrestrial individuals are associated with *Brachyglottis kirkii* var. *angustior*, *B. kirkii* var. *kirkii*, *G. xanthocarpa*, *I. brexioides* and *Nestegis* species. Across the Coromandel Range, rupestral individuals are found on high altitude rocky outcrops, with epiphytic and terrestrial individuals found in similar associations, but also with *Ascarina lucida* var. *lucida* and *P. tetrapetala* (Moore 1973).

37–39° S - Kaimai Ranges to Lake Taupo

Pittosporum kirkii is rare in the Waikato and King Country, being restricted to higher altitudes across the Kaimai Ranges and Mamaku plateau, and epiphytically on Mount Pirongia, Mount Karioi and Mount Te Aroha. Growing terrestrially, *P.*

kirkii is found in association with *I. brexioides* in old-growth and regenerating podocarp forest across the Kaimai Ranges (K.M. Jones, Department of Conservation, pers. comm. 2011). Associated understory across the Kaimai Ranges include, *Phyllocladus alpinus* and *Astelia nervosa* (Moore 1973). Common associated epiphyte species include, *Astelia solandri* and *Collospermum hastatum*; Orchidaceae, *Ichthyostomum pygmaeum*, *Earina autumnalis* *E. mucronata*, *Drymoanthus adversus*, and *Winika cunninghamii*; ferns, *Asplenium flaccidum*, *A. bulbiferum*, and *A. polyodon*; climbing *Metrosideros* species; shrubs, *Brachyglottis kirkii* var. *kirkii*, *Pittosporum cornifolium* and *G. lucida*; Hymenophyllaceae, *C. reniforme* and *Hymenophyllum* species; other species include, *Huperzia varia*, *Grammitis* species, *Ripogonum scandens* and *Rubus australis* (Cheeseman 1879; Gudex 1963; Moore 1973). On the Herangi Range in the Western King Country, *P. kirkii* has been found as an epiphyte on *Quintinia serrata* on the margin of a *Dracophyllum traversii*/sphagnum bog (B.D. Clarkson, University of Waikato, pers. comm. 2012)

39–39°38' S - Turangi to Matemateaonga Range.

Pittosporum kirkii is sparsely distributed, growing epiphytically in old-growth forest at Erua, on Mount Taranaki and at high altitudes across the Matemateaonga Range. At these populations, *P. kirkii* are most commonly associated with nest epiphytes, *Astelia solandri* and *Collospermum microspermum*; ferns, *A. flaccidum*, *A. polyodon*, *Hymenophyllum* species, and *M. pustulatum subsp.pustulatum*; Orchidaceae, *E. autumnalis*, *E. mucronata* and *W. cunninghamii*; *Metrosideros robusta* and *M. diffusa*; shrubs, *G. littoralis*, *Coprosma* species., and *P. cornifolium*, and also, *Pseudopanax crassifolius*, *Ripogonum scandens* and *Weinmannia racemosa* (Myron 2012).

4.11 Succession

The establishment and succession trajectory for vascular epiphytes positions *Pittosporum kirkii* as a late successional species, as evident by its frequent association with nest epiphytes in old-growth forests. As an epiphyte, *P. kirkii* commonly colonises in the deep humus supported in established nest epiphytes, *Astelia solandri*, *Collospermum hastatum* and *C. microspermum* (Dawson &

Sneddon 1969). Nest epiphytes frequently perch on large ramifications, collecting and accumulating leaf litter debris and dead organic matter through their long narrow leaves, creating moisture rich, albeit low nutrient, arboreal soil (Oliver 1930; Lüttge 2006). Found frequently hanging from the base of these nests, is a number of pendulous orchids, such as *Winika cunninghamii*; drooping ferns such as *Asplenium polyodon*; and epiphytic shrubs such as *P. kirkii*. This key association has been found by several authors and likely reflects the facilitative succession of vascular epiphytes generally on large canopy and emergent hosts (Johansson 1974; Dickinson et al. 1993; Hofstede et al. 2001). This is characterised by the initial establishment of desiccation-tolerant pioneering species such as lichens, which co-occur and ameliorate the bark surface allowing for the growth of epiphyte mats (Johansson 1974; Nadkarni 2000). Epiphyte mats retain water and nutrients, capture propagules and provide anchorage for vascular epiphyte seedlings (Nadkarni 1984a; Zotz & Vollrath 2003). By functioning in this manner, epiphyte mats ameliorate microclimatic conditions of the ramosphere (Freiberg 1996b, 2001), which creates favourable microhabitats for the growth of detritus collecting nest epiphytes (e.g. *Collospermum* species), which in turn ameliorate conditions for shrub epiphytes to colonise (Robertson 1964; Freiberg 1996b, 2001)

Persisting in a rupestral lifestyle across Mount Hobson (Great Barrier Island), individuals were found directly on rock and with moss clumps. The fine texture and structure of jagged rhyolitic outcrops provides habitat for the establishment of *P. kirkii*. Rhyolitic outcrops perforated with crevices that permit the build-up of detritus similar to nest epiphytes, which allows for the penetration of *P. kirkii* roots at exposed locations.

Terrestrial individuals grow directly beneath or in close proximity to large kauri. Kauri typically grow in strongly leached and low nutrient clay and loam soils upon ridges. Large kauri exacerbate these soil conditions through their highly acidic leaf litter which accumulate and decompose over extremely long periods of time. Coupled with this is the unique open architecture of kauri; creating open and well-lit microclimatic conditions throughout the canopy and understory. These conditions facilitate the continuing recruitment of *P. kirkii*, as only a limited

number of plants species can tolerate the environmental conditions that kauri create.

4.12 Pests, disease, and animal damage

The endemic fringed scale, *Kalasisis perforate* (Maskell), has been found on members of the genus *Pittosporum* in lowland and mixed broadleaf forest, including on *Pittosporum kirkii* (Henderson 2001). All endemic scale insects (Hemiptera: *Coccoidea*) are sexually dimorphic and survive and reproduce by sucking sap from their host (Henderson & Rhode 2001). Brushtail possums eat other endemic *Pittosporum* fruit (Ridley 1930), and new succulent growth and flowers (Ecroyd 1994; Townsend 1999; de Lange et al. 2011). But no published paper has been found quantifying possum browse impacts on *P. kirkii*.

4.13 Conservation and restoration

4.13.1 Conservation status

Pittosporum kirkii is currently listed as in decline and is nowhere common throughout its range (de Lange et al. 2009; Young 2010). It has been anecdotally reported that herbivory by the introduced brushtail possum (*Trichosurus vulpecular*) and forest clearance have led to the decline of *P. kirkii* (Brandon et al. 2004; Forester & Townsend 2004; Taranaki Regional Council 2009), although beyond these anecdotal reports no evidence has been presented in the scientific literature. However, direct observations of the limited North Island populations in contrast to the abundant population on possum-free Great Barrier Island, suggests that *P. kirkii* may be threatened by possum herbivory. This could be due to inadequate possum control at mainland populations and/or slow recovery rates after possum control. Historic destruction of upper lowland and lower montane forests (520–770 years ago) (McGlone 1989) has most certainly reduced the potential distribution and habitat to *P. kirkii* populations, as preferred hosts such as large kauri were preferentially selected due to their valuable wood qualities (Esler 1983). The conservation of this species is further impeded by the lack of information on its autecology and the extent, or likelihood of browsing by

introduced pests. Overall, there is uncertainty about the current declining *P. kirkii* threat listing due to the lack of published population monitoring results.

4.13.2 Conservation and restoration management

Informed conservation management is critical to the survival and regeneration of *P. kirkii* populations. Education would be a useful tool for increasing the appreciation of *P. kirkii*, but also to address the current information gap. Education could enable people to identify, assess and report the locations and condition of *P. kirkii* individuals; potentially leading to a better understanding of its natural range and threat status. On-going public education about kauri die back disease is also vital to protect terrestrial and epiphytic *P. kirkii* communities that exist in the unique conditions that large kauri create. This has two-fold importance, firstly to protect the current hosts, habitat and seed source of many *P. kirkii* individuals and secondly, to ensure the seed source of future kauri hosts and habitat.

There are many factors that are potentially causing the decline of *P. kirkii*, and these need to be adequately addressed in conservation and restoration plans. These factors include: the inherent slow growth rate that is a feature of vascular epiphytes in general (Benzing 1990; Schmidt & Zotz 2002); limited bird populations restricting seed dispersal; skewed sex ratios limiting regeneration and increasing the probability of inbreeding depression; intraspecific competition; poor habitat availability through the loss of suitable hosts and microhabitats; and possum browse. This species also should be considered for inclusion in suitable restoration plantings and reintroduction projects, given its sparse distribution and absence from predicted locations. Certainly, this has been recognised in a few restoration programmes which have included *P. kirkii* in their restoration planting plans, these include Matakohe/Limestone Island restoration plan (Ritchie 2000) and the Waitakere Ranges threatened species management plan (Waitakere Threatened Species Management Policy 2009).

4.14 Conclusion

Pittosporum kirkii has historically been described by Oliver (1930) as a typical epiphyte, as it commonly displays an epiphytic lifestyle. However epiphytic, terrestrial and rupestral lifestyles are all represented in *P. kirkii* populations. Hence, *P. kirkii* is better placed as a facultative epiphyte as defined by Benzing (1990). Facultative epiphytes can exist both in terrestrial and rupestral lifestyles interchangeably when favourable growing conditions within and beneath the canopy converge (Dawson & Sneddon 1969; Benzing 1990). Terrestrial and rupestral lifestyles are primarily restricted to and abundant only on offshore islands which are possum-free and where other browsing animals are also limited. Therefore the current lifestyle profile is probably skewed compared to pre-human environments. In all three lifestyles, *Pittosporum kirkii* individuals are exposed to a combination of the desiccating effects of high irradiance and wind; and limited by the availability and irregular supply of water and nutrients. Thus, *P. kirkii* exhibits and utilises a range of morphological and physiological features typical of xeromorphic plants to survive in these difficult habitats. The strong habitat and microhabitat preferences of *P. kirkii*, coupled with historic logging of preferred hosts, restrict it to upper lowland and lower montane forested ecosystems. This has likely rendered the species sparsely distributed and exacerbates its potential decline. Informed conservation management is critical to the survival and regeneration of *P. kirkii* with on-going public education, particularly about kauri die back disease. This species also warrants inclusion in relevant restoration projects as a focal species. Future research should focus on quantifying browsing impacts and on sexual expression of *P. kirkii*, including dispersal and pollination studies.

Chapter five: Synthesis

5.1 Main findings

This research has contributed to our understanding of the autecology of the endemic shrub epiphyte *Pittosporum kirkii*, which is currently listed as in decline and data poor. Ecological field surveys were carried out to determine the current ecological status of five populations across the known latitudinal range. Habitat, host preferences and vascular epiphyte species found in close association were recorded to comprehensively characterise the habitat requirements of *P. kirkii*. Ecological data and supplementary data sets were combined to develop observed and predicted environmental distribution maps and relevant environmental variables that influence distribution were revealed (chapter two). Chapter two forms the bulk of this study; from it chapter four was developed and a paper for submission to the New Zealand Journal for the biological flora of New Zealand series is presented. A water relations experiment investigated morphological and physiological responses that *P. kirkii* and congener *P. cornifolium* exhibit under desiccation stress to identify the stress strategy of each species. The results of this experiment provide insight into the adaptations of New Zealand's vascular epiphytes that assist their survival in the harsh conditions of epiphytic, as well as rupestral and terrestrial habitats.

The ecological assessment of five mainland *P. kirkii* populations including offshore island population on Great Barrier Island confirmed that *P. kirkii* distribution is restricted both by altitude and latitude. *Pittosporum kirkii* habitat is restricted primarily to old-growth upper lowland and lower montane forested ecosystems, where individuals commonly adopt an epiphytic lifestyle. Under Benzing's (1990) life history classification scheme, *P. kirkii* is classified alongside *P. cornifolium* as a facultative epiphyte (Clarkson et al. *In press*), as individuals of both species adopt epiphytic, terrestrial and rupestral lifestyles. This is in contrast to the shrub epiphyte *Griselinia lucida* which has been argued to be an obligate epiphyte (Bryan et al. 2011).

Pittosporum kirkii is adapted to high light conditions but individuals can also tolerate semi-shaded conditions in open well-lit forests and are frequently found in high concentrations directly beneath or in the close vicinity of large kauri under these conditions. Large and often remnant, canopy and emergent hosts act as an ecological refuge and are important for the dispersal and regeneration of *P. kirkii*. Epiphytic congener, *P. cornifolium* is also thought to rely on these large hosts while *G. lucida* can be found growing on host trees from a range of sizes classes (Bryan 2011).

Evidence from ecological surveys found that *P. kirkii* has specific microhabitat preferences on hosts and occurs most commonly on a narrow range of specific host species. This has perhaps rendered the species sparsely distributed and thus, naturally uncommon across a narrow range of ecosystems. This contrasts with other endemic epiphytes, *G. lucida* and congener *P. cornifolium*, which are found more widely distributed across lowland and coastal ecosystems (Bryan et al. 2011; Clarkson et al. *In press*). The environmental factors that likely further limit distribution include low elevation, low solar radiation, low mean daily temperatures, low mean annual rainfall and high vapour pressure deficits. Similar to *P. cornifolium* the main agent proposed as detrimental to regeneration, possum herbivory was not detected and regeneration failure was not evident for *P. kirkii*. However, the results were not conclusive, due to the relative inaccessibility of the epiphytic lifestyle, and the fact that all study sites had adequate possum control.

Functional dioecy was apparent in the population data analysed. However no inconstant males were recorded so, gynodioecy as the main breeding system remains unsubstantiated. In comparison to endemic epiphytic species, *P. cornifolium*, is unisexual in function and gynodioecious while, *G. lucida* is known to be dioecious (Bryan 2011; Clarkson 2011).

A physiological drought response experiment revealed that *P. kirkii* seedlings are able to postpone the effects of drought stress predominantly through morphological adaptations. Under decreasing soil water content (increased stress) *P. kirkii* seedlings rapidly responded by reducing stomatal conductance and rates of photosynthesis. This response sustained relatively high leaf water potentials,

which maintained leaf turgor and reduced continual water loss. Morphological features contributing to this stress responses include variations in plant size and leaf characteristics. *Pittosporum kirkii* xeromorphic leaf characteristics allow for the postponement of desiccation stress by reducing water loss and contribute to water storage which is significant in drought conditions. Some of these characteristics include; small relative leaf area, coriaceous, thick leaves which are dark green in colour with substantial upper cuticle, upper and lower hypodermis. Desiccation postponement has been reported as the main stress strategy employed by epiphyte *G. lucida* under drought conditions, however this species utilises greater physiological adjustments in comparison to *P. kirkii* to delay the effects of drought (Bryan 2011). In contrast, *P. cornifolium* strongly aligns with the desiccation tolerance stress strategy, as evident through greater utilisation of physiological adjustments (discussed below).

The desiccation postponement strategy of *P. kirkii* aligns with the distribution range and habitat types discussed in chapter two. The rapid reduction of photosynthetic function during drought conditions is likely to be the key mechanism that allows this species to survive in the extreme conditions of upper lowland and lower montane forests. Nest epiphytes in the canopy, rock crevices on cliff faces and acidic litter under kauri trees all have limited water holding capacity and thus, *P. kirkii* has adapted to survive frequent, short term drought but also regain function rapidly when the water becomes available. The comparable hydrology of *P. kirkii* habitat types is supported by the similar water-use efficiencies of plants growing in all three of them.

The comparison of stress strategies for *P. kirkii* and *P. cornifolium* showed that *P. kirkii* does not maintain growth during drought. This indicates a preference for survival instead of growth. This trade-off may be related to the narrow habitat range of *P. kirkii* as it is likely out-competed by vascular epiphytes that can maintain growth during drought, such as *P. cornifolium*. In contrast to tropical epiphyte species, *P. kirkii* is more sensitive to desiccation stress, as shown by the rapid reduction of photosynthetic function and postponement of growth with onset of drought conditions. This is apparent when comparing *P. kirkii* with tropical

epiphyte species (e.g. bromeliads), which are prominently desiccation tolerators that are able to sustain growth under desiccation stress.

The results of both ecological field surveys and water relations of *P. kirkii* are relevant to inform conservation management and ecologically suitable restoration plantings and reintroduction projects.

In New Zealand there is a general lack of botanical information on our endemic plants and this is especially applicable for our vascular epiphytes. To date, only two known vascular epiphyte species have been the subject of extensive autecological studies (Bryan et al. 2011; Clarkson et al. *In press*). Therefore, this study represents a significant contribution to our understanding of native vascular epiphytes and also, the *Pittosporum* genus.

The majority of epiphyte research has been undertaken in tropical forests with the importance of these species being widely documented. This present research on *Pittosporum kirkii* is a contribution to the currently small body of knowledge for temperate epiphytes. It is hoped that it will help highlight the importance of these plants in non-tropical environments and lead to further autecological research.

5.2 Directions for future research

Future research is important for *Pittosporum kirkii* as the data quality available on the possible threats is poor and as a result uncertainty remains about the current declining threat status of *P. kirkii*. Future research would enhance the knowledge on the possible threats and would also be beneficial to the conservation of this species and its inclusion into relevant restoration and reintroduction plans.

Palatability to possums has been suggested a main agent of decline of *P. kirkii*, but evidence is anecdotal and circumstantial. Hence, further research on the possum palatability is undoubtedly required to clarify the current threat listing. A small trial with captive possums could be undertaken. This would entail wild possums being captured, acclimatised in captivity, and then fed a combination of plants already known to be palatable alongside *P. kirkii*. Mallinson & Hickling

(1993) provide a detailed outline that could be followed to undertake this research. Another method to address this question would be to monitor browsing in forests which are possum free (e.g. on Great Barrier Island) to forests where possums are abundant. The foliar browse index (Payton et al. 1999) would be a suitable method to assess differences between sites.

To build on the population data reported in the present research detailed research including hand-pollination experiments and flower dissections would clarify sexual expression in particular gynodioecy in *P. kirkii* populations. This would enable better understanding of the relationship between populations that are strongly male skewed and long term regeneration patterns. It is also important to restoration planting and reintroductions, as balanced numbers of both sexes may be needed for projects to be successful in the long term.

Genetic analysis of offshore island populations (e.g. Great Barrier Island) in comparison to mainland populations is also recommended. Significant morphological differences of Great Barrier Island individuals noted may point to the existence of a variant distinct from mainland populations. Eco-sourcing of seed for restoration plantings maybe needed to ensure that genetic diversity is not lost through hybridisation of variants.

Further research on flower pollinators and dispersal mechanisms of *P. kirkii* would also be beneficial.

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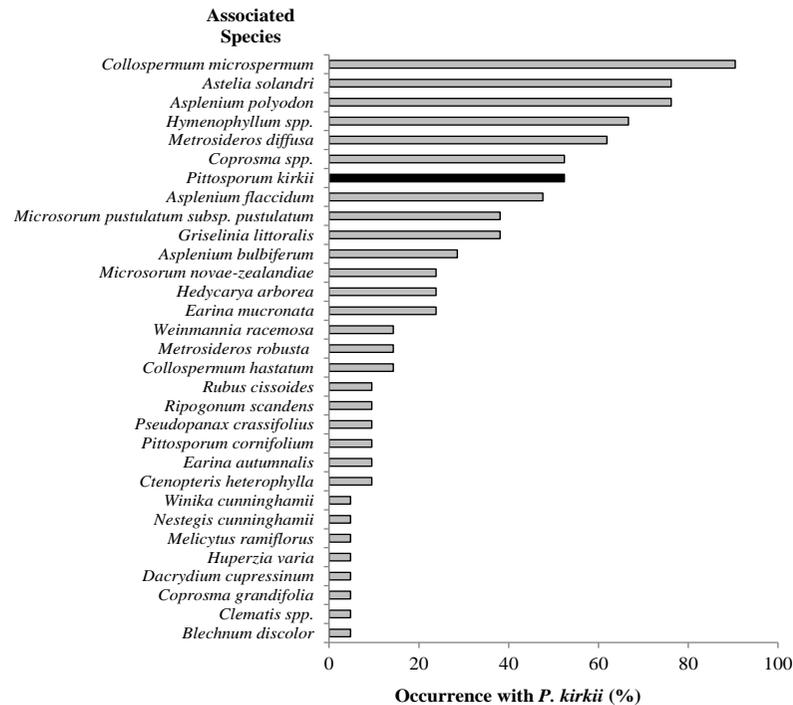
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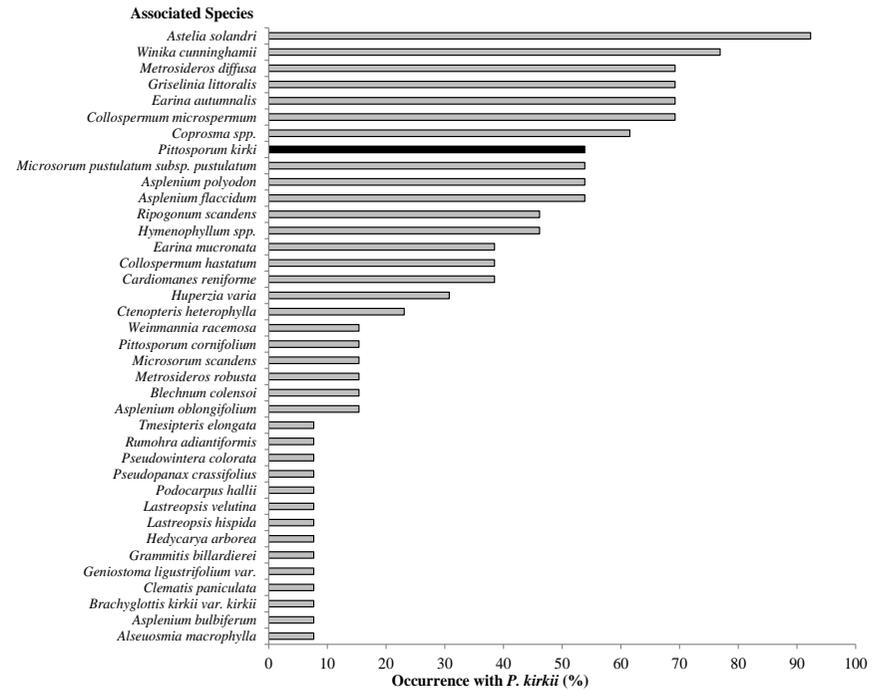
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Appendices

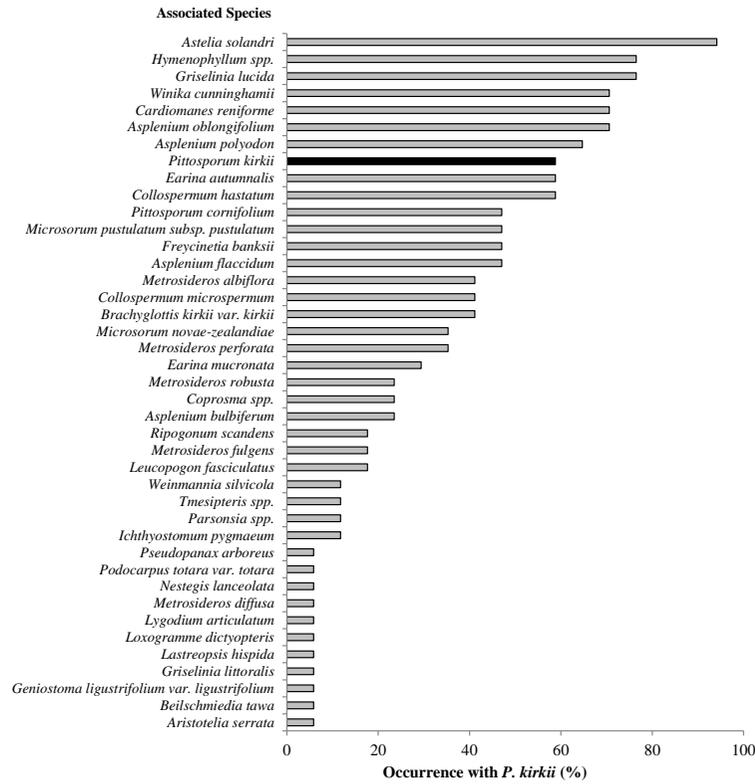
Appendix 1: Associated vascular epiphyte and vine species at each of the four North Island populations surveyed. Mount Hobson (Great Barrier Island) is omitted as only one host (one *Pittosporum kirkii* epiphytic individual) were surveyed.



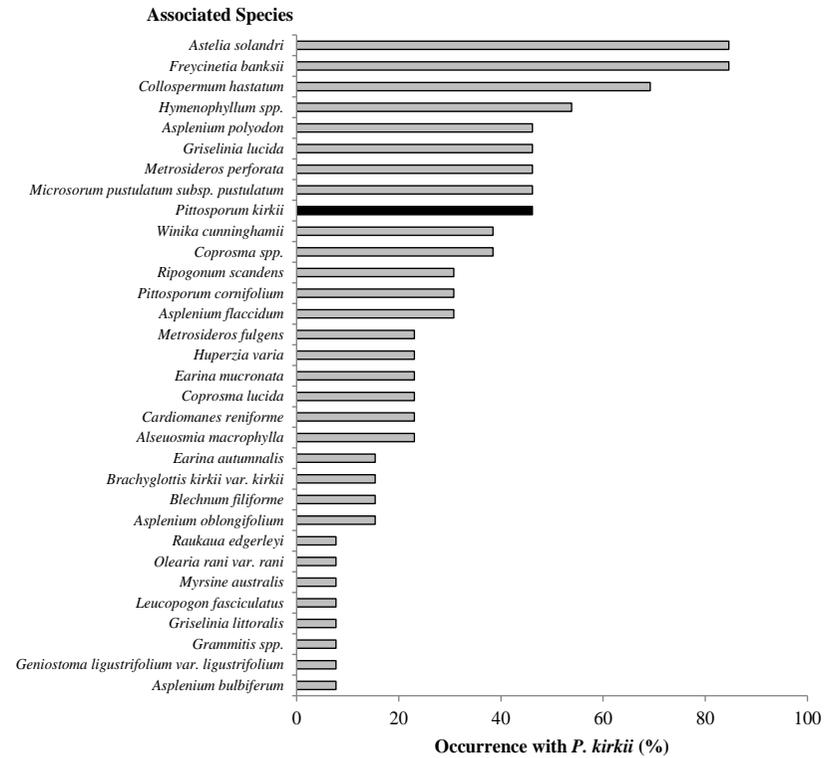
The vascular epiphyte and vine species ($n = 30$) associated with *Pittosporum kirkii* (occurring on the same host) and frequency of occurrence (percent) at Erua Forest. *Pittosporum kirkii* is highlighted.



The vascular epiphyte and vine species ($n = 38$) associated with *Pittosporum kirkii* (occurring on the same host), and frequency of occurrence (percent) at Mount Taranaki. *Pittosporum kirkii* is highlighted.

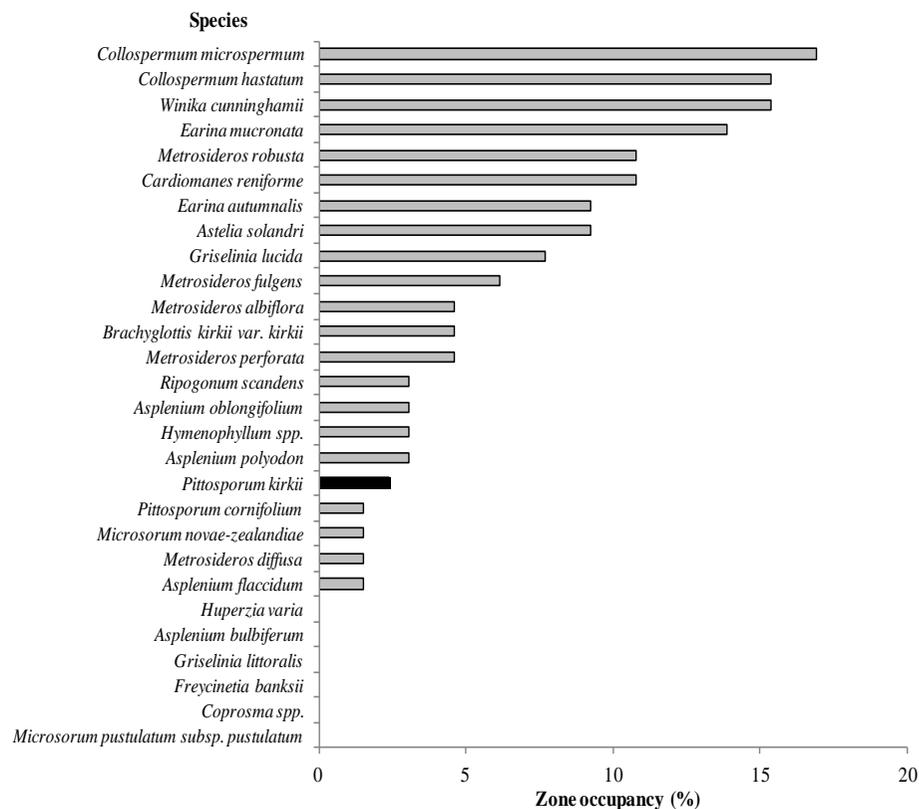


The vascular epiphyte and vine species ($n = 41$) associated with *Pittosporum kirkii* (occurring on the same host), and frequency of occurrence (percent) at Waipoua Forest. *Pittosporum kirkii* is highlighted.

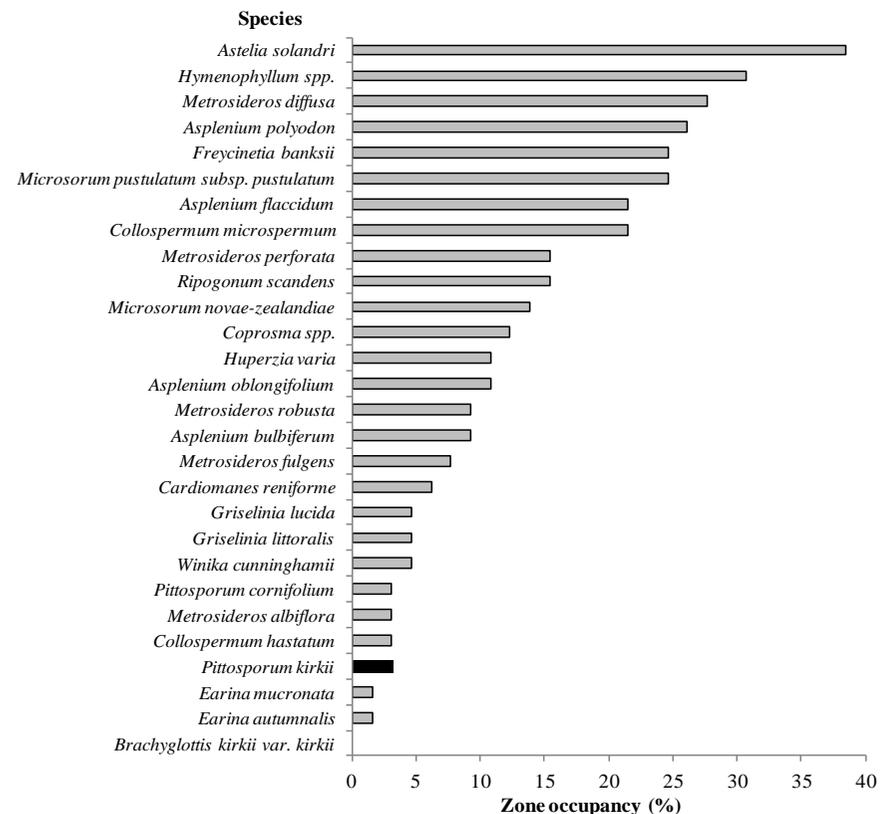


The vascular epiphyte and vine species ($n = 41$) associated with *Pittosporum kirkii* (occurring on the same host), and frequency of occurrence (percent) at the Waitakere Ranges. *Pittosporum kirkii* is highlighted.

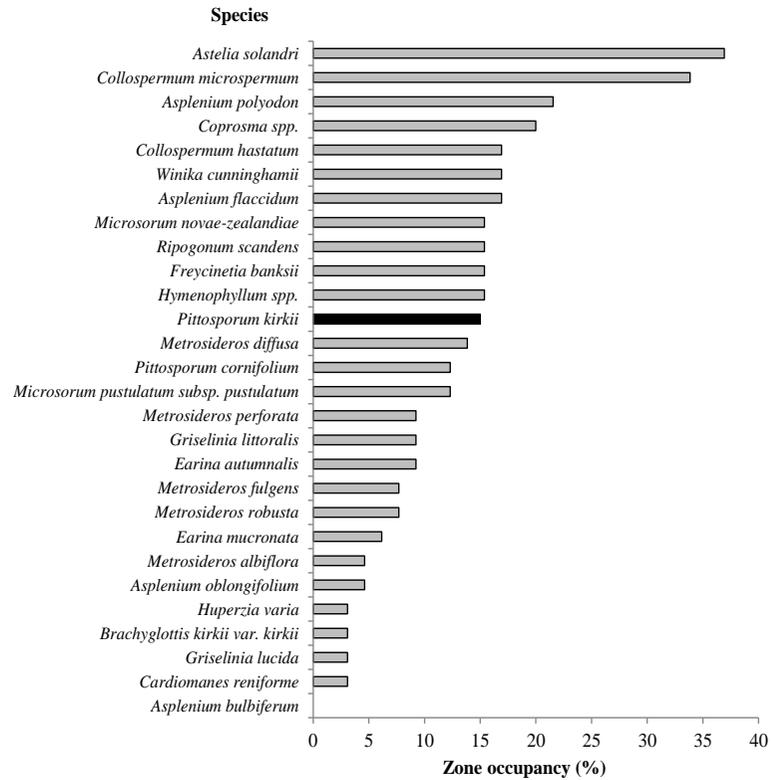
Appendix 2: The complete list of associated vascular epiphyte and vine species present in each of the five host occupancy zones (percent), combined across the four surveyed populations. Species that occurred in less than ten percent overall were predominantly ephemeral (accidental) epiphytes and were omitted.



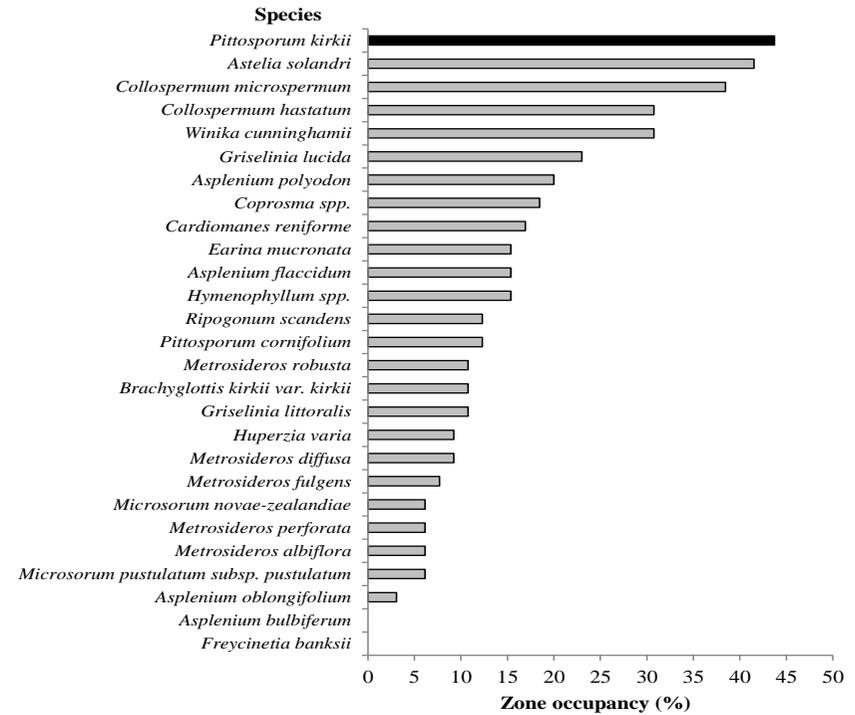
Associated vascular epiphyte and vine species present in zone one ($n = 21$). Species with no bar shown were absent from this zone.



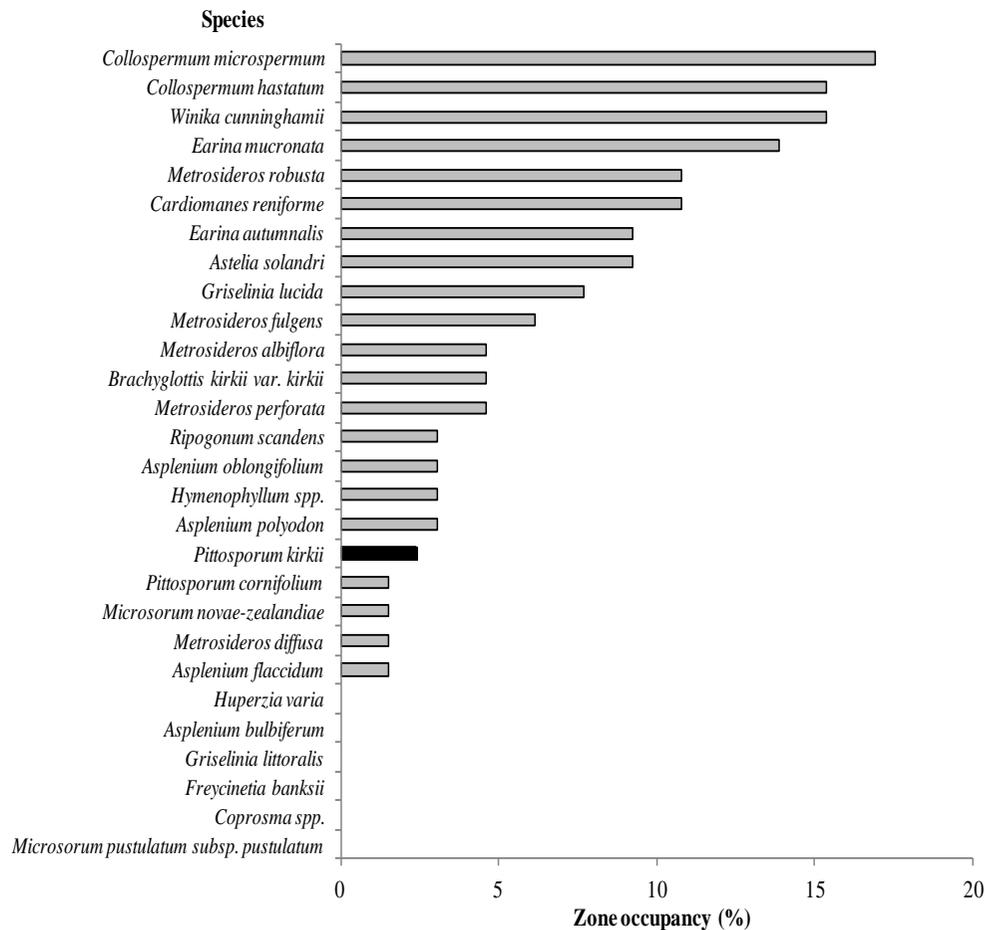
Associated vascular epiphyte and vine species present in zone two ($n = 27$). *Brachyglottis kirkii* var. *kirkii* was absent from this zone. *Pittosporum kirkii* is highlighted.



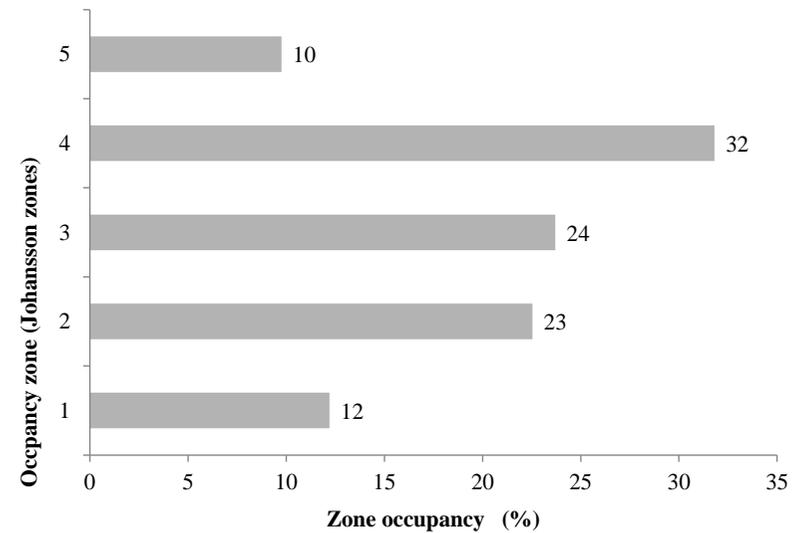
Associated vascular epiphyte and vine species present in zone three ($n = 27$). *Asplenium bulbiferum* was absent from this zone. *Pittosporum kirkii* is highlighted.



Associated vascular epiphyte and vine species present in zone four ($n = 27$). Species with no bar was absent from this zone. *Pittosporum kirkii* is highlighted.

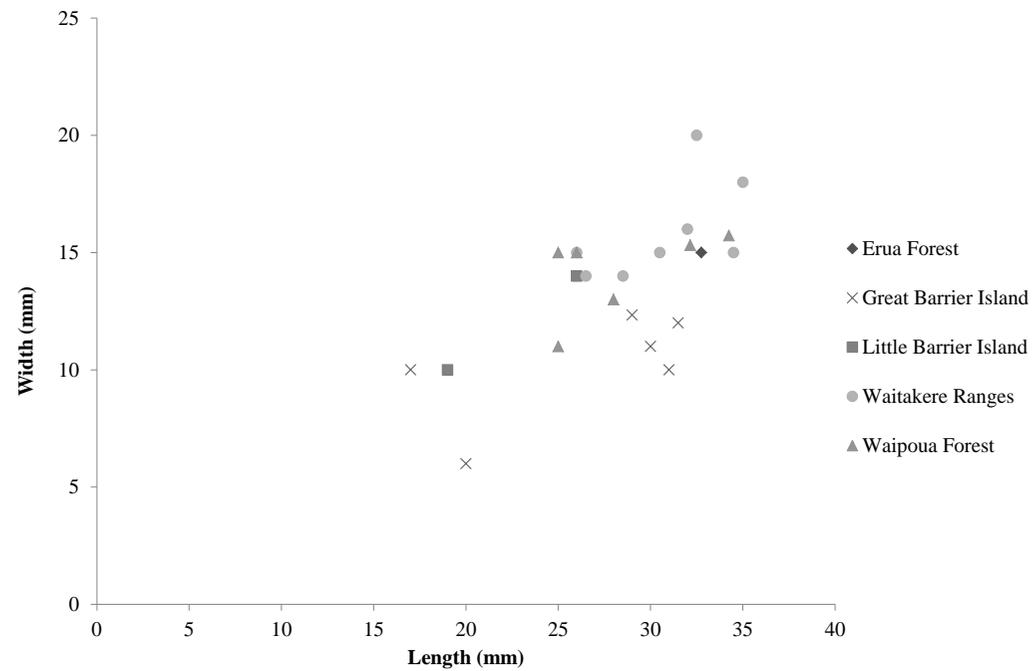


Associated vascular epiphyte and vine species present in zone five ($n = 22$). Species with no bar was absent from this zone. *Pittosporum kirkii* is highlighted.



Combined frequency of occupancy of all associated vascular epiphytes and vine species across the four surveyed populations. The percent present each zone is shown at the end of each bar.

Appendix 3: Capsule morphology



Mean length and width (millimetres) comparisons of *Pittosporum kirkii* capsule size. Combined from herbarium records and field surveys across five populations: Erua Forest ($n = 1$), Great Barrier Island ($n = 6$), Little Barrier Island ($n = 2$), Waipoua Forest ($n = 6$), Waitakere Ranges ($n = 7$). No precise capsule measurements have been recorded for Mount Taranaki.