Treeline vegetation composition, structure and dynamics across the AD 1655 Burrell Lapilli deposit, Mt Taranaki, New Zealand

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Jackson Tai Efford

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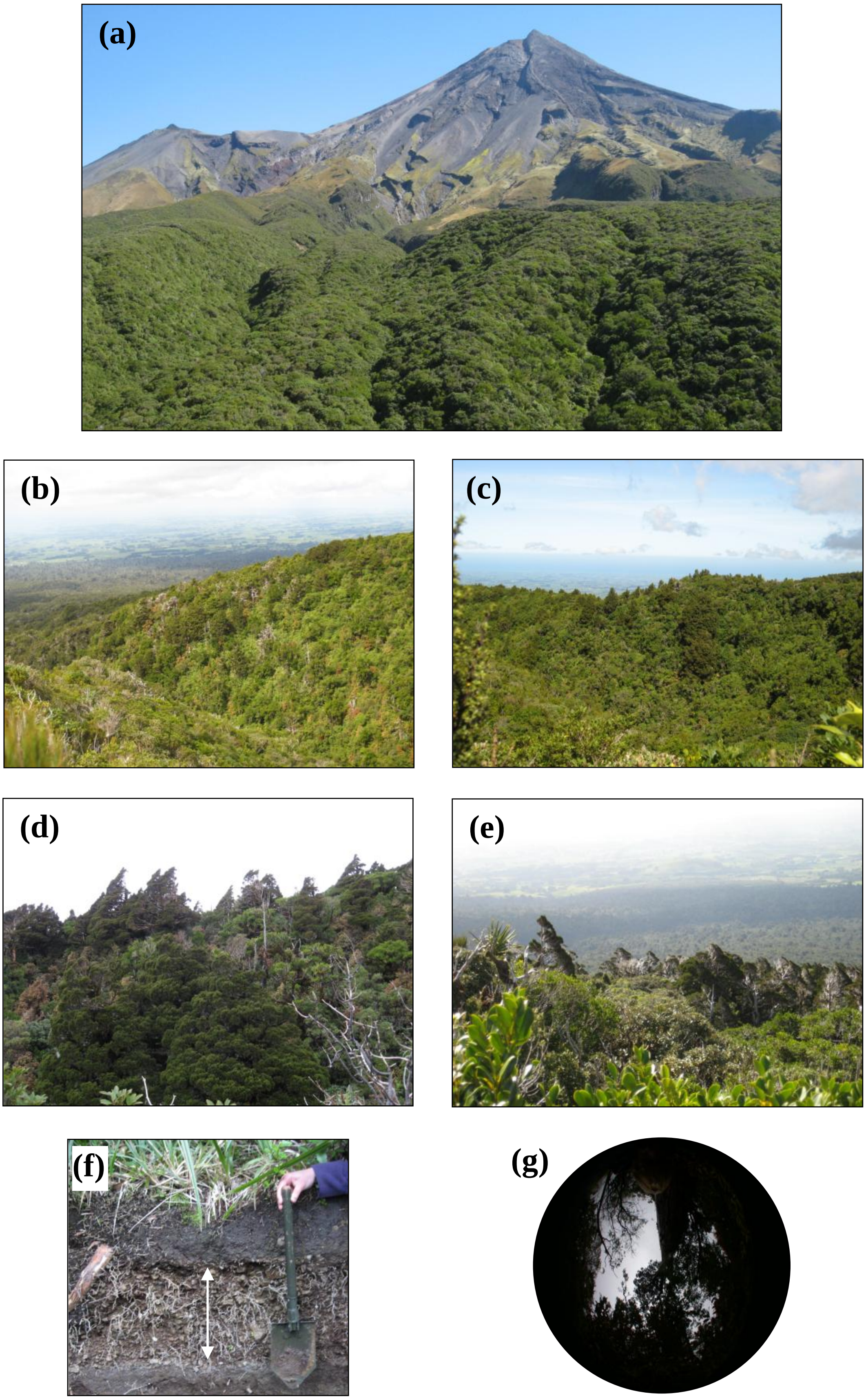

Frontispiece: (a) Mt Taranaki summit and satellite cone Fanthams Peak. **(b,c)** Treeline vegetation near The Plateau with emergent *Podocarpus hallii*. **(d,e)** Treeline vegetation near North Egmont with emergent *Libocedrus bidwillii*. **(f)** Burrell Lapilli deposit (35 cm thick) near Dawson Falls. **(g)** Hemispherical photo of treeline vegetation.

Abstract

Research was conducted on Mt Taranaki, North Island, New Zealand, to examine how the composition, structure and dynamics of treeline vegetation has been influenced by the AD 1655 Burrell Lapilli eruption. Treeline is considered as “the connecting line between the uppermost forest patches on the mountain, with trees upright and at least 3 m in height and growing in groups”. The Burrell Lapilli was deposited at a thickness of 1–40 cm over c. 150 km^2 of the eastern flanks of Mt Taranaki, and is thought to have inflicted widespread mechanical and chemical damage to vegetation at the time of eruption. Isopach maps of the Burrell Lapilli distribution reveal an eruption axis exists south-eastwards from the summit towards somewhere between Dawson Falls and Stratford Mountain House; out from which the thickness of lapilli decreases in all directions.

Vegetation at the treeline position (c. 1000–1100 m above sea level) was measured across this lapilli distribution with thirty-five 10 × 15 m quadrats and six variable length 5 × 35–120 m belt transects. An additional three quadrats were located on the treeline of the adjoining Pouakai Range, an area which has not suffered any recent volcanic disturbance. Across the survey area on Mt Taranaki, winter (24/7/2011–17/10/2011) temperature measurements were recorded using eighteen micro data loggers. The light requirements of selected treeline species (juveniles) were quantified *in situ* using canopy openness measurements made with hemispherical photography, in order to gain an insight into how species may have responded to increased light levels associated with vegetation damage by the Burrell Lapilli.

Daily average minimum temperatures ranged from 0.64–1.26 °C, average daily maximum temperatures ranged from 5.37–7.24 °C, and average daily means ranged from 3.07–3.71 °C. No major temperature anomalies were detected across the survey area.

Within the quadrats, a total of 57 vascular taxa were identified, all of which were indigenous and typical of either montane forest or shrubland vegetation types on the mountain. Quadrats were grouped based on the thickness of the Burrell Lapilli at the sites; quadrats where lapilli was 20–40 cm thick are referred to as ‘severe’, those with lapilli 1–20 cm thick as ‘minor’, and those outside the distribution of lapilli on Mt Taranaki as ‘outside’. Total basal area of trees >2 cm diameter at ground height (dgh)

increased progressively from 165 to 265 m^2 ha^{-1} across the severe, minor, outside, and Pouakai Range quadrat groups. Total density of trees displayed the inverse trend, with higher stocking rates in the severe (6615 stems ha^{-1}) and minor (8370 stems ha^{-1}) groups, compared with the outside (5422 stems ha^{-1}) and Pouakai Range (5822 stems ha^{-1}) groups.

The contributions of four potential canopy/emergent species (*Podocarpus hallii, Griselinia littoralis*, *Libocedrus bidwillii*, *Weinmannia racemosa*) varied markedly at the treeline. Across the severe, minor, outside and Pouakai Range groups, basal area of *Podocarpus* was 30, 40, 26 and 20 m^2 ha^{-1} respectively; *Griselinia* was 57, 58, 52, 6 m^2 ha^{-1}; *Libocedrus* was 10, 22, 93, 7 m^2 ha^{-1} and *Weinmannia* was 0, 1, 24, 161 m^2 ha^{-1}. Vegetation of each group was accordingly classified as:

Severe: *Podocarpus* / *Griselinia* scrub
Minor: *Podocarpus – Libocedrus* / *Griselinia* scrub
Outside: *Libocedrus – Podocarpus* / *Griselinia – Weinmannia* scrub
Pouakai Range: *Podocarpus* / <u>*Weinmannia*</u> scrub

Belt transect surveys across the treeline ecotone revealed that maximum tree diameters decreased markedly (c. 100 to 30 cm dgh) with increased elevation. Maximum tree heights also decreased with elevation, with emergent *Libocedrus* (c. 13 m) capable of attaining greater heights than emergent *Podocarpus* (c. 8 m) near the treeline position. Spatial configuration of trees implied that large canopy trees suppressed the number and size of stems in close proximity, and in areas away from canopy trees, clusters of smaller stems occurred (predominantly *Pseudowintera colorata* and *Coprosma tenuifolia*).

Common treeline species were ranked in order from most shade-tolerant to least shade-tolerant (i.e., light demanding) using the 10th percentile of the distribution of light environments occupied by each species as an approximation of the minimum light levels tolerated: *Coprosma tenuifolia* > *Pseudowintera colorata* > *Raukaua simplex* > *Griselinia* > *Podocarpus* > *Weinmannia* > *Libocedrus*. Consequently, diameter frequency distributions of light demanding species tended to display cohort population structures, implying they were incapable of regenerating below a closed canopy; while more shade-tolerant species displayed all-sized or reverse “J” structures, indicating their ability to regenerate continuously.

It is speculated that *Libocedrus*, being a tall emergent, was eliminated from the most severely affected areas because it suffered a direct impact from the lapilli and has poor resprouting capabilities. It did not successfully regenerate there because (1) seed dispersal did not occur, (2) it was competitively excluded, (3) or it could not tolerate the new substrate. Where the effects of the eruption were less severe, *Libocedrus* was more successful, with an even-aged population initiated due to the increased light levels on the forest floor. *Griselinia* was most successful in areas severely affected by the eruption, probably because it could establish epiphytically on brightly lit snags well before suitable substrate developed. *Griselinia* has maintained its dominance due to its *in situ* mode of regeneration, whereby seedlings establish epiphytically in parent trees, combined with its ability to basally resprout. *Weinmannia* was not capable of capitalising on the severely affected areas in the same way, because at this elevation it is very close to its upper altitudinal limit, and would not have tolerated exposure associated with open sites; then, following canopy closure, light levels would have been too low for it to establish. *Podocarpus*, being a more shade-tolerant species, probably established within the eruption zone sometime after the event, and continues to regenerate below a closed canopy. Seedling and sapling data suggest that in the absence of severe disturbance, the compositional differences observed around the treeline of Mt Taranaki are likely to persist.

The explanation of vegetation patterns resulting from tephra eruptions elsewhere in the world may benefit from the findings that (1) emergent species suffer the most deleterious effects during a tephra eruption, (2) epiphytic regeneration may be an important mechanism for early arrivals into devastated areas, (3) light demanding species thrive as a result of openings created in the canopy, and (4) the successional trajectory of affected areas could be altered to the extent that vegetation patterns across tephra deposits may persist indefinitely.

Keywords: Mt Taranaki, Egmont, Burrell Lapilli, tephra eruption, treeline, vegetation, *Podocarpus*, *Libocedrus*, *Griselinia*, *Weinmannia*, light requirements, shade-tolerant, light demanding, succession.

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Chapter One: Introduction and study site

This thesis investigates treeline vegetation composition, structure and dynamics across the AD 1655 Burrell eruption lapilli deposit on Mt Taranaki. The present chapter provides a general introduction to treelines and the Mt Taranaki study site, followed by the thesis research objectives and outline.

1.1 Alpine treelines

The high altitude limit of forest, commonly referred to as the alpine treeline, timberline or forest line, is probably the best known and most studied of all distributional boundaries of trees (Körner 2003). In reality, a treeline is not usually a clearly defined line as such (although it may sometimes appear that way from a distance), but rather a transitional zone along which trees are replaced by non-trees (Stevens and Fox 1991). Providing that plant communities vary in some way at this transition, the expression treeline 'ecotone' is also a useful term (Allan & Walsh 1996). A myriad of definitions for treeline exist, with a range of different heights used to delineate a 'tree' from other vegetation types. For example, Wardle (1964, 1965, 1971) has used two different tree height definitions (1 m and 2 m high) in his studies of New Zealand treelines. In the present study, I follow Körner & Paulsen's (2004) definition of the treeline position as "the connecting line between the uppermost forest patches in an area, with trees upright and at least 3 m in height and growing in groups" (Figure 1.1).

There are an overwhelming number of possible mechanisms thought to cause alpine treelines, many of which are frequently debated in the scientific literature. A review by Stevens & Fox (1991) grouped these explanations into either 'stature-related' or 'growth-related' hypotheses. Stature-related hypotheses suggest that smaller plants are able to exploit the narrow zone of favourable conditions near the ground, while upright trees cannot. Growth-related hypotheses are concerned with the idea that photosynthetic rates decline with temperature, such that a treeline is located where the annual carbon fixation of trees does not balance the carbon lost to respiration.

On mountains in New Zealand, two visually distinct types of alpine treeline vegetation transition exist; those where *Nothofagus*[1] is present and dominant, and those where *Nothofagus* is absent (Wardle 1973; Figure 1.2). The most common type of treeline is the abrupt and level treeline formed where either of two species of *Nothofagus* are present. In this type of transition, a solid mass of closed-canopy, upright *Nothofagus* forest (often >12 m high) abruptly gives way to short alpine grassland or tussockland over a distance of only several metres, at an elevation of c. 1200–1500 m above sea level (asl). Where annual rainfall exceeds 2000 mm, *Nothofagus menziesii* is usually the dominant species, whereas dryer mountains with shallower soils support *Nothofagus solandri* var. *cliffortioides* (Wardle 2008). However, the distribution of *Nothofagus* across New Zealand is not continuous, with a total absence of the genus at locations with seemingly favourable conditions; such as Stewart Island, areas west of the Southern Alps, mountains either side of the Manawatu Gorge and on the dormant volcano Mt Taranaki. The likely explanation for the discontinuous distribution of *Nothofagus* across New Zealand relates to its failure to recover ground lost during the last glaciation, due to poor seed dispersal capabilities (Dawson 1988).

Where *Nothofagus* is absent, the treeline transition is much more gradual, and occurs at an elevation c. 100–200 m lower than *Nothofagus* dominated treelines. At non-*Nothofagus* treelines, mixed montane conifer-broadleaf forest diffusely gives way to alpine grassland via a belt of dense woody subalpine scrub or shrubland. In this type of transition, the growth form of montane forest genera (e.g., *Podocarpus*, *Libocedrus*, *Weinmannia*, *Metrosideros*, etc.,) displays a reduction in height with increased elevation, often gradually transitioning from vertical erect stems, to prostrate stunted shrub forms (Wardle 1973). In the absence of *Nothofagus*, it is possible to examine the competitive interactions between these species at the upper limits of their altitudinal distribution; as they would otherwise be suppressed and out-competed by *Nothofagus* at similar elevations elsewhere (Ogden 1971). In the subalpine scrub and shrubland vegetation associated above non-*Nothofagus* treelines, a mix of hardy shrubs in turn become shorter, and more sparse with increased elevation, before eventually reaching their upper limits, whereby vegetation merges into an alpine grassland or tussockland, then herbfield. This transition from montane forest to subalpine scrub and then grass or tussockland can take place over a distance of several kilometres,

[1]. Species nomenclature follows New Zealand Plant Conservation Network (2012) except for *Podocarpus hallii*, which follows Connor & Edgar (1987).

a strong contrast to the rapid transition where *Nothofagus* is dominant (Wardle 2008). On Mt Taranaki, the focus of the present study, the treeline (groups of trees >3 m) currently occurs at around 1000–1100 m asl. The dominant tree species here include *Podocarpus hallii*, *Griselinia littoralis*, *Libocedrus bidwillii* and *Weinmannia racemosa*, with every possible combination from co-dominance of all four species to single dominance of any one possible (Clarkson 1986). For the purposes of this study, a reference to treeline henceforward should not be considered as an exact line, but rather as the narrow (<100 m wide) belt of treeline vegetation occurring between the treeline position and the timberline position indicated in Figure 1.1.

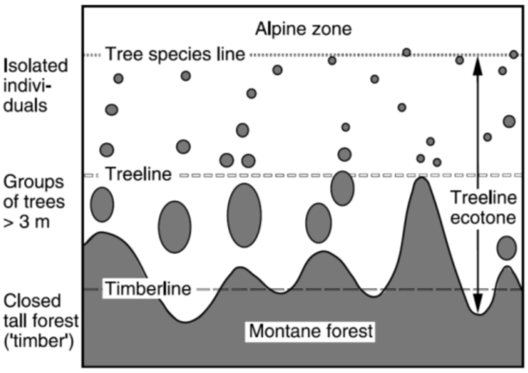

Figure 1.1: A schematic representation of the alpine treeline ecotone and treeline definition used in this study after Körner & Paulsen (2004).

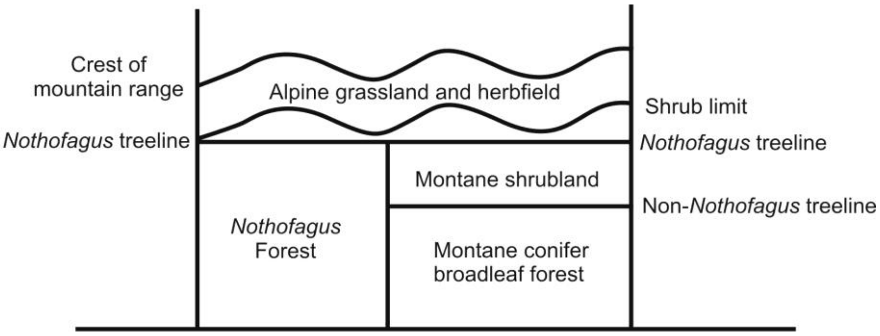

Figure 1.2: Differences in zonation near treeline where *Nothofagus* is present and dominant, and where *Nothofagus* is absent after Dawson (1988).

1.2 Mt Taranaki

Mt Taranaki (alternatively known as Mt Egmont) is a dormant strato-volcano on the western coast of the North Island of New Zealand. Towering an imposing 2518 m above the surrounding landscape, Mt Taranaki is central to the 33,500 ha Egmont National Park, and is isolated from the central mountains of the Tongariro Volcanic Zone (Figure 1.3). The majority of the present cone of Mt Taranaki has been built up by eruptions in only the last 10,000 years, and since c. AD 1500, Mt Taranaki has erupted at least nine times (Neall et al. 1986); though all these eruptions have occurred prior to the European occupation of New Zealand, and no Maori accounts are known (Lowe et al. 2002). Unlike any other Holocene volcano in New Zealand, the slopes of Mt Taranaki are clothed with largely intact natural vegetation. Both Druce (1966, 1974, 1976a, 1976b) and Clarkson (1977, 1981, 1986) have described Mt Taranaki's vegetation in detail, and recognised the influence that recent volcanic events have had on shaping the current vegetation pattern on the mountain.

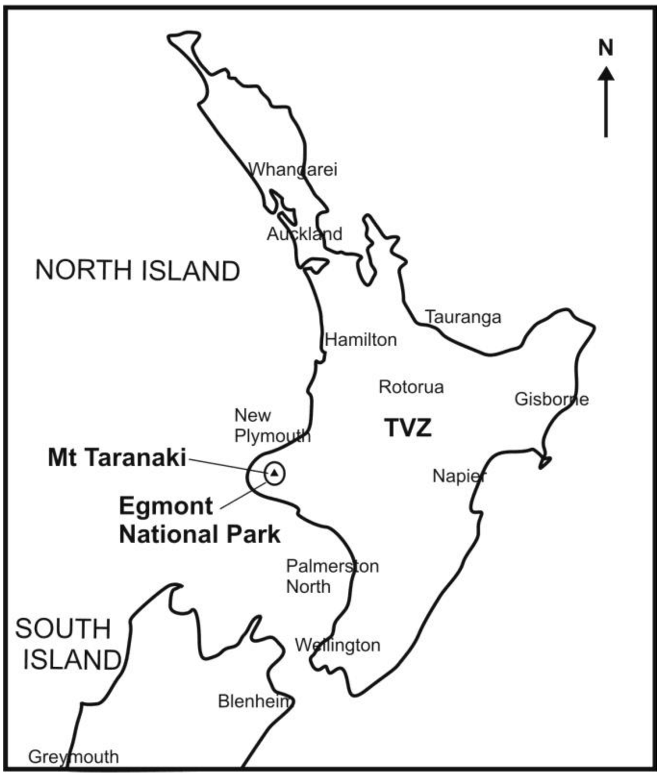

Figure 1.3: Location of Mt Taranaki, Egmont National Park and the Tongariro Volcanic Zone (TVZ) in the North Island of New Zealand.

1.2.1 Climate

A general description of the climate experienced by Egmont National Park and Mt Taranaki has been compiled by the New Zealand Meteorological Service (1976, 1980) and Clarkson (1981). This information, while somewhat dated, is deemed adequate in the context of the present study; and in addition, measurements of temperature at the treeline position were conducted as a component of this research (see Section 2.2). The height of Mt Taranaki (2518 m asl) and its position near the west coast of the North Island has a strong influence on the climate experienced at each location. This is depicted in the concentric zonation of the bioclimatic zones present, which range from coastal through to alpine in the Taranaki Region (Figure 1.4). Overall, the park has a temperate maritime climate like most of New Zealand, with continually alternating calm and stormy weather conditions. The range of seasonal contrast on the mountain is moderate, with frequent stormy conditions in winter and longer settled spells in summer.

Due to orographic effects influencing the prevailing moisture-laden winds from the Tasman Sea, precipitation increases concentrically around Mt Taranaki from a mean annual rainfall of 1100–1500 mm at the coast, through to 6500 mm at 1000 m asl, and finally to 8000 mm near the summit; with rainfall isopachs almost mirroring the elevation contours of the mountain (Figure 1.5). In the eastern sector of the mountain, where the present study is focused, available data suggests a slight rainfall increase towards the northeast; Dawson Falls (945 m asl) receives 6000 mm annually, compared to 6700 mm at Stratford Mountain House (846 m asl). These two monitoring stations are the closest located to the treeline area of focus. Daily rainfalls here have been as high as 443 mm, with rain occurring on an average of 192 days yr^{-1}, and the longest consecutive period without rain being 23 days. There is little information available for snowfall; Stratford Mountain House has an average of 14 snowfall days yr^{-1}, though this number undoubtedly increases with altitude. In rare instances, snow has engulfed all of the mountain and sections of the ringplain as far afield as Stratford, though it does not persist for more than a few days. Snowpack studies on the upper slopes have shown that during winter, temperatures can still be above freezing, causing precipitation to fall as rain and not snow. In winter, cloud and mist also frequently envelope Mt Taranaki, particularly in the afternoon, and fog is reported on average 49 days yr^{-1}

at Stratford Mountain House. As a consequence of frequent cloud cover, sunshine hours vary from 2110 hours yr^{-1} at New Plymouth (c. 50% of the total possible), through to less than 1000 hours yr^{-1} at Stratford Mountain House. Relative humidity also increases with elevation and distance from the coast. At New Plymouth at 9 am, the average relative humidity is 78%, while at Stratford Mountain House it is 87%.

With regards to temperature, the freezing level in the atmosphere over Mt Taranaki is approximately 2800–4200 m asl in mid-summer, and somewhere between 1150–2350 m asl in mid winter. The ground level air temperature on the mountain decreases at an average of 6 ^{o}C for every 1000 m of elevation gained. At Stratford Mountain House, summer (December–March) temperatures average 12–13 ^{o}C, while winter (June–August) temperatures average 4–5 ^{o}C. February is the only frost-free month, and occasionally summer temperatures have exceeded 25 ^{o}C; while winter minimums have been as low as -5 ^{o}C, with July usually being the coldest month.

Prevailing westerly winds are frequently salt laden and are diverted into a northwesterly airflow by the mass of the mountain, creating wind strengths as high as 186 km hr^{-1}, which were measured at The Plateau (1144 m asl) in December 1979. The salt which is blown inland has been known to cause damage to exposed tree crowns, particularly those of *Libocedrus bidwillii* (Druce 1966). As well as being channelled through the gap between Mt Taranaki and the Pouakai Range, wind is also channelled between Mt Taranaki and the Taranaki uplands to the east. This creates a prevailing southerly wind on the eastern flanks where the present study is focused, and consequently, westerly winds here are rare due to obstruction by the mountain. As a whole, the mountain strongly affects wind climate, and local modifications would occur in all parts of the park.

With the exception of the upper slopes of Mt Taranaki, climatic conditions in Egmont National Park are very favourable for almost year-round plant growth, with ample to excessive water supply, sufficient temperatures, and an absence of drought stress.

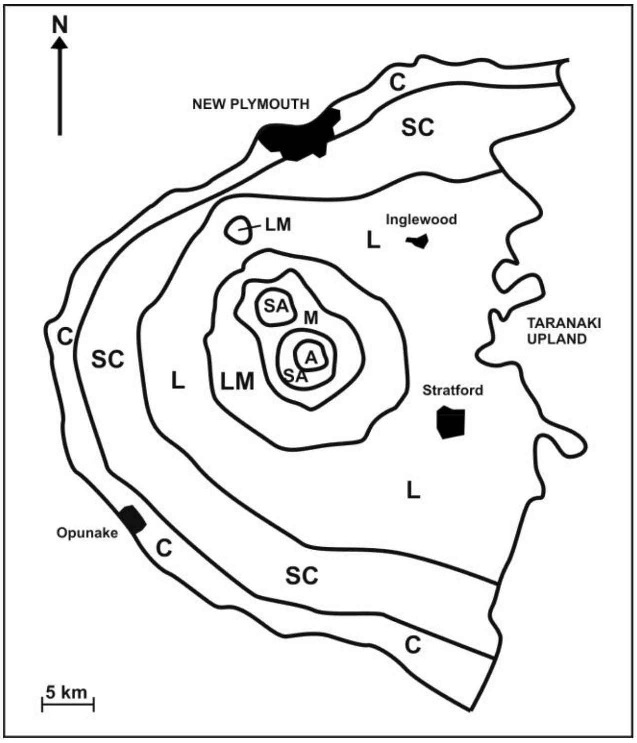

Figure 1.4: Bioclimatic Zones in the Taranaki Region after Lees and Neall (1993): C Coastal, SC Semi-coastal, L Lowland, LM Lowland Montane, M Montane, SA Sub-alpine, A Alpine.

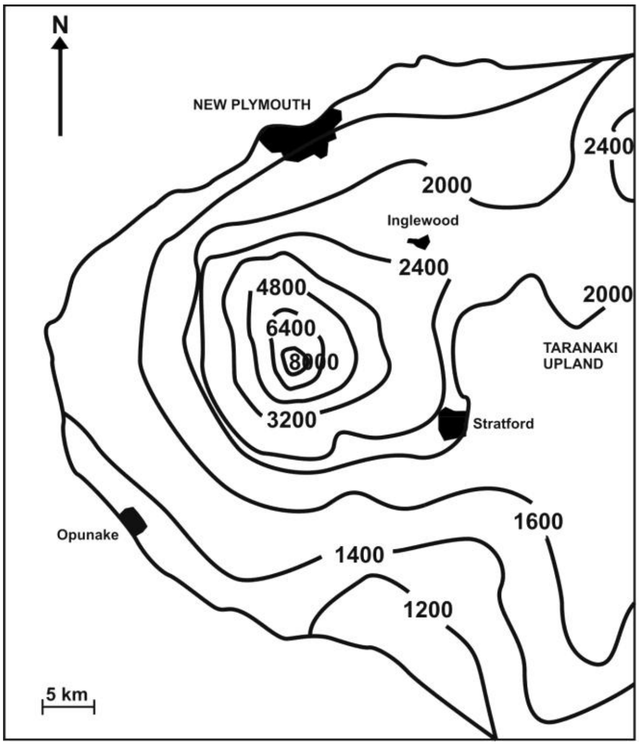

Figure 1.5: Distribution of mean annual rainfall (mm) in the Taranaki Region 1941–70 after Lees and Neall (1993).

1.2.2 Geology and volcanic history

The volcanic history of the Taranaki Region, and the recent eruptive events from Mt Taranaki, have been described at various levels of detail by Druce (1966), Topping (1972), Neall (1980), Neall et al. (1986), Platz et al. (2007) and Platz et al. (2012). Mt Taranaki, along with the progressively older Pouakai Range, Kaitake Range and Paritutu, define a Quaternary andesitic volcanic lineament known as the Taranaki Volcanic Succession, along which volcanism has migrated south-eastward through time (Figure 1.6). Last active c. 1.75 million years ago, Paritutu is the oldest volcano in the succession, and has been eroded to the extent that only small outcrops of volcanic breccias <80 m asl high remain (the Sugar Loaf Islands). The more extensive Kaitake Range was last active c. 575,000 years ago, and is estimated to have once been as large as Mt Taranaki; though now advanced erosion has reduced this volcano to a circular area of radiating ridges, rising to the central point Patuha at 684 m asl. Pouakai was last active c. 250,000 years ago, and is more intact than Kaitake with a height of 1377 m asl and a bordering ringplain of mass flow deposits. Pouakai was also probably once similar in height and shape to Mt Taranaki, but deeply dissecting erosion has left only the lower and middle portions of this volcano preserved.

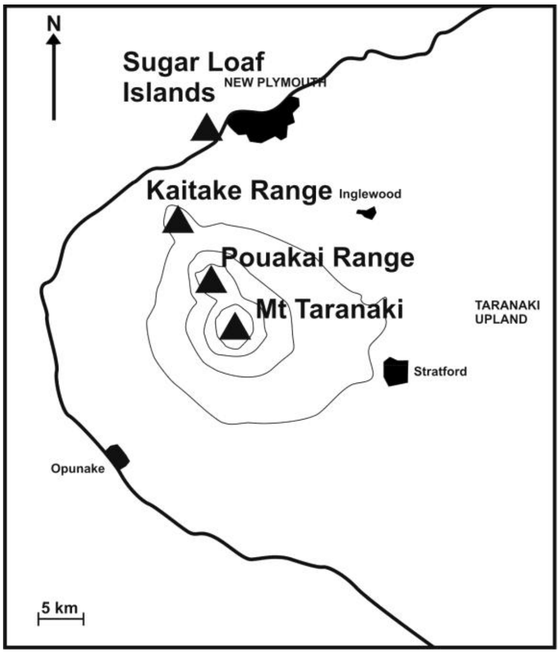

Figure 1.6: Southeast trending Taranaki Volcanic Succession after Platz et al. (2007).

Mt Taranaki, the youngest and most intact in the succession, is a strato-volcano with a near perfect cone rising to 2518 m asl at a vertical to horizontal ratio of 1:10. A parasitic or satellite cone known as Fanthams Peak (1962 m asl) is present off the southern flanks. Lahars, debris flows, lava flows, and tephra showers originating from Mt Taranaki have shaped the present day Taranaki landscape. The mountain first appeared c. 70,000 years ago, and by c. 35,000 years ago would have been a substantial cone similar in size to today. Mountain up-building through lava extrusion has been complimented with regular eruptions of tephra and mass flows, which now mantle the surrounding landscape. The upper section of the cone is comprised principally of lava flows extruded over the last 10,000 years, while the lower section represents detrital fragments of pre-existing cones that have been deposited by mass flows and floods throughout the duration of the mountain’s formation. These mass flow deposits are partially recognisable as an extensive hummocky ring plain around the mountain, and give the mountain a gradually tapering appearance around the flanks. Mt Taranaki is also dissected with a near perfect pattern of more than 50 radially draining streams and rivers.

The most recent period of volcanism on Mt Taranaki (Table 1.1) commenced with the AD 1500–1550 Newall and Waiweranui eruptions, followed by the AD 1655 Burrell eruption, the minor AD 1755 Tahurangi eruption, and finally the passive AD 1785–1820 Sisters eruption. These recent eruptions have been significant in shaping the present day vegetation pattern of the mountain. The Newall and Waiweranui eruptions comprised four pyroclastic flows (nuées ardentes), and are represented by ash and lapilli deposits to the northwest of the summit. During these eruptions, searing gases and hot block and ash flows cascaded through forest to the lower slopes of the volcano, burying and carbonising many trees, as well as starting forest fires which spread 3 km northwards across the flanks of the Pouakai Range. With the forest cover stripped, rain easily eroded away these and older pyroclastic flow deposits, with the material being transported down the Stony River and Waiwhakaiho River catchments.

Table 1.1: The most recent eruptions from Mt Taranaki after Topping (1972) and Platz et al. (2012).

Date (AD)	Eruption and formation name	Geological member
1785–1820	Sisters	NA
1755	Tahurangi	Tahurangi Ash
1655	Burrell	Puniho Lapilli 2 Puniho Lapilli 1 Burrell Lapilli Burrell Ash
1500–1550	Newall	Waiweranui Ash Waiweranui Lapilli Newall Lapilli Newall Ash

After around 100 years of dormancy, the AD 1655 Burrell eruption occurred when a small scale dome effusion event was suddenly terminated by an explosive sub-plinian eruption. Prior to 1883, it had not been suspected that Mt Taranaki had erupted so recently, until A.W. Burrell found lapilli in the forks of a living *Prumnopitys taxifolia* tree that had just been felled. Then in 1929, the discovery of a Maori oven buried just below the Burrell eruption deposit implied an eruption had occurred since the Polynesian occupation of New Zealand, which was later confirmed by radiocarbon dating of charcoal found in the oven (Wellman 1962). Through dendrochronological dating of both pre/post Burrell eruption *Libocedrus bidwillii*, and post-Burrell *Kunzea ericoides*, Druce (1966) was able to give a likely eruption date of AD 1655. The Burrell eruption comprised of two small pyroclastic flows to the west of the summit, known as Puniho Lapilli 1 and 2, followed by a large tephra eruption. This eruption is divided into two main phases, the first being the ejection of the Burrell Ash. The Burrell Ash is described as a firm, shower-bedded, greyish brown, coarse-fine ash, which mantles the slopes of the mountain concentrically above 1000 m, with a slightly skewed lobe to the northwest of the summit on account of prevailing wind at the time of the eruption. This was succeeded sometime later by the ejection of the Burrell Lapilli, which was shower deposited extensively over 150 km^2 of the eastern flanks of the mountain between Lake Dive and Ahukawakawa Swamp.

The lapse of time which occurred between the ejection of the Burrell Ash and the Burrell Lapilli has been a point of conjecture for some researchers. Druce (1966) identified the presence of a thin organic horizon between the two deposits at one of his sample sites. At first he thought this was due to a soil-forming break between the two eruptions, but later concluded that this was the result of buried litter, due to leaf fall after the deposition of the Burrell Ash; and thus there had been no significant time lapse between the two events. In a later study, Tonkin (1970) identified this humus layer as an inbuilt B horizon, attributed to melanisation downwards by illuviation. Most recently, in a peat core pollen study on the mountain, Lees and Neall (1993) concluded that this organic layer was formed over a >70 year period which occurred between the deposition of the Burrell Ash and the Burrell Lapilli.

The Burrell Lapilli is the eruption of interest for the present vegetation study, for although the Burrell Ash would also have had an impact on vegetation, it is distributed evenly around the mountain and only a trace is found at the treeline position. The Burrell Lapilli deposit consists of up to 40 cm of loose white pumiceous blocks, lapilli and coarse ash, with some andesitic conduit fragments also present. Both Druce (1966) and Topping (1972) independently mapped the distribution of Burrell Lapilli over Mt Taranaki (Figure 1.7 and Figure 1.8), with their resulting maps being almost identical. Both studies indicated tephra fallout to the east-southeast of the summit with a dispersal axis located somewhere between Dawson Falls and Stratford Mountain House. Topping (1972) also recognised three distinct dispersal lobes to the northeast, southeast, and east-southeast based on a grain size iso-sorting analysis (Figure 1.9), though the northeast lobe is not reflected in the thickness contours of the deposit. He concluded that the lapilli distribution was influenced by high level southerly or south-westerly winds, and that three consecutive eruptive phase’s had created the distinct lobes.

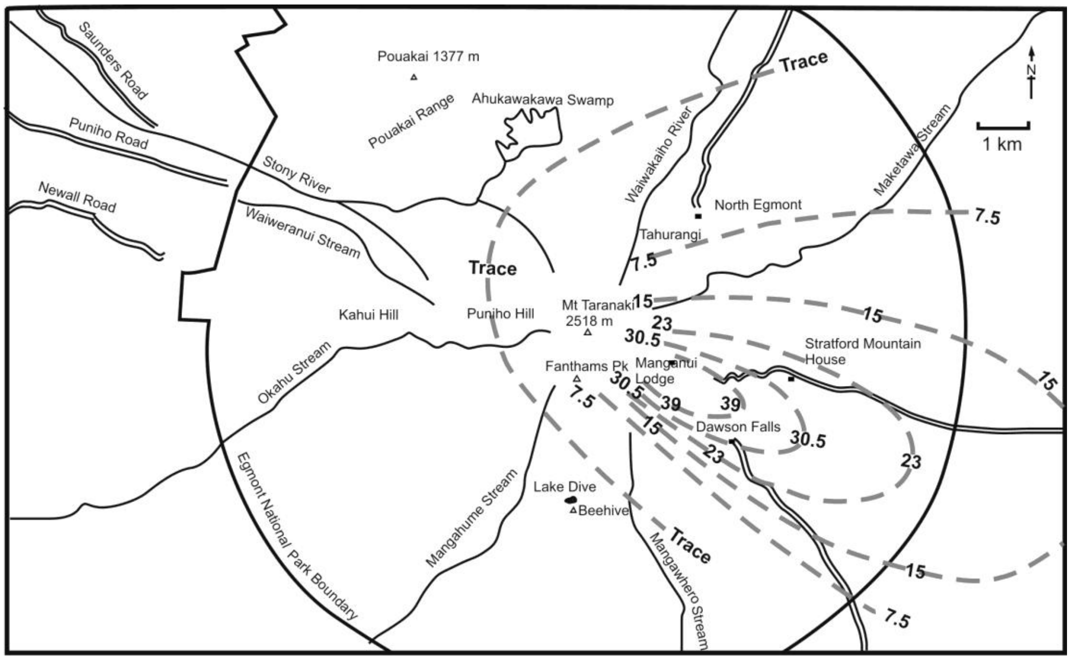

Figure 1.7: Distribution of Burrell Lapilli in cm after Druce (1966).

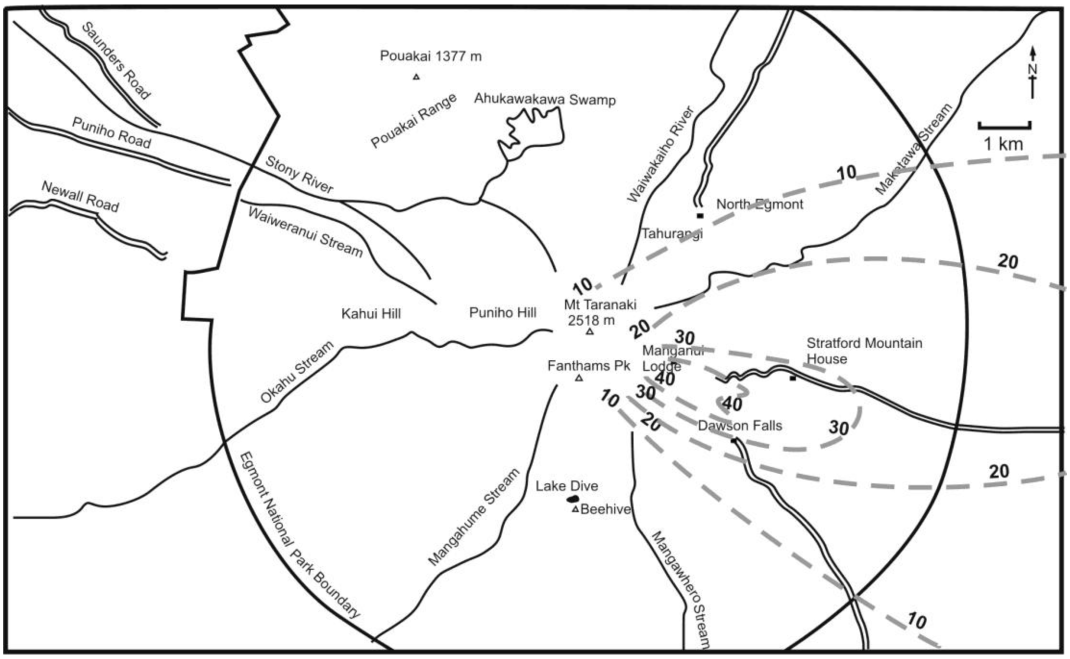

Figure 1.8: Distribution of Burrell Lapilli in cm after Topping (1972)

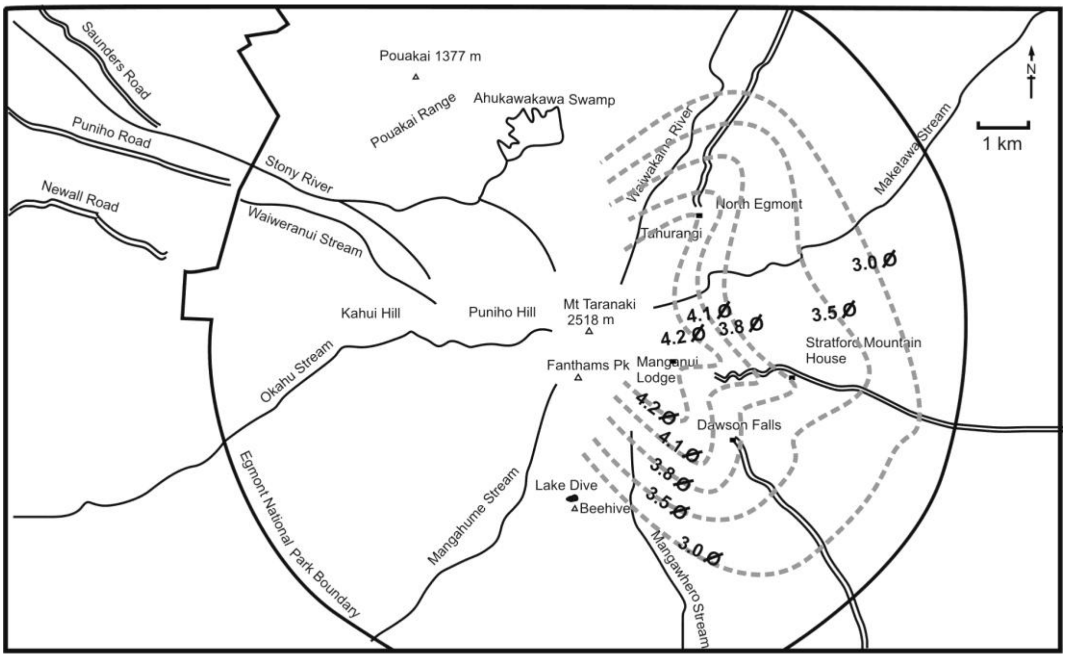

Figure 1.9: Iso-sorting map (contoured sorting values) of Burrell Lapilli in phi deviation after Topping (1972).

Druce (1966) suspected that the most recent eruption from Mt Taranaki was the minor Tahurangi eruption, which he tentatively dated at around AD 1755; although the discovery of exotic pollen within this ash by Lees and Neall (1993) suggests a date much closer to European arrival, perhaps as recently as AD 1860. The Tahurangi Ash is a fine ash, distributed up to 12 cm thick across the upper slopes of the mountain where it has contributed to the formation of the present soil. Although this ash may have had some impact on vegetation, the effects would have probably been equivalent around the mountain, given its concentric distribution, and thus it is not considered in the present study. Recent research by Platz et al. (2012) revealed that Mt Taranaki has erupted even more recently, with the passive effusion of a large (c. 5.9 million m^3) dome at the summit of the mountain sometime between AD 1785–1820, which they term the Sisters eruption. Any explosions that would have been associated with the dome emplacement are unlikely to have affected any vegetation on the mountain. Around 70 years after the Sisters emplacement however, around one third of the dome was destroyed by a mass flow which transported debris over 5 km. The instability of the dome was attributed to its position on a steep flank of unconsolidated breccias, hydrothermal alteration of the core, and rapid cooling associated with heavy rain. The flow was thought to be triggered by a heavy rain storm or an earthquake. Although no other eruptions have occurred since the Sisters event, erosion has been significant, mostly due to the heavy rainstorms which batter the mountain. At least 11 major debris flows, more common than volcanic eruptions on Mt Taranaki, have originated over the last 400 years. These water based debris flows have been mostly caused by the collapse of loosely jointed lava flows resting upon unconsolidated gravels. They have flattened great tracts of forest, with the most recent event occurring around 100 years ago and destroying a 1 × 6 km strip of vegetation extending to the park boundary in the northwest.

1.2.3 Soils

Soils of the south-eastern sector of Mt Taranaki have been described in detail by Tonkin (1970), and summarised by Clarkson (1981). They are predominantly recent/raw volcanic soils developed from andesitic tephra. The two major soil groups identified, the Burrell and Tahurangi Soils, have developed on Burrell Lapilli, and Tahurangi Ash respectively. The Tahurangi Soils are mainly subalpine (990–1371 m asl), though can exceed down to 670 m asl in places; while the Burrell Soils are upland temperate soils below 990 m asl. The treeline vegetation zone (900–1100 m asl), in which the present study is focused, is thus situated at the overlap of these two soil types, although it was not possible to determine exactly which of the two soils were present at each quadrat location. Both the Burrell and Tahurangi soils are coarse-textured and relatively unweathered mineral soils, and due to percentage base saturations of the mineral horizons being very low, they are consequently impoverished. It is instead the litter layer which provides a source of nutrients to the vegetation.

High rainfall on Mt Taranaki is the significant factor affecting the soils, causing leaching losses, a humus shift in the porous A horizon and, because of the stratified nature of the soil body, a significant lateral movement of water containing dissolved materials such as iron hydroxides. When this iron precipitates at the surface it creates a deposit known as kokowai, which was prized by local Maori as a source of ochre for ceremonial and artistic purposes (Molloy 1998). Soil chemistry does not change significantly across the range of slopes and altitudes in these soils, although gross features such as the thickness of the A horizon, stability, and drainage characteristics are strongly correlated with increasing slope angles recorded at higher elevations on the mountain. Other soil types present on the mountain include those developed on recent alluvium, and those associated with peat at poorly drained sites (though neither are found within the study area).

1.2.4 Vegetation

Note:

The following species' names frequently reoccurring throughout this thesis are referred to henceforward by genus only: *Podocarpus hallii*, *Griselinia littoralis*, *Libocedrus bidwillii*, *Weinmannia racemosa*, *Raukaua simplex*, *Fuchsia excorticata*, *Kunzea ericoides*, *Brachyglottis elaeagnifolia* and *Pseudowintera colorata*. In selected figures, six-letter species codes (first three letters of plant genus in uppercase, and first three letters of species name in lowercase) are also used. However, two of the species' codes are non-intuitive; PSWcol for *Pseudowintera colorata*, and PSPcol for *Pseudopanax colensoi*.

Vegetation

Around 80%–90% of the total 340 km^2 area of Egmont National Park is covered with intact native vegetation. The most obvious vegetation pattern displayed is the concentric zonation associated with elevation. The deterioration of climatic conditions with elevation is reflected in the composition, growth form and stature of the vegetation present. The climatically favourable lower slopes of the mountain are capable of supporting tall forest trees, but with increased elevation, climatic conditions become harsher and trees become progressively shorter, until they are replaced by a hedge-like shrubland above the treeline. Above this, tussock becomes the dominant plant form, which is then eventually replaced by low growing herbs, the only plants which can survive in the alpine environment. Mt Taranaki thus exhibits the full altitudinal range of vascular plants in this part of New Zealand.

A review of botanical literature relating to Egmont National Park has been compiled by Clarkson (1977). Acknowledgment is given in particular to the late A.P Druce, for his extensive botanical work on the mountain spanning over three decades (1953–1976). Most notably, Druce (1966) identified that volcanic eruptions had played a significant role in determining the current vegetation composition, and furthermore, his dendrochronological analysis provided likely dates for these recent pre-European volcanic events. Building on the work of Druce more recently, B.D Clarkson has comprehensively analysed and described the vegetation of Mt Taranaki and Egmont National Park (Clarkson 1977, 1980, 1981, 1986). Based on Clarkson's publications, a concise description of the vegetation types (Figure 1.10) present on Mt Taranaki and Pouakai Range is given here. Species' common names are given for those which appear as vegetation types in Figure 1.10.

Lowland forest

Over half of the park (>16,765 ha) is covered in lowland forest, in which there are nine main forest types present across 500–750 m asl elevation range. These forests have canopies up to 20 m tall with emergent trees occasionally reaching >25 m. The most extensive lowland forest type is *Dacrydium cupressinum – Metrosideros robusta* / *Weinmannia* (rimu – rata / kamahi) forest, which forms a wide belt around the flanks of Mt Taranaki and the Pouakai Range. In the south-eastern section of this lowland zone, *Dacrydium cupressinum – Metrosideros robusta* / *Melicytus ramiflorus* (rimu – rata / mahoe) forest is present, probably due to increased soil fertility associated with tephra addition from the Burrell eruption. On the more poorly drained eastern flanks of Mt Taranaki, *Dacrycarpus dacrydioides – Dacrydium cupressinum – Weinmannia* (kahikatea – rimu / kamahi) forest dominates. To the west, *Metrosideros robusta – Weinmannia* (rata – kamahi) forest is associated with the lower slopes of the Maero debris flow fans produced during the AD 1500 Newall eruption; above which *Weinmannia – Myrsine salicina* (kamahi – toro) forest becomes more common. On south-western Pouakai, a section of forest dominated by *Metrosideros robusta* exists. This is thought to have developed through the epiphytic establishment of rata onto burnt logs created by forest fires of the Newall eruption. Common understory constituents of lowland forest types on Mt Taranaki include *Melicytus ramiflorus*, *Myrsine salicina*, *Cyathea smithii*, *Dicksonia squarrosa*, *Coprosma grandifolia*, *Coprosma lucida*, *Coprosma tenuifolia*, *Uncinia* spp., *Microlaena avenacea*, *Blechnum discolour*, *Asplenium* *bulbiferum*, *Carpodetus serratus*, *Geniostoma rupestre*, *Hedycarya arborea*, *Pseudowintera axillaris, Ripogonum scandens* and *Astelia solandri*.

Montane forest

Montane forest is present across the 750–1100 m asl elevation range of Taranaki and Pouakai, making up approximately one third of the total park area (11,165 ha). At least seven types of montane forest have been identified, though only one, *Weinmannia – Podocarpus* (kamahi – mountain totara) forest, is widespread. In this forest type, *Griselinia* (broadleaf) can also contribute to the canopy, and emergent *Prumnopitys ferruginea* (miro) may be present. With increasing altitude, the stature of montane forest becomes shorter (<10 m) and tree crowns merge closely together creating a more compact hedge-like canopy. Montane forest *Weinmannia* grows in a multi-stemmed form, and frequently has a gnarled and irregular shape which is possibly due to nutrient deprivation caused through rain leached soil. Epiphytically derived 'compound trees', where multiple species such as *Griselinia*, *Weinmannia*, *Raukaua* and *Pseudopanax colensoi* intertwine together are also common here as a result of the high humidity, which also permits much of the forest to be festooned with mosses, liverworts and filmy ferns. Common understory species present in montane forest include *Pseudowintera*, *Myrsine salicina*, *Myrsine divaricata*, *Coprosma grandifolia*, *Coprosma tenuifolia*, *Coprosma dumosa*, and *Astelia* sp. unnamed aff. *nervosa* (referred to henceforward as *Astelia nervosa*). The most common ground cover contributors here are *Blechnum procerum*, *Blechnum fluviatile* and *Pseudowintera* seedlings, with other ferns *Leptopteris superba*, *Blechnum colensoi* and *Blechnum vulcanicum* also being prominent.

Other montane forest types include *Weinmannia – Podocarpus* with *Kunzea* (kamahi – mountain totara with kanuka) forest, and *Podocarpus* / broad leaved shrubs forest, present where the effects of the Burrell eruption were the most severe. In these forest types, it is suspected that the dominant species originally colonised into gaps created when the Burrell eruption destroyed many of the canopy trees, of which evidence exists in the presence of standing dead trees killed by the eruption. The abundance of *Kunzea*, as well as *Fuchsia* in these forest types is an indication of well-lit sites having been available for their establishment and continued growth. Outside of the Burrell eruption zone, *Podocarpus – Libocedrus /* broad leaved shrubs forest is more common, with *Libocedrus* being excluded from treeline areas severely affected by the Burrell eruption. At the upper limits of montane forest on Mt Taranaki, the treeline vegetation is comprised of mostly *Podocarpus* and *Griselinia,* either with or without *Libocedrus*, overtopping tree-sized shrubland species *Brachyglottis*, *Pseudopanax colensoi* and *Raukaua*. *Weinmannia* does not reach as higher elevations in montane forest on Mt Taranaki as it does on the older Pouakai Range, which has not been subjected to recent volcanic disturbance. At the treeline around Mt Taranaki, there is considerable variation in the distribution and abundance of *Podocarpus*, *Libocedrus*, *Griselinia* and *Weinmannia*, with every possible combination from co-dominance of all four species to single dominance of any one possible. The most probable reason for this is related to the distribution of the Burrell Lapilli, and the present study investigates this phenomenon in further detail using a quantitative survey targeting the treeline vegetation specifically.

Other montane forest types present include *Libocedrus – Podocarpus* / *Weinmannia* forest, present on a debris fan bordering the Ahukawakawa Swamp; *Libocedrus / Brachyglottis* scrub and *Libocedrus* / *Weinmannia* forest on the slopes and ridges above Ahukawakawa Swamp; and *Weinmannia* forest and *Brachyglottis* scrub above the Stony River where the Newall eruption pyroclastic flows were most severe.

Subalpine scrub and shrubland

Montane forest gives way to scrub or shrubland vegetation at around 1100 m asl, forming a belt of vegetation up to 1 km wide and reaching to an elevation of 1400 m asl. This shrubland vegetation appears hedge-like from a distance, with a uniform canopy <2.5 m high of closely spaced crowns. The dominant species is *Brachyglottis,* interspersed with *Pseudopanax colensoi*, *Raukaua*, *Dracophyllum filifolium*, *Hebe stricta* var. *egmontiana* (referred to henceforward as *Hebe* "*egmontiana*"), *Coprosma pseudocuneata*, *Coprosma dumosa* and stunted *Podocarpus* and *Griselinia* (leatherwood scrub and shrubland). With increasing elevation, the vegetation becomes progressively shorter, and *Brachyglottis* becomes less prominent as it is replaced by *Cassinia vauvilliersii*, *Hebe odora*, *Myrsine divaricata*, and *Dracophyllum filifolium*. Towards the upper altitudinal limit of shrubland, *Chionochloa rubra* tussock becomes increasingly common amongst the shrubs until it assumes dominance as the next vegetation belt, alpine tussockland.

Subalpine and alpine tussockland

Tussockland vegetation between 75–120 cm tall occurs in a narrow 500 m wide belt between 1400–1600 m asl. The dominant species is *Chionochloa rubra*, with *Poa colensoi* an important associate. At the lower altitudinal range of this belt and where drainage is not too poor, dwarfed *Hebe odora*, *Cassinia vauvilliersii*, *Dracophyllum filifolium*, *Brachyglottis*, and *Coprosma depressa* shrubs are scattered amongst the tussock. At the upper range of the belt, patches of herbfield exist between the clumps of tussocks. *Ourisia macrophylla* and *Ranunculus nivicola* are commonly found in such patches.

Alpine herbfield

Above the upper limit of *Chionochloa rubra* at around 1600 m asl, a carpet of small herbs <15 cm high exists. Common herbfield species includes *Celmisia gracilenta* var., *Celmisia glandulosa* var. *latifolia*, *Helichrysum* sp. aff. *bellidiodes*, *Anisotome aromatica*, *Forstera bidwillii*, *Poa colensoi*, dwarf shrubs *Coprosma pumila* and *Gaultheria* sp. aff. *depressa*, clubmoss *Lycopodium fastigiatum* and moss *Racomitrium lanuginosum*. Above 1650 m asl, plant cover becomes more patchy over raw substrates which are referred to as gravelfield, stonefield, boulderfield, and rockland depending on the dominant substrate size. Most of the herbfield species reach their upper limits between 1700–1900 m asl, with *Poa colensoi* a common species at this elevation. Between 2000–2500 m asl, less than 12 vascular species are capable of surviving, including *Poa novae-zelandiae*, *Carex pyrenaica* var. *cephalotes* and *Colobanthus* sp. unnamed, which reaches a higher elevation than any other vascular species on the mountain. Above 2500 m asl, mosses, lichens and algae are the only life forms able to tolerate the harsh climatic conditions.

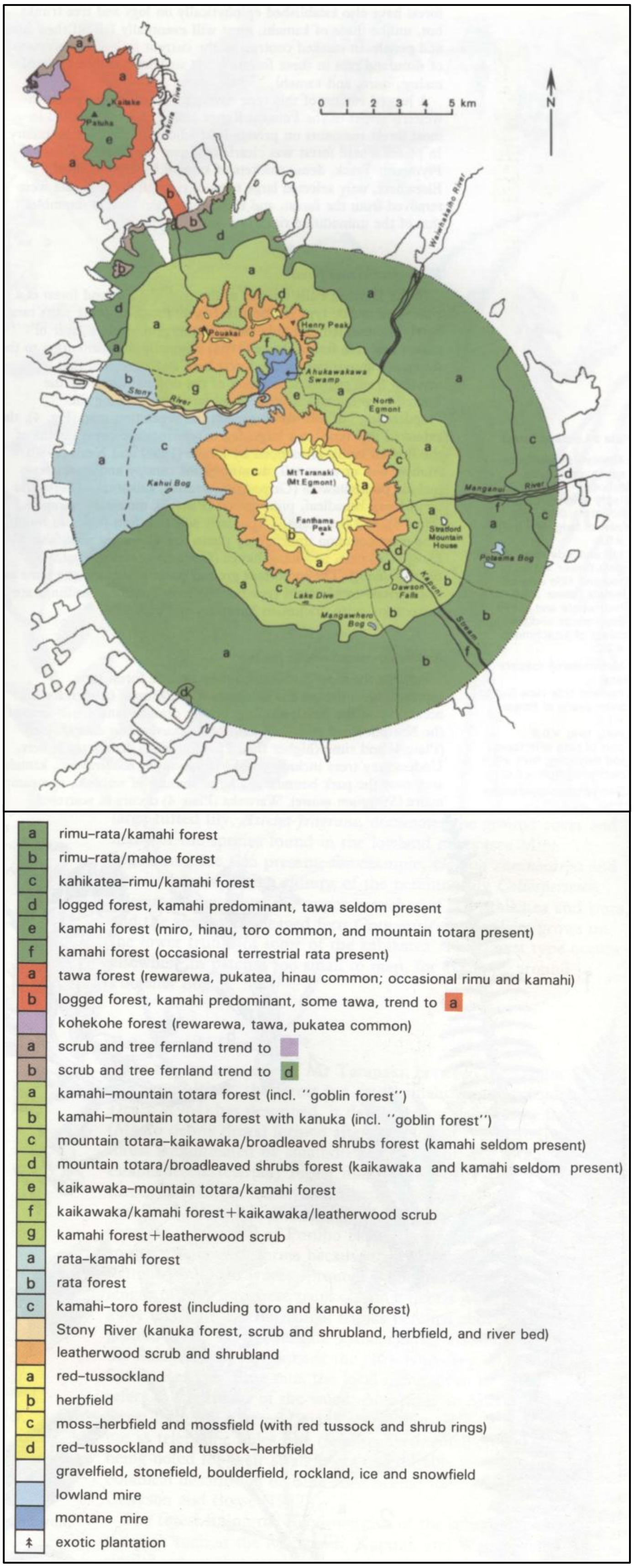

Figure 1.10: Vegetation map of Egmont National Park (Clarkson 1986).

1.2.5 The effects of recent eruptions on Mt Taranaki vegetation

By examining pollen from mire cores taken on Mt Taranaki, McGlone et al. (1988) and Lees & Neall (1993) have determined how vegetation is likely to have responded to volcanic events over the last 3500 years. Of particular relevance to the present study, they noted that the abundance of *Libocedrus* and *Weinmannia* in the montane forest has varied somewhat, with *Libocedrus* more common between c. 2500–3000 years ago, and between c. 450–1400 years ago, with the intervening periods being characterised by a greater abundance of *Weinmannia*. They attributed the dominance of *Libocedrus* to greater slope instability during cooler, stormier conditions; and the dominance of *Weinmannia* to volcanic eruptions (AD 1500 Newall and AD 1655 Burrell) which initiated secondary succession.

It is thought that falling Burrell Lapilli probably decapitated emergent trees and destroyed the canopy within a few hours, and the increased light availability allowed resilient species to recover quickly. In some places, it is unlikely that the lapilli fall was hot enough to scorch vegetation, but damage would have occurred via mechanical stripping of leaves, twigs and branches, or by chemical effects associated with the acidic tephra (Druce 1966; Wilmshurst & McGlone 1996). Those species capable of rapid invasion or adjustment (including lianes and epiphytes) temporarily thrived before the canopy again became closed. In places, the succession following the eruption was dominated firstly by light demanding *Coriaria arborea*, followed by *Kunzea* and *Fuchsia*, and finally, dense stands of *Weinmannia*. Where vegetation damage was minor, *Weinmannia* probably expanded by coppicing; its abundant, light, wind dispersed seed could have also readily reoccupied the more severely affected areas. The *Weinmannia* stands are presently beginning to thin out, with the vegetation slowly returning to its pre-eruption state (Clarkson 1990). To this day, *Kunzea* and *Fuchsia* can still be found scattered in vegetation within the Burrell Lapilli distribution, testament to well lit sites having been available for their establishment and continued growth.

Other direct evidence of vegetation damage inflicted by the Burrell eruption also exists in the vegetation standing today. Druce (1966) identified that some *Libocedrus* trees on the mountain are without root flanges at the ground surface, and appear to plunge into the ground. Such trees have had their bases buried by the Burrell Lapilli, and thus pre-date the eruption. Standing dead boles of *Podocarpus*, also projecting through the Burrell Lapilli are common in areas most heavily affected by the eruption, and were likely to have been killed by the eruption (though a number of pre-Burrell *Podocarpus* trees are still alive today). Because pre-Burrell *Podocarpus* and *Libocedrus* generally have shorter boles than post-Burrell trees, Druce (1966) concluded that at the time of the eruption, these trees were not of a significant size. It is likely that in some areas, most emergent trees would have been killed by a direct impact of Burrell Lapilli, while those juveniles in the understory were partially protected and survived. Druce (1966) also considered the possibility that the Burrell eruption may have affected the uptake of nutrients by buried root systems, because the nutrient return from litter would have been reduced for several years until a new layer formed on top of the lapilli bed.

1.3 Research objective

The objective of this research is to examine treeline vegetation composition structure and dynamics across the AD 1655 Burrell eruption lapilli deposit on Mt Taranaki. Four interlinked field research components address this objective:

1) An intensive quadrat survey of treeline vegetation across the Burrell Lapilli deposit;
2) Measurement of treeline temperatures across the quadrat survey area;
3) A belt transect survey of the altitudinal vegetation transition through the treeline position (i.e., treeline ecotone);
4) Characterisation of the light environments occupied by juveniles of treeline species using hemispherical photography.

1.4 Thesis outline

Chapter One: Introduction and study site

This chapter provides background information on alpine treelines in general, and relevant aspects of the Mt Taranaki study site including climate, geology, and vegetation. It then outlines the research objectives and summarises the thesis content.

Chapter Two: Composition of treeline vegetation in relation to Burrell Lapilli thickness

This chapter represents the principal research component of this thesis, an intensive quadrat survey of treeline vegetation across the AD 1655 Burrell Lapilli deposit. A supplementary survey measuring treeline temperatures across the study site is also presented in this chapter.

Chapter Three: Vegetation composition, stature and spatial configuration across the treeline ecotone

This chapter presents a belt transect survey of treeline vegetation on Mt Taranaki, conducted to supplement the quadrat survey by providing details on spatial configuration of stems and vegetation change with elevation across the treeline ecotone.

Chapter Four: Demography and light requirements of key treeline species

This chapter examines the demography and light requirements of key species found at the treeline, to aid with the explanation of compositional differences detected across the Burrell Lapilli distribution.

Chapter Five: Synthesis

This chapter concludes the thesis by bringing together all the key findings of the research, and recommending further experimental studies to extend explanation of treeline vegetation on Mt Taranaki.

Chapter Two: Composition of treeline vegetation in relation to Burrell Lapilli thickness

2.1 Introduction

Volcanic eruptions represent infrequent, intense, and unpredictable large-scale disturbance (Turner et al. 1988). Of all vegetation disturbances which can result from volcanic eruptions, tephra fall is the most widespread (Antos & Zobel 2005). Tephra is fragmental material ejected into the air by an eruption, with material <2 mm Ø referred to as ash, and 2–64 mm Ø as lapilli. The response of vegetation to burial by tephra has been discussed in a review by Kent et al. (2001). There is a close link between vegetation burial and the concepts of plant succession, with burials being retrogressive events which initiate either primary and/or secondary succession, depending on the severity of the eruption and the proximity to the source. Antos & Zobel (1987) made the comment that data on vegetation changes caused by volcanic eruptions were sparse and mostly anecdotal; though the 1980 eruption of Mt St. Helens (Washington, America) has since stimulated numerous studies of succession (reviewed by Dale et al. 2005), as have eruptions in Japan (e.g., Tsuyuzaki 1989, 1991; Nakashizuka et al. 1993; Titus & Tsuyuzaki 2003) and elsewhere in the world (e.g., Clarkson 1990; Whittaker et al. 1992; Oner & Oflas 1997; Clarkson 1998); though many of these studies focus on the effects of volcanic disturbances other than tephra fall (e.g., lava, debris flow, pyroclastic flow).

In the North Island of New Zealand, numerous geologically-young volcanoes (Rangitoto Island, White Island, Mts Tarawera, Ruapehu, Ngauruhoe, Tongariro and Mt Taranaki) provide sites for the study of both primary and secondary succession initiated by volcanic eruptions. The analysis of plant macrofossils and pollen preserved in organic sediments across the North Island has often been used to determine board scale vegetation change associated with volcanic disturbances (e.g., McGlone et al. 1988; Lees & Neall 1993; Clarkson et al. 1988, 1995; Wilmshurst et al. 1997; Horrocks & Ogden 1998; Giles et al. 1999), though given that the life span of many late successional New Zealand trees is potentially >500 years, present-day spatial differences in forest structure and floristic composition can also be related directly back to volcanic events (Clarkson 1990). Studies have indicated that emergent, canopy and senescent vegetation are the most susceptible to damage by tephra, while juvenile, robust or vigorous survivors have better chances of survival and are able to exploit forest gaps, thus facilitating forest regeneration (Kent et al. 2001).

By examining plant macrofossils within tephra deposits in New Zealand, Vucetich & Pullar (1963) attempted to determine critical tephra depths (thicknesses) with which damage to vegetation would occur. They concluded that >38 cm of tephra burial would probably result in complete destruction of trees, 30–38 cm in almost complete destruction, and 23–30 cm in partial destruction. On Mt St. Helens, thinner 1–15 cm depositions of tephra were not enough to kill canopy trees, but damage to the forest understory (i.e., shrubs, groundcovers, seedlings) could still be severe, and influence the successional trajectory of vegetation (Antos & Zobel 1985, 1986, 2005). A number of confounding factors other than tephra thickness also determine the effect that tephra will have on vegetation. These include differences in the stature, morphology and eco-physiology of taxa involved, availability of microsites for protection, tephra chemistry and the occurrence of rain or snow at the time of deposition (Kent et al. 2001).

In montane forest around Mt Taranaki, the thickness of the AD 1655 Burrell Lapilli ranges from 0–40 cm over an extensive sector of the mountain. Druce (1966) and Clarkson (1981, 1986, 1990) have identified that across this lapilli distribution, vegetation composition differs somewhat, particularly with regards to the occurrence of potential canopy species *Podocarpus, Libocedrus*, *Weinmannia* and *Griselinia*. In this chapter, I quantify these differences for the first time using a quadrat based survey of treeline vegetation across the Burrell Lapilli deposit. The vegetation sampling method is described and justified, and the results of the survey are presented and then discussed.

As a supplementary study, winter air temperatures were also recorded around the vegetation survey area using 18 micro data loggers, the purpose being to evaluate whether or not compositional differences in vegetation around the mountain could potentially be correlated to climatic variation, as opposed to lapilli thickness. The results of this study are presented as a sub-section of this chapter before the main vegetation survey component.

2.2 Treeline temperature measurements across the survey area

2.2.1 Sampling method

Eighteen micro data loggers (Maxim hygrochron iButtons®, DS1923) were deployed to quantify treeline temperature trends around the mountain over a winter period from 24/07/2011–17/10/2011. The loggers recorded measurements hourly, with a resolution of 0.0625 °C. Each logger was housed within a cylindrical, five-gill radiation shield (Ø = 7 cm × 15 cm high) to give ventilation while protecting the sensor from severe weather and heating via direct and reflected solar rays. The shields were constructed from plastic components to minimise any heat absorption.

The location where each data logger was placed on the mountain is summarised in Table 2.1 and Figure 2.1. Specific criteria were used in the placement of loggers to ensure that microclimates at each logger were as close to one another as possible; the overall treeline temperature trends around the mountain, as opposed to microclimate or altitudinal variations, were the focus of this investigation. Accessible locations for the loggers were selected in treeline forest on the ridges of the valleys which radially dissect the mountain; valley floors, which are known to funnel cold air down from higher elevations, were avoided. The loggers were positioned in treeline vegetation around the mountain at irregular intervals ranging 50–1500 m apart. The elevation where loggers were located ranged from 1020–1100 m asl. All loggers were suspended at a height of 1.5 or 2 m above ground, using the limbs of large (3–5 m high) *Podocarpus* trees. The loggers were positioned along limbs to be at a distance of 1–1.5 m from the main trunk of the tree. Despite extreme weather conditions including heavy snowfall and high winds, all logger shields remained intact and in place for the duration of the investigation.

Table 2.1: Summary of the position of each data logger at the Treeline of Mt Taranaki.

Data logger ref. and position around mountain (ordered from west-east)		GPS reference (NZTM)		Elevation (m asl)	Straight-line distance between each data logger location (m)	Data logger height above ground (m)	Tree height (m)
		Easting	Northing				
A	Lake Dive	1692697	5646175	1035	-	1.5	3
B	Lake Dive	1692964	5646231	1020	300	2	5
C	Dawson Falls	1694224	5647209	1060	1500	2	6
D	Dawson Falls	1694478	5647682	1045	500	2	4
E	The Plateau	1694562	5648181	1100	500	1.5	2
F	The Plateau	1695279	5647985	1065	600	2	5
G	The Plateau	1695425	5648462	1035	500	1.5	4
H	The Plateau	1695258	5648702	1080	300	2	5
I	The Plateau	1695086	5648699	1080	200	2	6
J	Curtis Falls	1695536	5650089	1030	1500	2	4
K	Curtis Falls	1695466	5650561	1020	500	2	5
L	Curtis Falls	1695070	5650787	1065	500	2	4
M	Maketawa Hut	1694822	5651387	1065	700	1.5	3
N	Maketawa Hut	1694706	5651409	1045	100	1.5	3
O	North Egmont	1694209	5651787	1065	600	1.5	3
P	North Egmont	1694182	5651781	1100	50	2	3
Q	North Egmont	1694040	5652100	1070	300	1.5	3
R	North Egmont	1693818	5652059	1090	200	2	4

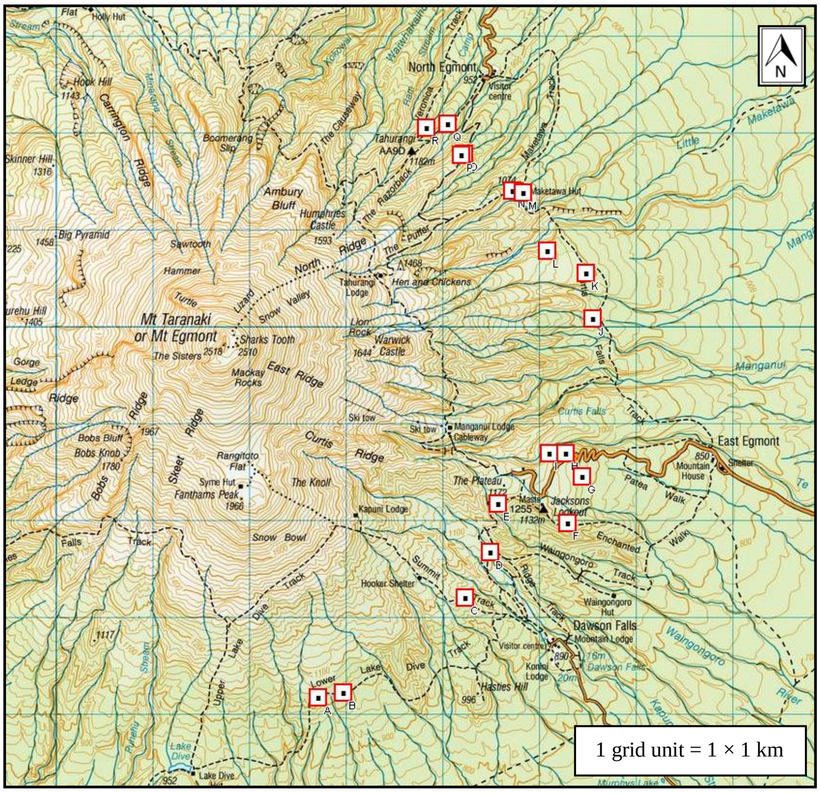

Figure 2.1: Location of the eighteen micro data loggers (labelled A–R) at the treeline position on Mt Taranaki.

2.2.2 Results

Results of the treeline temperature measurements around Mt Taranaki are presented as both absolute temperatures recorded by each logger (Table 2.2 and Figure 2.2), and daily average temperatures recorded by each logger (Table 2.3 and Figure 2.3). Absolute temperatures were derived from the raw (hourly) temperatures recorded by each logger. For example, the absolute maximum temperature of logger A represents the single highest temperature recorded while the logger was operating (24/7/2011–17/10/2011); the absolute mean represents an average of every single temperature recorded by the logger for this period. Daily temperature statistics (minimum, maximum and mean) for each logger were then computed for the calculation of all average daily temperatures. For example, the average daily maximum of logger A represents the mean of every daily maximum recorded while the logger was in operation; the average daily mean represents the average of all daily means recorded by the logger for this period. Differences in treeline temperature around Mt Taranaki can be depicted by sixth-order polynomial trend lines fitted to the temperature data in Figure 2.2 and Figure 2.3.

Absolute maximum treeline temperatures (Table 2.2 and Figure 2.2) recorded by each logger around the mountain ranged from 11.62–15.89 °C, absolute minimum temperatures ranged from -6.98–-4.66 °C, and absolute mean temperatures ranged from 3.07–3.74 °C. In terms of the absolute minimum treeline temperatures around the mountain, the range of only 2.32 °C between sites suggests that no area there was spared from the cool temperatures. The slightly higher range of absolute maximum treeline temperatures around the mountain (4.27 °C) suggests that some areas of the treeline were warmer than others. Two likely explanations for these higher maximum temperatures are considered. First, the higher maximum temperatures of some loggers could be an artefact of where the loggers were suspended. Those loggers which displayed higher absolute maximum temperatures (loggers D, F) were perhaps suspended in such a way that they received more direct sunlight due to openings in the canopy above the loggers, and thus they exhibited a higher degree of absorptive heating compared with loggers suspended in the shade. Second, the two loggers displaying the higher maximum temperatures were positioned at the most easterly section of the treeline on Mt Taranaki; perhaps they received a higher degree of irradiance in the course of a day than other loggers which may have been shaded by the tall peak of the mountain.

Table 2.2: Absolute temperatures (minimum, maximum and mean) recorded by each data logger around the treeline of Mt Taranaki (24/7/2011–17/10/2011).

iButton ref. and position around mountain (ordered from west–east)		Absolute treeline temperatures (°C) recorded around Mt Taranaki July 24 2011–November 17 2011		
		Mean	Maximum	Minimum
A	Lake Dive	3.38	11.62	-6.49
B	Lake Dive	3.23	12.07	-6.00
C	Dawson Falls	3.35	11.82	-6.17
D	Dawson Falls	3.51	15.16	-6.64
E	The Plateau	3.07	12.21	-6.20
F	The Plateau	3.71	15.89	-6.05
G	The Plateau	3.38	12.44	-6.98
H	The Plateau	3.02	14.26	-4.66
I	The Plateau	3.59	13.40	-6.22
J	Curtis Falls	3.45	12.37	-5.99
K	Curtis Falls	3.51	12.57	-5.81
L	Curtis Falls	3.22	12.44	-6.16
M	Maketawa Hut	3.49	12.75	-6.66
N	Maketawa Hut	3.36	12.34	-6.28
O	North Egmont	3.35	12.13	-6.48
P	North Egmont	3.74	14.07	-6.22
Q	North Egmont	3.64	12.81	-5.73
R	North Egmont	3.57	12.37	-5.98

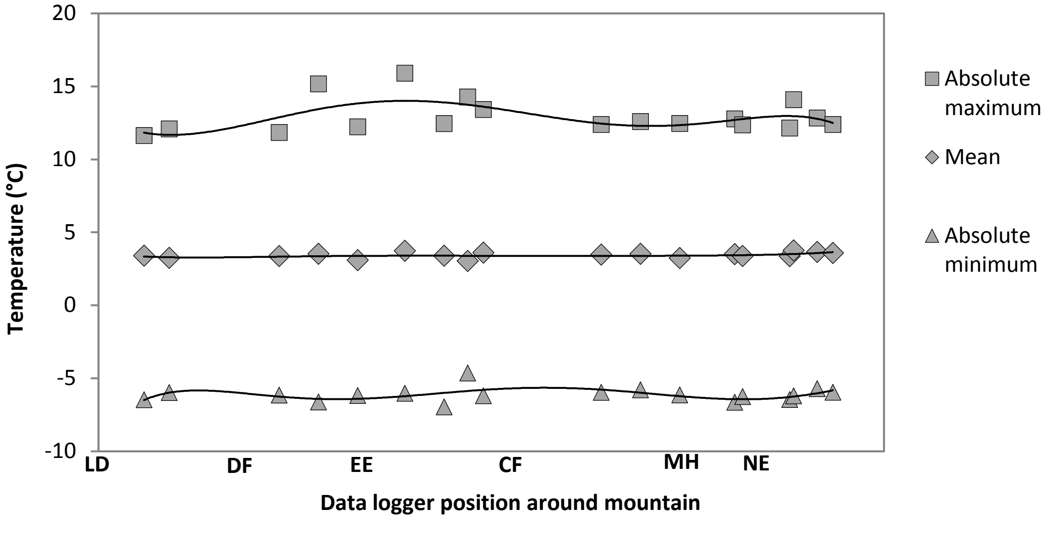

Figure 2.2 Absolute temperatures (minimum, maximum and mean) recorded by each data logger around the treeline of Mt Taranaki (24/7/2011–17/10/2011). A sixth-order polynomial trend line has been fitted to show how temperatures differ around the mountain. Labels on the x-axis are abbreviations for geographic locations near to which the loggers were positioned. Arranged from west–east (anti-clockwise around summit) they are; LD Lake Dive, DF Dawson Falls, EE East Egmont, CF Curtis Falls, MH Maketawa Hut, NE North Egmont. For the actual straight-line distances between each logger refer to Table 2.1

Average daily minimum temperatures (Table 2.3 and Figure 2.3) recorded by each logger ranged from 0.64–1.26 °C, average daily maximum temperatures ranged from 5.37–7.24 °C, and average daily means ranged from 3.07–3.71 °C. One-way Analysis of Variance (ANOVA) and *a posteriori* (post-hoc) Fisher LSD tests were used to detect whether or not average daily temperatures around the mountain differed significantly. Around the mountain, there were no significant differences between the average daily minimum temperatures ($F = 0.43$; d.f. = 17, 1512; $P = 0.98$), or average daily mean treeline temperatures ($F = 0.50$; d.f. = 17, 1512; $P = 0.95$). However, there was a very significant difference detected between the average daily maximum temperature around the mountain ($F = 2.30$; d.f. = 17, 1512; $P < 0.01$). The majority of these differences were associated with only three of the eighteen data loggers (loggers F, H, P).

The average daily maximum temperature of logger F, located near The Plateau, was significantly higher than ten other loggers around the mountain ($P < 0.05$ for loggers C, G, J, N, R; $P < 0.01$ for loggers B, C; and $P < 0.001$ for loggers A, E, H). The average daily maximum of logger P, located near North Egmont, was also significantly higher than eleven other loggers around the mountain ($P < 0.05$ for loggers R, N, K, J, G; $P < 0.01$ for loggers C, E, L; and $P < 0.001$ for loggers A, B, H). Finally, the average daily maximum temperature of logger F, located near The Plateau, was significantly lower than seven other loggers around the mountain ($P < 0.05$ for loggers O, M, D; $P <0.01$ for loggers Q, I; and $P < 0.001$ for loggers P, F).

The results of the treeline temperature measurements around the mountain were not significantly different from place to place. Although average daily maximum temperatures varied somewhat around the mountain, it is more likely that average daily minimum temperatures would have a more deleterious effect on vegetation, and these did not differ significantly. Consequently, any differences detected in the treeline vegetation around the mountain are more likely to be a related in some way to another variable (such as the Burrell eruption), than to temperature. Other climatic variables which could also possibly differ around the treeline, such as wind and rainfall, were not able to be measured here, though Mt Taranaki climate has been reviewed in Section 1.2.1.

Table 2.3: Average daily temperatures (± SEM) (average daily minimum, average daily maximum and average daily mean) recorded by each data logger around the treeline of Mt Taranaki (24/7/2011–17/10/2011).

Data logger ref. and position around Mt Taranaki (ordered from west–east)		Average treeline temperatures (°C) around Mt Taranaki July 24 2011–November 17 2011		
		Daily mean ± SEM	**Daily maximum ± SEM**	**Daily minimum ± SEM**
A	Lake Dive	3.38 ± 0.28	5.59 ± 0.32	1.26 ± 0.28
B	Lake Dive	3.23 ± 0.28	5.64 ± 0.34	0.99 ± 0.27
C	Dawson Falls	3.35 ± 0.28	5.99 ± 0.33	1.09 ± 0.27
D	Dawson Falls	3.51 ± 0.28	6.53 ± 0.37	0.84 ± 0.28
E	The Plateau	3.07 ± 0.28	5.95 ± 0.34	0.71 ± 0.27
F	The Plateau	3.71 ± 0.29	7.24 ± 0.40	1.21 ± 0.28
G	The Plateau	3.38 ± 0.28	6.21 ± 0.34	0.75 ± 0.29
H	The Plateau	3.02 ± 0.28	5.37 ± 0.41	1.21 ± 0.24
I	The Plateau	3.59 ± 0.29	6.82 ± 0.36	1.14 ± 0.28
J	Curtis Falls	3.45 ± 0.29	6.26 ± 0.33	0.89 ± 0.29
K	Curtis Falls	3.51 ± 0.29	6.31 ± 0.34	1.02 ± 0.29
L	Curtis Falls	3.22 ± 0.28	5.83 ± 0.32	0.94 ± 0.28
M	Maketawa Hut	3.49 ± 0.29	6.53 ± 0.36	0.82 ± 0.29
N	Maketawa Hut	3.36 ± 0.28	6.20 ± 0.33	0.95 ± 0.29
O	North Egmont	3.35 ± 0.29	6.37 ± 0.35	0.64 ± 0.28
P	North Egmont	3.74 ± 0.28	7.31 ± 0.37	0.86 ± 0.29
Q	North Egmont	3.64 ± 0.28	6.75 ± 0.34	0.98 ± 0.29
R	North Egmont	3.57 ± 0.28	6.10 ± 0.33	1.18 ± 0.27

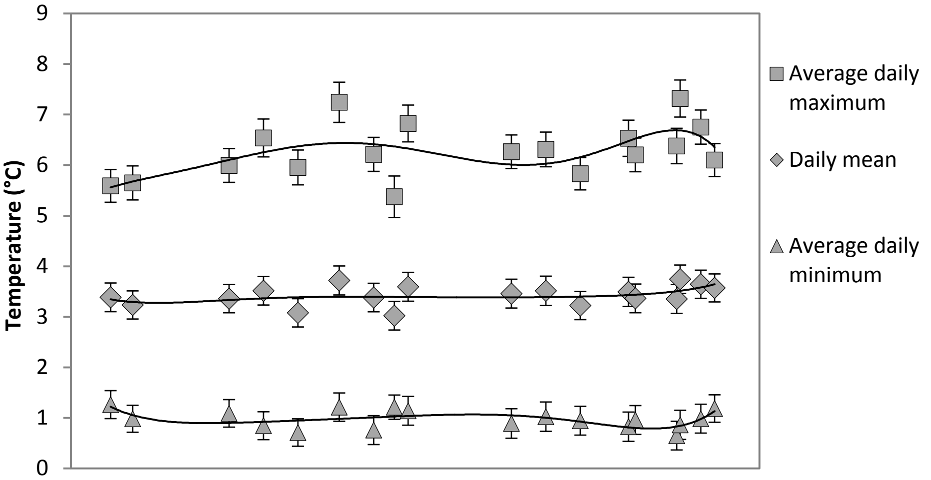

Figure 2.3: Average daily temperatures (± SEM) (average daily minimum, average daily maximum and average daily mean) recorded by each data logger around the treeline of Mt Taranaki (24/7/2011–17/10/2011). A sixth-order polynomial trend line has been fitted to show how temperatures differ around the mountain. Labels on the x-axis are abbreviations for geographic locations near to which the loggers were positioned. Arranged from west–east (anti-clockwise around summit) they are; LD Lake Dive, DF Dawson Falls, EE East Egmont, CF Curtis Falls, MH Maketawa Hut, NE North Egmont. For the actual straight-line distances between each logger refer to Table 2.1

2.3 Quadrat survey sampling methods

2.3.1 Quadrat size and justification

Using nested quadrat minimal area checks, Clarkson (1977) and Efford (2010) have determined an adequate quadrat size of 150 m^2 (10 × 15 m) for sampling treeline vegetation on Mt Taranaki. The point at which species representation levels off to within 5%–10% of the value recorded in the preceding sample area is generally accepted as the minimal area to be sampled if a representative combination of species is to be achieved (Clarkson 1977). As a further justification for this quadrat size, Mueller-Dombois & Ellenberg (1974) have recommended 15 × 15 m and 10 × 10 m quadrat sizes for sampling scrub-forest and scrub in temperate-zone vegetations.

2.3.2 Quadrat positioning

When implementing representative vegetation sampling designs, objective positioning of quadrats (either systematically or randomly) in the study area is generally favoured in order to eliminate the subjective bias of the researcher (Hurst & Allen 2007). This is most favourable when vegetation patterns are nondistinct or unclear to the investigator (Mueller-Dombois & Ellenberg 1974; Moore & Chapman 1986). Objective sampling is not favoured in every instance however, because it suffers from inflexibility (Mueller-Dombois & Ellenberg 1974) and may be restricted by factors such as topography and time available for the study.

The steep radially dissected terrain of Mt Taranaki combined with the impenetrably dense stature of shrubland vegetation above treeline, renders fully objective positioning of quadrats practically impossible. Given that the purpose of this study was to examine treeline vegetation differences across the Burrell Lapilli deposit, a set of criteria for determining quadrat location were devised, resulting in stratified quadrat positioning which could be referred to as ‘subjective without preconceived bias’; a method regarded with validity by Mueller-Dombois & Ellenberg (1974). The existing networks of tracks present on the mountain were invaluable for accessing the treeline area, and thus influenced the location of quadrats to a degree. These criteria used to position quadrats provided a vital level of consistency between the quadrats (i.e., variables held at a constant), which is necessary when comparing vegetation over a large area.

Foremost, quadrats were positioned in vegetation which fell within the stature constraints of: a canopy 2–3 m high over ≥50% of the plot; with a minimum of two or more prominently emergent trees ≥3 m tall present. The area targeted by the survey was thus located between the 'treeline' and 'timberline' positions (Figure 1.1) defined by Körner & Paulsen (2004). Quadrats were positioned at least 5 m away from active water courses, cleared tracks and cliffs/bluffs; drainage class within the quadrat was required to be good–moderate, with no poorly drained or saturated areas present; quadrats were oriented with the longer axis (15 m) positioned horizontally across the slope; and multiple quadrats in the same vicinity were positioned with intervals of >50 m between each. It was impossible to maintain a constant aspect between plots as done by Clarkson (1977) previously. An attempt was made to have a number of quadrats located within each of the Burrell Lapilli isopachs identified by Druce (1966), as well as a number outside the Burrell Lapilli distribution, including on the Pouakai Range.

2.3.3 Quadrat survey method

Stem 'diameter at ground height' (henceforward referred to as dgh) as opposed to 'diameter at breast height' was deemed appropriate for basal area calculations and demographic analyses for the following reasons. The low stature and multi-branched growth form of species at the treeline makes dbh measurements difficult to obtain, and none of the treeline species display any excessive root buttressing, which would usually prevent the use of dgh measurements. Furthermore, due to bole taper, dgh measurements provide the most realistic indication of basal area.

Within each 10 × 15 m quadrat, all individuals ≥2 cm dgh (hereafter referred to as trees) were recorded by species and measured for dgh using a soft diameter tape. In a randomly selected 5 × 15 m (½) subset of the quadrat, all individuals <2 cm dgh but >50 cm high (hereafter referred to as saplings) were recorded by species and tallied. In a randomly selected 7.5 × 5 m (¼) subset of the quadrat, stems 5–

50 cm high (hereafter referred to as seedlings) were recorded by species and approximately tallied.

Within the entire 10 × 15 m quadrat, the following was conducted; a search was made for the presence of additional vascular species which had not previously been recorded in the quadrat; epiphytes and lianes were ranked based on cover; the dominant ground covering species were ranked based on cover; the overall percentage contributions of vegetation, litter, non-vascular, bare ground and bare rock to the total ground cover of the quadrat were estimated; canopy height and emergent tree heights were estimated, with the dominant canopy and emergent species being noted; the presence of mammalian browse on each species was ranked by severity; quadrat slope, aspect, elevation and GPS position were recorded; and additional notes were made on any relevant observations such as physiognomy and structure of the vegetation.

2.3.4 Tephra measurement

Initially, it was the intention that at one or two locations within each quadrat, a small hole (c. 30 cm width × 30–60 cm depth) would be excavated for the purposes of a soil profile description and assessment of the Burrell Lapilli deposit thickness. This would permit an analysis of any relationship between tephra thickness (a proxy for eruption severity) and the current vegetation in each quadrat. The profile location within the quadrat was to be selected on the basis of topography; with a gentle incline or flat area being desirable in order to minimise/standardise the implication of colluvial tephra redeposition.

Unfortunately, after this procedure was attempted it was abandoned for several reasons. First, the abundance of thick root mats over the soil surface and throughout the profile made digging very difficult, exacerbated further by the inclination of the ground. Second, leaching of dark organic matter through the profile made it difficult to determine the upper and lower limits of the Burrell Lapilli deposit, as the lapilli was intermixed with humus and no longer in its recognisably white-coloured state. Fortunately, previous measurements of the Burrell Lapilli deposit by Druce (1966) and more recently Topping (1972), have produced eruptive isopach maps which are utilised as an alternative to my own measurements. These maps are at a broader scale than is probably ideal, as their tephra measurements have not targeted the treeline area specifically, but nevertheless, still allow for general relationships between the Burrell eruption and vegetation to be inferred.

2.3.5 Data collection

Fieldwork was conducted intermittently from March–October 2011. Vegetation data was collected from thirty-eight 10 × 15 m quadrats at the treeline position on Mt Taranaki. Of the quadrats, thirty-two were distributed across the eastern half of Mt Taranaki between the treeline above Lake Dive and North Egmont (Kokowai Track); a zone which spans the full extent of the Burrell Lapilli deposit. Outside the Burrell eruption zone, on the western side of the mountain, one quadrat was located above Brames Falls, and two quadrats were located near Kahui Hut and Puniho Track. A further three quadrats were located at the treeline on the adjoining Pouakai Range near the Mangorie Track.

2.3.6 Data analysis

Because of the number of quadrats surveyed, a logical way to examine differences in treeline vegetation was to allocate quadrats into a smaller number of groups, in which vegetation data could be pooled and then compared. Quadrats were assigned to one of four quadrat groups (Table 2.4) based on their geographic location in relation to the Burrell Lapilli distribution identified by Druce (1966). The quadrat located at Puniho Hill was excluded from the analyses because this area is known to have been heavily affected by a different volcanic eruption (AD 1500 Newall eruption). The four groups utilised were as follows: ‘severe’, where Burrell Lapilli was deposited at a thickness 20–40 cm; ‘minor’, where Burrell Lapilli was deposited at a thickness of 1–20 cm; ‘outside’, where quadrats were situated on Mt Taranaki outside the Burrell Lapilli distribution; and ‘Pouakai Range’, where plots were located on the Pouakai Range, also outside the Burrell Lapilli distribution. These groups provide the basis for the comparison of treeline vegetation in this study.

Table 2.4: Allocation of the thirty-eight quadrats into four groups to analyse the effect of the Burrell eruption on treeline vegetation.

Group name	**Burrell lapilli thickness (cm)**	**Number of quadrats**	**Total area surveyed (m^2)**	**Sampling intensity[1] (%)**
Severe	20–40	13	1950	0.010
Minor	1–20	18	2700	0.005
Outside	0	4	600	0.001
Pouakai Range	0	3	450	0.001
Total	-	38	5700	-

[1]. approximation only

In comparing the treeline vegetation between these groups, The Pouakai Range site could be considered as the 'climax' treeline vegetation for the region, because there has been no recent volcanic disturbance there. Mt Taranaki is a geologically younger formation, and although an area of treeline vegetation not affected by the Burrell eruption was surveyed (outside group), there are a number of other eruptions which have occurred which would have affected the vegetation on Mt Taranaki outside the Burrell eruption distribution, but not on the Pouakai Range. Vegetation in the minor group would not have been affected by the Burrell eruption as heavily as the severe group, and thus the successional trajectories in each group may have been altered in different ways. In one sense, the four quadrat groups can thus be considered in a similar way to a chronosequence, with each representing a different position along a successional pathway; though given the differing levels of disturbance, the trajectory of each group may not necessarily reach the same climax vegetation.

For tree species (≥2 cm dgh) in each group, mean basal area and mean density were computed, along with standard deviations and relative contributions. For major sapling (<2 cm dgh, >50 cm high) and seedling (5–50 cm high) species in each group, mean density, standard deviations, and relative contributions were computed. All density and basal area values were standardised to units of stems per hectare and m^2 per hectare respectively. A vegetation naming unit and a description were produced for each quadrat group, and finally, a multivariate ordination of quadrats was conducted.

Justification of quadrat grouping

Grouping of quadrats (pooling data) in the way used here to describe differences in treeline vegetation, is just one of many approaches that could potentially be used, and thus the issues associated with such an approach are considered briefly. A limitation which arises is the fact that the Burrell Lapilli distribution essentially represents a continuous gradient of lapilli thickness on the landscape (from which I have inferred a gradient of eruption-inflicted vegetation damage), rather than discrete zones of eruption severity which the groupings suggest. For example, two quadrats located near to one another in the landscape may be assigned into two different ‘groups’, when in fact both quadrat locations were affected by the eruption to a similar degree. Furthermore, although the Burrell Lapilli isopach map suggests a continuous distribution of lapilli over the landscape, it is likely that erosion and re-deposition would undoubtedly have altered the Burrell Lapilli deposit at many locations (though one would assume at the time of deposition it would have been more uniform). Another limitation which arises with the quadrat groupings used here is the fact that the zones do not have an equal number of quadrats allocated to each; ideally an equal number would permit the most statistically robust comparison of vegetation, but due to time and treeline access constraints this was not achievable. Nonetheless, the use of these discrete ‘groups’ remains a logical way of interpreting any treeline vegetation differences related to the Burrell eruption.

2.4 Quadrat survey results

2.4.1 Site attributes

A summary of site attributes (including GPS reference, elevation, slope, aspect, and quadrat group) for each of the thirty-eight 10 × 15 m quadrats surveyed is presented in Table 2.5 alongside the expected thicknesses of the Burrell Lapilli deposit according to the isopach maps of Druce (1966) and Topping (1972). The position of each quadrat on the mountain is mapped in Figure 2.4. Quadrat elevations (and thus the approximate treeline position on the mountain) ranged from 900–1100 m asl, with an average elevation of 1040 m asl. Quadrat slopes ranged from 0–25° inclination, but were generally around the 5° mark. The variable range of quadrat aspects (0–343°) reflects both the radially dissected terrain of Mt Taranaki and the large spread of quadrats around the mountain itself.

Table 2.5: Summary of site attributes from thirty-eight 10 × 15 m quadrats surveyed at the treeline position on Mt Taranaki and the Pouakai Range. For explanation of group names see Section 2.3.6

Site # (ordered from west-east)	**Proximate geographic reference**	**GPS Reference (NZTM)**		**Elevation (m asl)**	**Slope (°)**	**Aspect (°)**	**Landform: Concave (CC) Convex (CX) Linear (L)**	**Burrell Lapilli thickness from Druce (1966) (cm)**	**Burrell Lapilli thickness from Topping (1972) (cm)**	**Quadrat group**
		Easting	**Northing**							
31	Puniho Hill	1687564	5650999	900	5	240	L	0	0	Outside
30	Kahui Hut	1687609	5650025	900	5	240	CX	0	0	Outside
38	Brames Falls	1689167	5647508	1070	5	310	L	0	0	Outside
25	Lake Dive	1691577	5646211	1060	10	90	L	0	0	Outside
10	Lake Dive	1692683	5646234	1050	5	60	CC	2.5	0	Minor
11	Lake Dive	1692735	5646290	1050	10	130	CX	2.5	0	Minor
12	Lake Dive	1692944	5646357	1050	10	180	CX	2.5	0	Minor
35	Dawson Falls	1693595	5646653	1040	5	90	L	2.5	10	Minor
5	Dawson Falls	1694289	5647132	1045	5	170	L	15	30	Minor
2	Dawson Falls	1694526	5647718	1055	25	200	CC	30.5	40	Severe
18	Dawson Falls	1694527	5647359	1000	10	60	CX	23	40	Severe
1	Dawson Falls	1694556	5647604	1020	25	200	L	30.5	40	Severe
19	Dawson Falls	1694442	5647637	1030	5	80	CC	30.5	40	Severe
3	Dawson Falls	1694477	5647691	1045	15	60	CX	30.5	40	Severe
4	Dawson Falls	1694225	5647212	1065	15	20	CC	15	30	Minor
17	Dawson Falls	1694531	5647764	1050	10	60	CX	30.5	40	Severe
9	The Plateau	1695332	5647954	1055	20	120	CC	30.5	40	Severe
27	The Plateau	1695427	5648462	1030	5	30	L	30.5	30	Severe
26	The Plateau	1695464	5648542	1015	5	90	L	30.5	30	Severe
20	The Plateau	1695419	5648610	1040	5	120	L	30.5	30	Severe
7	The Plateau	1695254	5648708	1075	10	340	CC	30.5	30	Severe
8	The Plateau	1695083	5648696	1080	10	320	CX	30.5	30	Severe
37	The Plateau	1695459	5648955	1050	5	40	L	30.5	30	Severe
16	Curtis Falls Track	1695511	5650122	975	5	140	L	15	20	Minor
15	Curtis Falls Track	1695446	5650554	1005	5	140	CC	15	10	Minor
14	Curtis Falls Track	1695306	5650690	1010	5	50	L	15	10	Minor
13	Curtis Falls Track	1695184	5650772	1020	5	60	CX	15	10	Minor
22	Maketawa Hut	1694911	5651418	1040	5	40	CC	7.5	10	Minor

Table continues over page

Table 2.5 (continued)

Site # (ordered from west-east)	Proximate geographic reference	GPS Reference (NZTM)		Elevation (m asl)	Slope $(^{O})$	Aspect $(^{O})$	Landform: Concave (CC) Convex (CX) Linear (L)	Burrell Lapilli thickness from Druce (1966) (cm)	Burrell Lapilli thickness from Topping (1972) (cm)	Quadrat group
		Easting	Northing							
24	Maketawa Hut	1694839	5651503	1055	5	60	CX	7.5	10	Minor
23	Maketawa Hut	1694710	5651418	1070	15	290	L	7.5	10	Minor
6	North Egmont	1694176	5651777	1100	20	270	CC	7.5	10	Minor
21	North Egmont	1694258	5651832	1090	5	40	L	7.5	10	Minor
28	North Egmont	1694040	5652100	1075	5	310	L	7.5	0	Minor
29	North Egmont	1693818	5652059	1090	10	343	CX	7.5	0	Minor
36	Kokowai Track	1692941	5653269	1030	5	270	CC	2.5	0	Minor
33	Pouakai Hut	1689292	5657459	1000	5	270	L	0	0	Pouakai Range
34	Pouakai Hut	1689594	5657359	1045	10	270	CX	0	0	Pouakai Range
32	Pouakai Hut	1689332	5657678	990	5	270	L	0	0	Pouakai Range

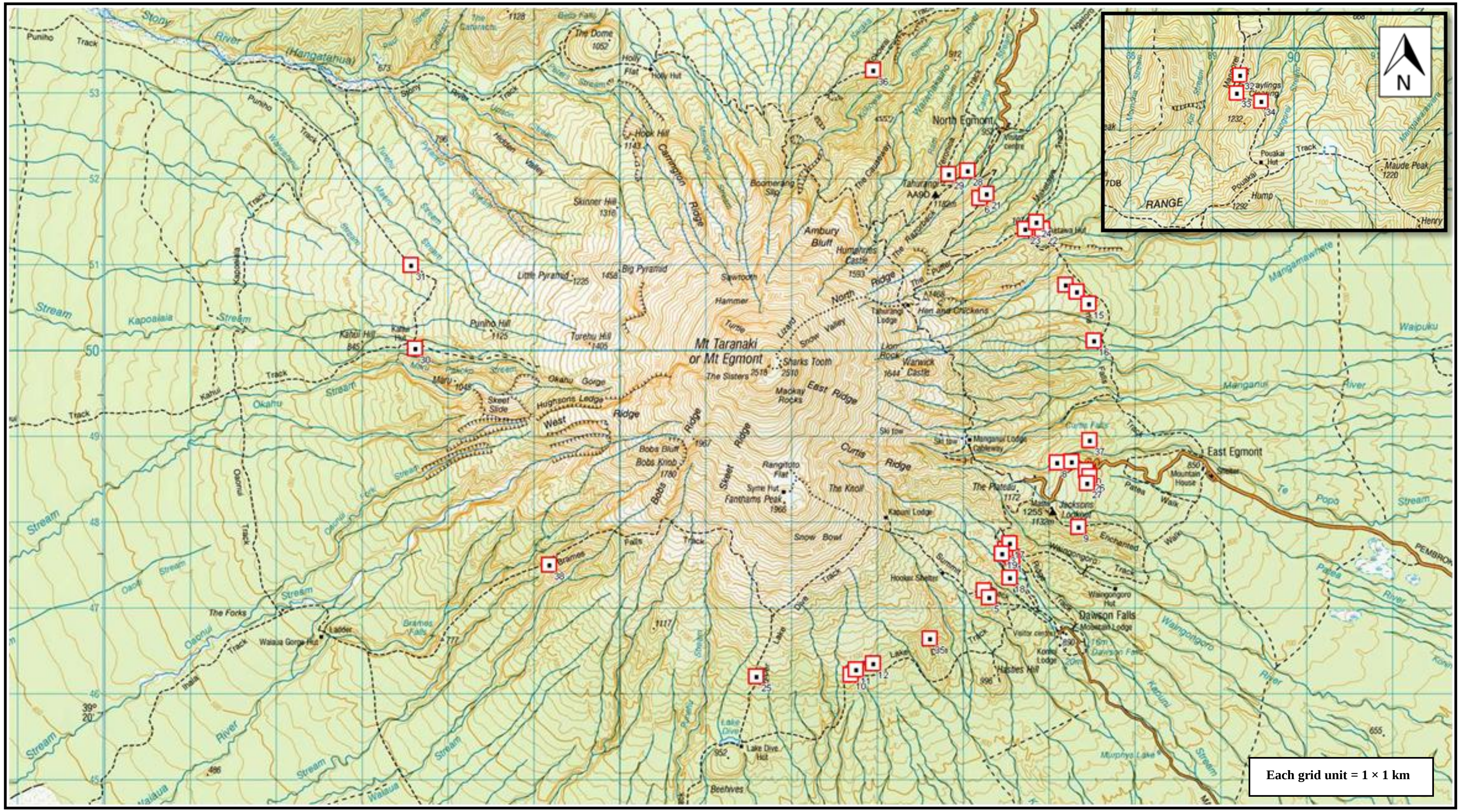

Figure 2.4: Location of the thirty-eight quadrats at the treeline position on Mt Taranaki and Pouakai Range (inset).

2.4.2 Flora

In the 5700 m^2 area surveyed at the treeline position on Mt Taranaki, a total of 57 vascular taxa were identified (Table 2.6), all of which have been previously recorded on Mt Taranaki by Druce (1992). All treeline flora were indigenous, and constituted a mix of species typical of montane forest and shrubland vegetation types on the mountain.

Table 2.6: Vascular flora recorded in quadrats at the treeline position of Mt Taranaki.

Vascular treeline flora, Mt Taranaki	
Alseuosmia macrophylla	*Hymenophyllum multifidum*
Alseuosmia pusilla	*Hymenophyllum pulcherrimum*
Aristotelia serrata	*Hymenophyllum sanguinolentum*
Asplenium bulbiferum	*Libertia micrantha*
Asplenium flaccidum	*Libocedrus bidwillii*
Astelia sp. unnamed (aff. *nervosa*)	*Luzuriaga parviflora*
Blechnum chambersii	*Melicytus lanceolatus*
Blechnum fluviatile	*Microlaena avenacea*
Blechnum montanum	*Microsorum scandens*
Blechnum procerum	*Myrsine divaricata*
Brachyglottis elaeagnifolia	*Myrsine salicina*
Cardamine debilis agg.	*Nematoceras trilobum*
Carmichaelia australis	*Olearia arborescens*
Carpodetus serratus	*Ourisia macrophylla*
Coprosma grandifolia	*Pittosporum tenuifolim*
Coprosma pseudocuneata	*Podocarpus hallii*
Coprosma dumosa (syn. *C. tayloriae*)	*Polystichum vestitum*
Coprosma tenuifolia	*Pseudopanax colensoi*
Cyathea smithii	*Pseudopanax crassifolius*
Dracophyllum filifolium	*Pseudowintera colorata*
Elaeocarpus hookerianus	*Raukaua simplex*
Fuchsia excorticata	*Rubus cissoides*
Gaultheria antipoda	*Schefflera digitata*
Grammitis billardierei	*Uncinia drucei*
Grammitis magellanica	*Uncinia involuta*
Griselinia littoralis	*Uncinia silvestris*
Hebe stricta var. *egmontiana* (*H.“egmontiana”*)	*Uncinia uncinata*
Hebe macrocarpa	*Weinmannia racemosa*

2.4.3 Densities and basal areas of trees

Summaries of the basal area and density of all species by individual quadrat are provided in the appendices. Densities and basal areas of trees ≥2 cm dgh in the four quadrat groups are presented in Table 2.7 and Table 2.8 respectively, along with the relative (percent) contributions of each species to the groups. Large standard deviation values displayed for some species indicates significant variation in abundance between quadrats which were combined to create the groups. Figure 2.5 and Figure 2.6 give the density and basal area of selected species in each group simultaneously, visually illustrating how these values are related to one another, and how they vary between the groups.

Total density in each group ranged from 5422–8370 stems ha^{-1}, with considerably higher densities found in the groups affected by the Burrell Lapilli (severe and minor) than the outside and Pouakai Range groups. Total basal area for each group ranged from 165.5–265.7 m^{2} ha^{-1}, with the lowest basal area found in the severe group, and increasing progressively across the minor, outside and Pouakai Range groups. The densities and basal areas of some species differed significantly between the groups. Results show that the way in which the basal area and density values for each species varies across groups can be broadly classed as one of three trends. There are those species which are more common within the Burrell Lapilli distribution than outside, those which are more common outside the Burrell Lapilli distribution than within, and finally those which are equally common both inside and outside the Burrell Lapilli distribution. For each of the key species, the variation in basal area and density values across each group is described.

Table 2.7: Mean (± SD) and relative density of trees (stems ha^{-1}, ≥2 cm dgh) in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range.

Group name	**Mt Taranaki**						**Pouakai Range (no lapilli)**	
	Severe (20–40 cm Burrell Lapilli)		**Minor (1–20 cm Burrell Lapilli)**		**Outside (no lapilli)**			
Species	**Density (No. stems ha^{-1} ≥2 cm dgh)**	**Relative density (%)**	**Density (No. stems ha^{-1} ≥2 cm dgh)**	**Relative density (%)**	**Density (No. stems ha^{-1} ≥2 cm dgh)**	**Relative density (%)**	**Density (No. stems ha^{-1} ≥2 cm dgh)**	**Relative density (%)**
Podocarpus hallii	846 ± 506	13.3	1107 ± 643	13.5	311 ± 308	5.8	1266 ± 546	21.8
Podocarpus hallii Dead	46 ± 92	0.7	44 ± 79	0.5	0	0	0	0
Libocedrus bidwillii	15 ± 55	0.2	133 ± 186	1.6	89 ± 102	1.6	66 ± 115	1.1
Libocedrus bidwillii Dead	0	0	52 ± 87	0.6	22 ± 38	0.4	133 ± 176	2.3
Griselinia littoralis	769 ± 449	12.1	385 ± 293	4.7	311 ± 252	5.8	22 ± 38	0.4
Weinmannia racemosa	0	0	19 ± 64	0.2	800 ± 1386	14.8	1000 ± 133	17.2
Fuchsia excorticata	77 ± 200	1.2	0	0	0	0	0	0
Aristotelia serrata	77 ± 149	1.2	0	0	0	0	0	0
Raukaua simplex	256 ± 237	4.0	559 ± 559	6.8	89 ± 102	1.6	178 ± 192	3.1
Pseudowintera colorata	1318 ± 868	20.7	4056 ± 1600	49.3	2889 ± 2721	53.5	1667 ± 1073	28.6
Brachyglottis elaeagnifolia	308 ± 447	4.8	185 ± 594	2.3	0	0	22 ± 38	0.4
Hebe "egmontiana"	149 ± 283	2.3	211 ± 200	2.6	22 ± 38	0.4	67 ± 115	1.1
Pseudopanax colensoi	97 ± 146	1.5	63 ± 130	0.8	0	0	0	0
Coprosma grandifolia	882 ± 1241	13.8	285 ± 689	3.5	22 ± 38	0	0	0
Coprosma dumosa	272 ± 297	4.3	300 ± 268	3.6	222 ± 234	4.1	111 ± 102	1.9
Coprosma tenuifolia	1000 ± 365	15.7	581 ± 564	7.1	267 ± 200	4.9	67 ± 67	1.1
Myrsine divaricata	149 ± 134	2.3	167 ± 162	2.0	111 ± 38	2.1	133 ± 115	2.3
Myrsine salicina	0	0	0	0	111 ± 192	2.1	1089 ± 674	18.7
Carpodetus serratus	62 ± 203	1.0	30 ± 57	0.4	111 ± 38	2.1	0	0
Cyathea smithii	26 ± 43	0.4	30 ± 89	0.4	22 ± 38	0.4	0	0
Others[1]	29 ± 100	0.5	18 ± 77	0.2	2 ± 13	0	0	0
TOTAL	6615	100	8370	100	5422	100	5822	100

[1]. *Alseuosmia macrophylla*, *Carmichaelia arborea*, *Coprosma pseudocuneata*, *Dracopyllum filifolium*, *Melicytus lanceolatus*, *Olearia arborescens*, *Pittosporum tenuifolium*, *Rubus cissoides*, *Schefflera digitata*.

Table 2.8: Mean (± SD) and relative basal area of trees (m^2 ha^{-1}, stems ≥2 cm dgh) in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range.

Group name	**Mt Taranaki**						**Pouakai Range (no lapilli)**	
	Severe (20–40 cm Burrell Lapilli)		**Minor (1–20 cm Burrell Lapilli)**		**Outside (no lapilli)**			
Species	**Basal area (m^2 ha^{-1})**	**Relative basal area (%)**	**Basal area (m^2 ha^{-1})**	**Relative basal area (%)**	**Basal area (m^2 ha^{-1})**	**Relative basal area (%)**	**Basal area (m^2 ha^{-1})**	**Relative basal area (%)**
Podocarpus hallii	30.5 ± 19.5	18.6	39.9 ± 27.0	22.8	25.7 ± 40.8	11.5	20.2 ± 21.1	7.6
Podocarpus hallii Dead	25.6 ± 48.7	15.6	7.3 ± 15.0	4.2	0	0	0	0
Libocedrus bidwillii	10.1 ± 36.5	6.2	21.6 ± 26.7	12.3	93.4 ± 98.2	41.8	7.5 ± 12.9	2.8
Libocedrus bidwillii Dead	0	0	11.8 ± 26.6	6.7	4.1 ± 7.0	1.8	49.3 ± 76.1	18.6
Griselinia littoralis	57.4 ± 36.0	35.0	58.3 ± 41.4	33.3	51.8 ± 35.1	23.1	6.0 ± 10.3	2.2
Weinmannia racemosa	0	0	1.1 ± 4.4	0.6	24.0 ± 41.6	10.7	161.1 ± 29.1	60.6
Fuchsia excorticata	12.5 ± 38.8	7.6	0	0	0	0	0	0
Aristotelia serrata	1.8 ± 3.7	1.1	0	0	0	0	0	0
Raukaua simplex	4.2 ± 4.2	2.6	9.2 ± 7.1	5.2	1.9 ± 2.1	0.8	1.3 ± 1.6	0.5
Pseudowintera colorata	3.5 ± 3.4	2.1	14.5 ± 7.5	8.3	12.9 ± 11.9	5.8	3.9 ± 3.0	1.5
Brachyglottis elaeagnifolia	5.0 ± 7.1	3.1	2.0 ± 5.3	1.1	0	0	0.2 ± 0.3	0.1
Hebe “egmontiana”	2.7 ± 6.4	1.6	2.7 ± 3.8	1.5	0.5 ± 0.8	0.2	0.1 ± 0.3	0.1
Pseudopanax colensoi	3.0 ± 7.9	1.8	0.9 ± 2.3	0.5	0	0	0	0
Coprosma grandifolia	1.9 ± 2.1	1.1	0.6 ± 1.6	0.3	0	0	0	0
Coprosma dumosa	1.5 ± 1.9	0.9	1.5 ± 1.8	0.8	1.5 ± 1.7	0.7	0.3 ± 0.3	0.1
Coprosma tenuifolia	2.4 ± 1.6	1.5	1.2 ± 1.6	0.7	0.5 ± 0.3	0.2	0.2 ± 0.3	0.1
Myrsine divaricata	0.6 ± 0.6	0.4	0.9 ± 1.0	0.5	1.3 ± 0.8	0.6	0.2 ± 0.2	0.1
Myrsine salicina	0	0	0	0	3.0 ± 5.2	1.4	15.4 ± 7.2	5.8
Carpodetus serratus	0.5 ± 1.3	0.3	0.7 ± 2.7	0.4	2.6 ± 1.3	1.2	0	0
Cyathea smithii	0.8 ± 2.0	0.5	1.0 ± 3.1	0.6	0.6 ± 1.1	0.3	0	0
Others[1]	0.1 ± 0.5	0.1	0.1 ± 0.6	0.1	0	0	0	0
TOTAL	165.5	100	170.0	100	223.7	100	265.7	100

[1] *Alseuosmia macrophylla*, *Carmichaelia arborea*, *Coprosma pseudocuneata*, *Dracopyllum filifolium*, *Melicytus lanceolatus*, *Olearia arborescens*, *Pittosporum tenuifolium*, *Rubus cissoides*, *Schefflera digitata*.

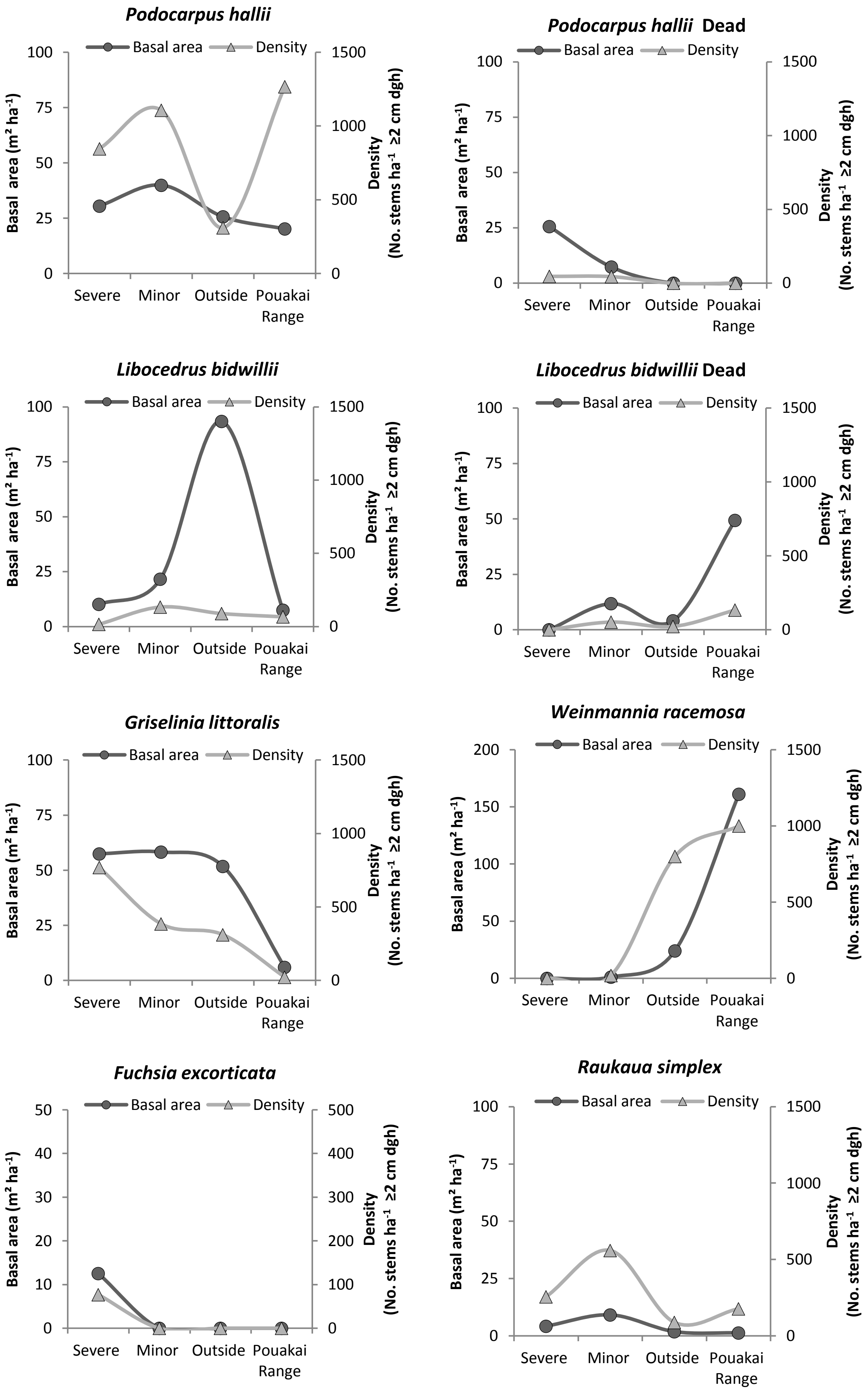

Figure 2.5: Mean basal area (m^2 ha^{-1}, stems ≥2 cm dgh) and mean density (stems ha^{-1}, ≥2 cm dgh) of selected species in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range. Note that axis scaling varies between graphs.

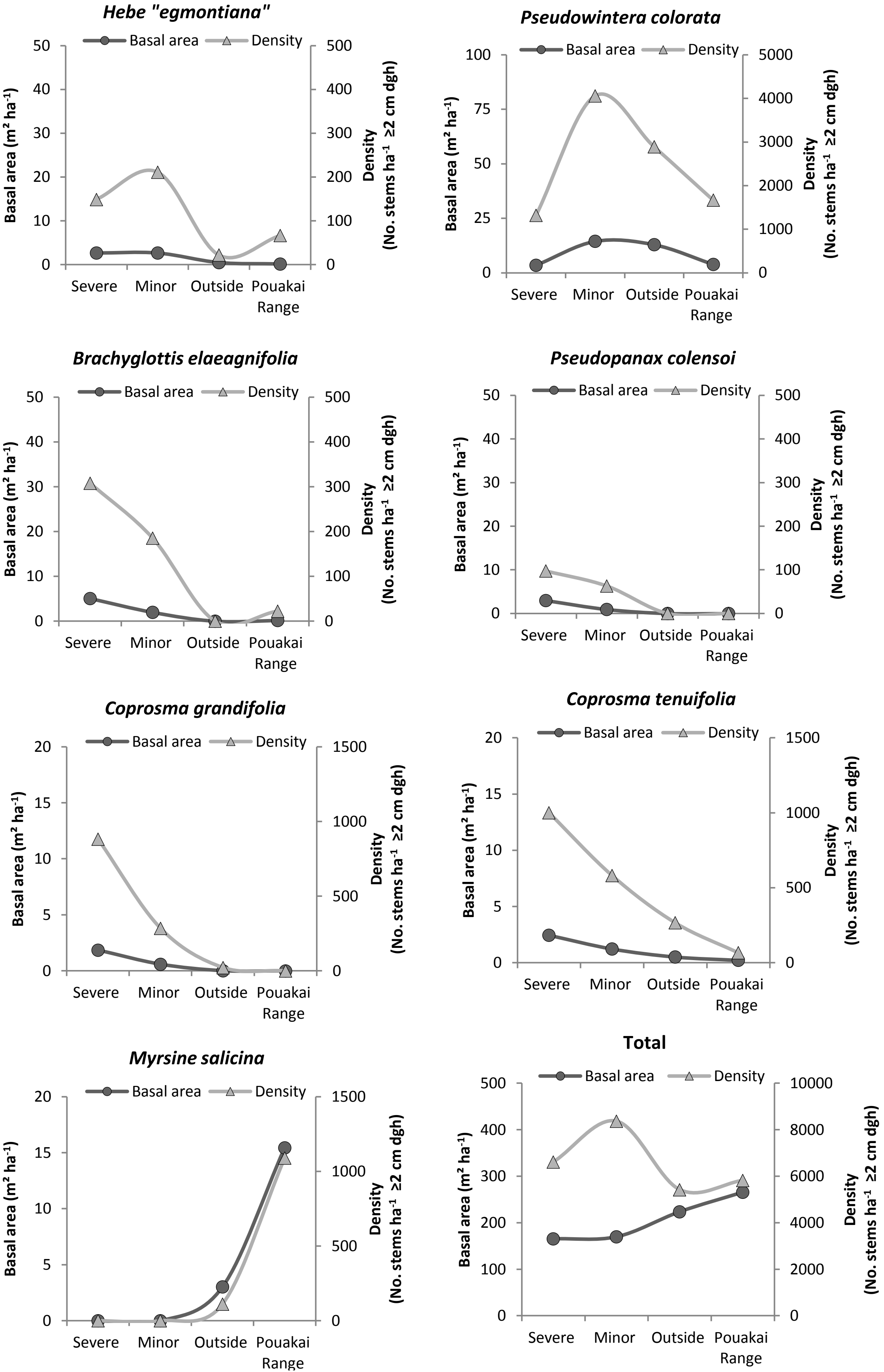

Figure 2.6: Mean basal area (m^2 ha^{-1}, stems ≥2 cm dgh) and mean density (stems ha^{-1}, ≥2 cm dgh) of selected species in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range. Note that axis scaling varies between graphs.

Density of *Podocarpus* was highest in the Pouakai Range group (1266 stems ha^{-1}), and least common in the outside group (311 stems ha^{-1}), with the severe and minor groups having similar densities (846 cf. 1107 stems ha^{-1}). Basal area of *Podocarpus* was higher in the severe (30.5 m^{2} ha^{-1}) and minor (39.9 m^{2} ha^{-1}) groups compared with the outside (25.7 m^{2} ha^{-1}) and Pouakai Range (20.2 m^{2} ha^{-1}) groups. Standing dead (snag) *Podocarpus* were only recorded in the two groups affected by the Burrell eruption; with the basal area of dead *Podocarpus* (25.6 m^{2} ha^{-1}) almost equalling that of the living *Podocarpus* in the severe group. However, the density of the dead stems was much lower than living stems there (46 cf. 846 stems ha^{-1}), which indicates the snags were of a much larger size than the living stems. In terms of basal area, *Podocarpus* is a dominant component of treeline vegetation across Mt Taranaki and the Pouakai Range.

Density of *Libocedrus* was highest in the minor group (133 stems ha^{-1}), and lowest in the severe group (15 stems ha^{-1}). Basal area of *Libocedrus* was notably higher in the outside group (93.4 m^{2} ha^{-1}) compared with all other groups which had values of 7.5–21.6 m^{2} ha^{-1}. The greatest density and basal area of dead *Libocedrus* was found in the Pouakai Range group; here the basal area of dead stems greatly exceeded that of the living stems (49.3 cf. 7.5 m^{2} ha^{-1}). Density of *Griselinia* progressively decreased from 769–22 stems ha^{-1} through the severe, minor, outside and Pouakai Range groups. Basal area of *Griselinia* was consistently high across the severe, minor and outside groups on Mt Taranaki (51.8–58.3 m^{2} ha^{-1}), making it a major component of the vegetation there, though on Pouakai Range, it decreased to only 6 m^{2} ha^{-1}.

Weinmannia was absent from the severe group, but progressively increased in basal area and density across the minor, outside and Pouakai Range groups to reach a notable contribution of 161.1 m^{2} ha^{-1} and 1000 stems ha^{-1}. *Myrsine salicina* also followed a similar pattern, being absent from the severe and minor groups but increasing from the outside to Pouakai Range groups to a total of 15.4 m^{2} ha^{-1} and 1089 stems ha^{-1}. *Pseudowintera* had the highest density of all species in each of the groups (1318–4056 stems ha^{-1}); but the comparatively insignificant basal area values (<15 m^{2} ha^{-1}) in each group indicate that while a large number of individuals were present, they were only of a small diameter. Both density and basal area of *Pseudowintera* were highest in the minor group. Both *Fuchsia* and *Aristotelia serrata* were only found in the severe group and nowhere else, with basal areas of 12.5 m^2 ha^{-1} and 1.8 m^2 ha^{-1} respectively. *Coprosma tenuifolia*, *Coprosma grandifolia*, *Coprsoma dumosa*, *Pseudopanax colensoi*, and *Brachyglottis* generally decreased progressively in basal area and density across the severe, minor, outside and Pouakai Range groups.

2.4.4 Densities of saplings

Because individuals recorded in the saplings class are often juvenile, they can be helpful in determining future vegetation trends as well as quantifying the understory. Densities of saplings <2 cm dgh and >50 cm high in the four quadrat groups are presented in Table 2.9; a selection of these are graphed alongside seedlings in Figure 2.7. Total density in each group ranged from 8605–15,155 stems ha^{-1}, with similar total densities in the severe, minor and Pouakai Range groups, and the largest total density being found in the outside group.

Across all groups, *Pseudowintera* was the most abundant sapling species, with densities ranging from 2472 stems ha^{-1} in the severe group to 6044 stems ha^{-1} in the outside group, making it a very significant component of the understory vegetation. Another common sapling, *Coprosma tenuifolia*, decreased progressively from 1477–311 stems ha^{-1}, through the severe, minor, outside and Pouakai Range groups. The density of *Coprosma grandifolia* saplings was greatest in the outside group (5556 stems ha^{-1}), though this species was found across all the groups. The tufted lily *Astelia nervosa* decreased progressively from 1836–444 stems ha^{-1} across the severe, minor and outside groups, but was absent from the Pouakai Range group. *Myrsine salicina* saplings were absent from the severe and minor groups, but were common in the outside (844 stems ha^{-1}) and Pouakai Range groups (622 stems ha^{-1}). *Weinmannia* saplings were most abundant in the Pouakai Range group (222 stems ha^{-1}), and had low densities in the other groups. *Podocarpus* saplings increased progressively from 185–978 stems ha^{-1} across the severe, minor, outside and Pouakai Range groups, as did *Raukaua* saplings (205–1333 stems ha^{-1}). *Griselinia* saplings were most common in the minor group (256 stems ha^{-1}), with lesser amounts in the severe and

Pouakai Range, and none recorded in the outside group. *Libocedrus* saplings were virtually nonexistent in all four groups.

2.4.5 Densities of seedlings

Densities of seedlings and ground covers 5–50 cm high in the four quadrat groups are presented in Table 2.10; a selection of these are graphed alongside saplings in Figure 2.7. Total seedling density in each group ranged from 31,111–56,533 stems ha^{-1}, and as with trees, total seedling density was higher in the severe and minor groups affected by the Burrell eruption, compared with the outside and Pouakai Range groups. Across all groups, *Pseudowintera* was the most abundant seedling/groundcover species, with densities ranging from 9222 stems ha^{-1} in the outside group to 17,289 stems ha^{-1} in the minor group.

With regards to the canopy species, *Podocarpus* seedlings were found at high densities in the minor (785 stems ha^{-1}) and Pouakai Range (711 stems ha^{-1}) groups, but at low densities in the severe (226 stems ha^{-1}) and outside (89 stems ha^{-1}) groups. *Griselinia* seedlings increased progressively in abundance through the severe, minor, outside and Pouakai Range groups (738–3378 stems ha^{-1}), the inverse trend to that displayed by *Griselinia* trees. *Weinmannia* seedlings were not overly common and only found in the minor (119 stems ha^{-1}) and Pouakai Range (356 stems ha^{-1}) groups at low densities. No *Libocedrus* seedlings were found in any of the quadrats surveyed. The density of *Raukaua* seedlings was higher in the severe (3713 stems ha^{-1}) and minor (2415 stems ha^{-1}) groups than the outside (1689 stems ha^{-1}) and Pouakai Range (2044 stems ha^{-1}) groups. *Coprosma grandifolia* was an import seedling in the severe group (5108 stems ha^{-1}), and to a lesser extent in the minor group (1514 stems ha^{-1}), but was absent from the other groups. *Brachyglottis* seedlings decreased progressively from 2790–356 stems ha^{-1} across the severe, minor, Pouakai Range and outside groups, as did *Brachyglottis* trees. *Myrsine salicina* seedlings were absent in the severe group but increased progressively from 59–800 stems ha^{-1} through the minor, outside and Pouakai Range groups. *Blechnum procerum* was an important ground cover across all groups 2215–3556 stems ha^{-1}. *Blechnum fluviatile* was common across the groups on Mt Taranaki (3378–5867 stems ha^{-1}), as was *Polystichum vestitum* (1511–2756 stems ha^{-1}), but both species were absent from the Pouakai Range group.

Table 2.9: Mean (± SD) and relative density of saplings (stems ha^{-1}, <2 cm dgh, >50 cm high) in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range.

Group name	**Mt Taranaki**						**Pouakai Range (no lapilli)**	
	Severe (20–40 cm Burrell Lapilli)		**Minor (1–20 cm Burrell Lapilli)**		**Outside (no lapilli)**			
Species	**Sapling density (No. stems ha^{-1} <2 cm dgh, >50 cm high)**	**Relative density (%)**	**Sapling density (No. stems ha^{-1} <2 cm dgh, >50 cm high)**	**Relative density (%)**	**Sapling density (No. stems ha^{-1} <2 cm dgh, >50 cm high)**	**Relative density (%)**	**Sapling density (No. stems ha^{-1} <2 cm dgh, >50 cm high)**	**Relative density (%)**
Pseudowintera colorata	2472 ± 1617	29.0	3148 ± 1416	38.4	6044 ± 1309	40.1	4133 ± 3716	49.1
Griselinia littoralis	103 ± 146	1.2	259 ±376	3.2	0	0	89 ± 77	1.1
Podocarpus hallii	185 ± 334	2.2	215 ± 510	2.6	267 ± 462	1.8	978 ± 1231	11.6
Coprosma tenuifolia	1477 ± 1238	17.3	1156 ± 1157	14.1	1067 ± 1313	7.1	311 ± 429	3.7
Coprosma grandifolia	1159 ± 1345	13.6	689 ± 1170	8.4	5556 ± 9051	36.9	133 ± 133	1.6
Coprosma dumosa	164 ± 238	1.9	200 ± 311	2.4	133 ± 133	0.9	178 ± 77	2.1
Schefflera digitata	72 ± 222	0.8	7 ± 31	0.1	44 ± 77	0.3	0	0
Astelia nervosa	1836 ± 1497	21.5	1193 ± 1083	14.6	444 ± 407	2.9	0	0
Asplenium bulbiferum	72 ± 193	0.8	7 ± 31	0.1	0	0	0	0
Aristotelia serrata	31 ± 111	0.4	0	0	0	0	0	0
Carpodetus serratus	31 ± 111	0.4	67 ± 160	0.8	89 ± 154	0.6	0	0
Pseudopanax colensoi	369 ± 676	4.3	296 ± 912	3.6	0	0	133.0	1.6
Blechnum montanum	246 ± 623	2.9	215 ± 528	2.6	0	0	0	0
Brachyglottis elaeagnifolia	21 ± 74	0.2	37 ± 89	0.5	0	0	0	0
Raukaua simplex	205 ± 406	2.4	511 ± 555	6.2	578 ± 505	3.8	1333 ± 1392	15.8
Myrsine divaricata	10 ± 37	0.1	30 ± 98	0.4	0	0	133 ± 231	1.6
Olearia arborescens	51 ± 185	0.6	59 ± 166	0.7	0	0	0	0
Libocedrus bidwillii	0	0	7 ± 31	0.1	0	0	0	0
Myrsine salicina	0	0	0	0	844 ± 1463	5.6	622 ± 468	7.4
Weinmannia racemosa	10 ± 37	0.1	44 ± 189	0.5	0	0	222 ± 278	2.6
Others[1]	8 ± 62	0.1	52 ± 354	0.6	8 ± 32	0.1	149 ± 446	1.8
TOTAL	8605	100	8711	100	15155	100	9911	100

[1]. *Alseuosmia pusilla, Alseuosmia macrophylla, Blechnum chambersii, Blechnum discolor, Coprosma pseudocuneata, Cyathea smithii, Fuchsia excorticata, Gaultheria antipoda, Hebe "egmontiana", Melicytus lanceolatus*.

Table 2.10: Mean (± SD) and relative density of seedlings and ground covers (stems ha^{-1}, 5–50 cm high) in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range.

Group name	**Mt Taranaki**						**Pouakai Range (no lapilli)**	
	Severe (20–40 cm Burrell Lapilli)		**Minor (1–20 cm Burrell Lapilli)**		**Outside (no lapilli)**			
Species	**Seedling density (No. stems ha^{-1} 5–50 cm high)**	**Relative density (%)**	**Seedling density (No. stems ha^{-1} 5–50 cm high)**	**Relative density (%)**	**Seedling density (No. stems ha^{-1} 5–50 cm high)**	**Relative density (%)**	**Seedling density (No. stems ha^{-1} 5–50 cm high)**	**Relative density (%)**
Alseuosmia macrophylla	0	0	15 ± 63	0.1	0	0	4978 ± 4598	15.5
Asplenium bulbiferum	1415 ± 2338	3.1	252 ± 815	0.5	178 ± 308	0.6	0	0
Astelia nervosa	2215 ± 3538	4.9	2193 ± 1474	4.2	1422 ± 2019	4.8	1778 ± 937	5.5
Blechnum fluviatile	5620 ± 5120	12.9	5867 ± 5486	11.3	3378 ± 1563	11.4	0	0
Blechnum montanum	533 ± 1131	0.5	1259 ± 2754	2.4	356 ± 407	1.2	0	0
Blechnum procerum	2215 ± 3920	4.9	2963 ± 2261	5.7	2222 ± 2268	7.5	3556 ± 1469	11
Brachyglottis elaeagnifolia	2790 ± 7261	6.1	1156 ± 3235	2.2	356 ± 308	1.2	444 ± 770	1.4
Cardamine debilis agg.	451 ± 1470	0.1	889 ± 357	0.3	0	0.3	0	0
Coprosma grandifolia	5108 ± 10512	11.2	1514 ± 1605	3	0	0	0	0
Coprosma dumosa	328 ± 617	0.7	519 ± 795	1	267 ± 267	0.9	622 ± 407	2
Coprosma tenuifolia	3897 ± 4846	8.5	2385 ± 3228	4.6	978 ± 1694	3.3	711 ± 308	2.2
Fuchsia excorticata	226 ± 595	0.5	0	0	0	0	0	0
Griselinia littoralis	738 ± 1130	1.6	1185 ± 1731	2.3	1778 ± 3079	6	3378 ± 3204	10
Hebe “egmontiana”	103 ± 229	0.2	30 ± 126	0.1	89 ± 154	0	444 ± 555	1.4
Microlaena avenacea	636 ± 1730	1.4	5022 ± 5698	9.6	2933 ± 4406	9.9	1867 ± 1749	5.8
Myrsine divaricata	267 ± 738	0.6	1141 ± 2876	2.2	356 ± 616	1.2	0	0
Myrsine salicina	0	0	59 ± 195	0.1	978 ± 1694	3.3	800 ± 1386	2.5
Olearia arborescens	472 ± 1548	1.0	133 ± 391	0.3	0	0	0	0
Podocarpus hallii	226 ± 405	0.5	785 ± 1436	1.5	89 ± 154	0.3	711 ± 407	2
Polystichum vestitum	1395 ± 1203	3.1	2756 ± 3533	5.3	1511 ± 1078	5.1	0	0
Raukaua simplex	3713 ± 5548	8.1	2415 ± 1988	4.6	1689 ± 1516	6	2044 ± 857	6
Pseudopanax colensoi	246 ± 648	0.5	0	0	3556 ± 6158	12	0	0
Pseudowintera colorata	11815 ± 7190	25.9	17289 ± 9384	33.2	6222 ± 10777	21	8178 ± 6024	25.4
Schefflera digitata	492 ± 1115	1.1	30 ± 86	0.1	0	0	0	0
Uncinia spp.	1077 ± 1402	2	2815 ± 3453	5.4	1200 ± 1598	4	1644 ± 2006	5
Weinmannia racemosa	0	0	119 ± 503	0.2	0	0	356 ± 616	1.1
Others[1]	66 ± 472	0.1	41 ± 251	0.1	25 ± 99	0.1	692 ± 2856	2.1
TOTAL	47979	100	56533	100	31111	100	44622.0	100

[1]. *Alseuosmia pusilla*, *Aristotelia serrata*, *Blechnum chambersii*, *Carpodetus serratus*, *Coprosma pseudocuneata*, *Cyathea smithii*, *Elaeocarpus hookerianus*, *Libertia micrantha*, *Luzuriaga parviflora*, *Melicytus lanceolatus*, *Nematoceras trilobum*, *Ourisia macrophylla*, *Pseudopanax crassifolius*, *Prumnopitys ferruginea*.

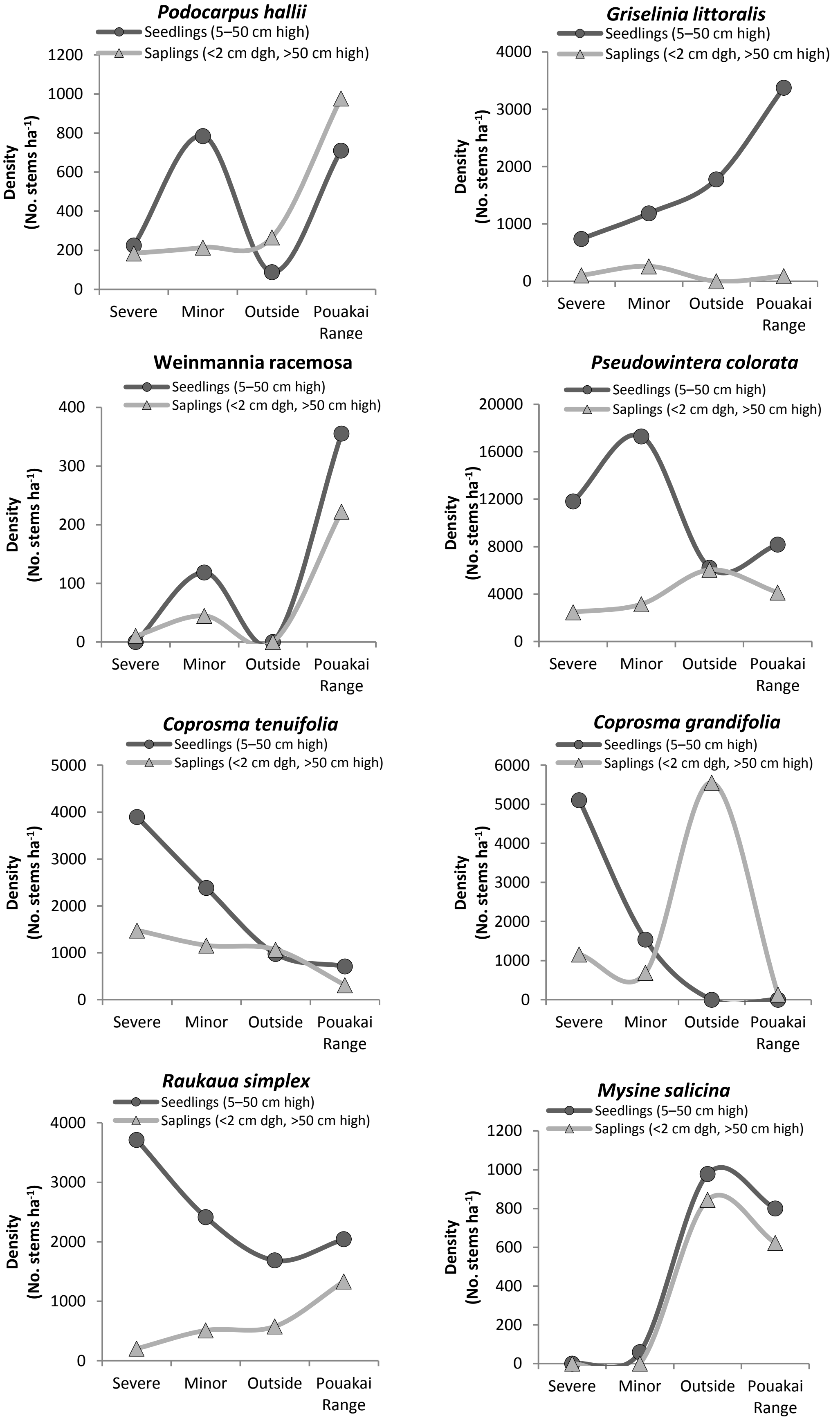

Figure 2.7: Mean density (stems ha^{-1}) of selected seedlings (5–50 cm high) and saplings (<2 cm dgh, >50 cm high) in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range.

2.4.6 Vegetation composition of each group

Using an adaptation of the vegetation naming system developed by Atkinson (1985), a compositional vegetation name is given for each of the four treeline quadrat groups (Table 2.11), and the vegetation of each group is described. In the naming system, a back slash (/) provides structural information by separating species that differ significantly in height, with the taller species being placed to the left of the symbol. Hyphens (–) are used to link species not greatly different in height, which form part of the same canopy layer. Species contributing >50% to the total basal area are signified by underlining. Atkinson's naming system was modified in the sense that all species contributing >10% to the total basal area (as opposed to the recommended >20%) were included in the name.

Atkinson (1985) makes no mention as to whether or not standing dead trees (henceforward referred to as snags) should be included in the name if they reach the >20% threshold. On Mt Taranaki, snags constitute a significant and conspicuous component of the treeline vegetation, so the decision was made to include them in the vegetation name where they met the >10% contribution to basal area criterion. It is known that large (and often emergent) snags at the treeline on Mt Taranaki are likely to be one of only two species, *Libocedrus* or *Podocarpus*, because these are the only two species present on Mt Taranaki capable of obtaining such large straight boles at this elevation. Once dead however, it is not a simple task to confidently distinguish between these species. The longer the tree has been deceased, the further this problem is exacerbated as the wood decays and limbs are shed from the snag. Although an educated best-guess was given as to which taxa snags belonged (presented in the basal area and density summaries), the vegetation names here use the conservative term of snag, for which contribution to total basal area was calculated by grouping those individuals identified as dead *Podocarpus* and dead *Libocedrus* together.

Atkinson (1985) also provides a list of diagnostic criteria in his naming system to determine which overall structural class the vegetation belongs to. Applying my quadrat data to Atkinson's structural class criteria yields 'scrub' as the most appropriate class, though unfortunately he provides no specific canopy heights in the criteria, which would have aided with the decision. Nonetheless, the treeline represents transitional vegetation between the montane forest and shrubland classes, so use of the scrub class, which falls between forest and shrubland on Atkinson's (1985) scale, is well justified.

Table 2.11: Treeline vegetation types identified in the quadrat survey. An adaptation of the Atkinson (1985) naming system was used.

Quadrat group	**Treeline vegetation type**
Severe	*Podocarpus hallii* – snag / *Griselinia littoralis* scrub
Minor	*Podocarpus hallii – Libocedrus bidwillii* – snag / *Griselinia littoralis* scrub
Outside	*Libocedrus bidwillii – Podocarpus hallii / Griselinia littoralis – Weinmannia racemosa* scrub
Pouakai Range	*Podocarpus hallii* – snag / *Weinmannia racemosa*

Podocarpus hallii – snag / *Griselinia littoralis* scrub

Treeline areas severely affected by the Burrell Lapilli were characterised by a dominance of *Podocarpus* and snags, emergent over *Griselinia*. Other canopy constituents included *Pseudowintera*, *Fuchsia*, *Brachyglottis*, *Raukaua*, and *Pseudopanax colensoi*. In this part of Mt Taranaki, *Libocedrus* was rare, and *Weinmannia* was totally absent at the treeline. Below the canopy, the most common trees were *Pseudowintera*, *Coprosma tenuifolia* and *Coprosma grandifolia*. *Pseudowintera* and *Astelia nervosa* were most common along with *Raukaua*, *Coprosma dumosa*, *Podocarpus*, *Pseudopanax colensoi* and *Blechnum montanum* in the sapling layer. The seedling and groundcover class was made up of mostly *Pseudowintera*, with lesser amounts of *Blechnum fluviatile*, *Asplenium bulbiferum*, *Coprosma grandifolia*, *Coprosma tenuifolia*, *Raukaua* and *Brachyglottis*.

Podocarpus hallii – Libocedrus bidwillii – snag / *Griselinia littoralis* scrub

At the treeline where the effects of the Burrell Lapilli were minor, vegetation was subtly different to areas severely affected, with *Podocarpus*, *Libocedrus* and snags emergent over *Griselinia*. Other canopy constituents included *Pseudowintera*, *Raukaua*, *Hebe "egmontiana"* and *Brachyglottis*. Below the canopy, the most common species were *Pseudowintera*, *Coprosma tenuifolia*, *Coprosma dumosa* and *Coprosma grandifolia*. *Pseudowintera* was the most abundant sapling, with lesser amounts of *Astelia nervosa*, *Coprosma tenuifolia*, *Coprosma grandifolia*, *Raukaua*, *Pseudopanax colensoi* and *Griselinia*. The seedling and groundcover class was made up of mostly *Pseudowintera*, along with *Blechnum fluviatile*, *Microlaena avenacea*, *Blechnum procerum*, *Polystichum vestitum*, *Uncinia* spp., *Raukaua*, *Coprosma tenuifolia* and *Astelia nervosa*.

***Libocedrus bidwillii* – *Podocarpus hallii* / *Griselinia littoralis* – *Weinmannia racemosa* scrub**

Treeline vegetation outside the Burrell Lapilli distribution on Mt Taranaki was characterised by *Libocedrus* and *Podocarpus* emergent over *Griselinia* and *Weinmannia*. Other canopy constituents were rare in comparison with the severe and minor group vegetation types, but included *Pseudowintera*, *Myrsine salicina*, *Carpodetus serratus* and snags. The seedling and groundcover class was made up of mostly *Pseudowintera*, along with *Pseudopanax colensoi*, *Blechnum fluviatile*, *Microlaena avenacea*, *Blechnum procerum*, *Griselinia*, *Raukaua*, *Polystichum vestitum* and *Astelia nervosa*.

***Podocarpus hallii* – snag / *Weinmannia racemosa* scrub**

On the Pouakai Range, the treeline area surveyed was characterised by *Podocarpus* and snags (most likely *Libocedrus*) emergent over almost pure *Weinmannia*. Some living *Libocedrus* were also emergent, and other less common canopy constituents included *Myrsine salicina*, *Griselinia* and *Raukaua*. It should be noted that although *Libocedrus* was not overly common at the treeline position here, it was much more abundant in the shrubland above the treeline position than on Mt Taranaki (pers. obs.). As in the other groups, *Pseudowintera* was the most abundant sapling, along with *Raukaua*, *Podocarpus*, *Myrsine divaricata*, *Coprosma tenuifolia*, *Weinmannia*, and *Coprosma dumosa*. The seedling and groundcover class was made up of mostly *Pseudowintera*, along with *Alseuosmia macrophylla*, *Blechnum procerum*, *Griselinia*, *Raukaua*, *Microlaena avenacea*, *Astelia nervosa*, *Uncinia* spp. and *Myrsine salicina*.

2.4.7 Ordination of quadrats

Ordination is a multivariate data exploratory technique that allows any number of variables to be scaled along multiple axes, resulting in a graphical representation of the dominant trends in the dataset (McCune & Grace 2002). Objects are positioned in the ordination space so that similar objects (in this case quadrats) are near to each other, and dissimilar objects are farther apart from each other. Although several types of ordination exist, Nonmetric Multidimensional Scaling (NMS), an indirect gradient analysis, is generally regarded as the best ordination type for ecological datasets because unlike other techniques, it avoids the assumption of linear relationships among variables (McCune & Grace 2002). To aid with the interpretation of NMS ordinations, known vector gradients (e.g. environmental, biotic, abiotic) or categorical groupings can be provided from a secondary 'explanatory' dataset, and overlaid onto the main ordination graphic.

NMS ordination of the dataset obtained from the quadrat survey of treeline vegetation on Mt Taranaki is utilised here to objectively summarise a large amount of quadrat data into one graphic illustrating potential compositional similarities and differences between quadrats. By overlaying the final ordination with the four groupings of quadrats used to quantitatively describe the treeline vegetation in this study (severe, minor, outside, Pouakai Range), it can be tested whether or not the use of these particular groupings of quadrats was justified; if quadrats naturally separate out into these four categories in the ordination space, then the quadrat groupings were appropriate.

NMS ordination was completed here using PC-ORD Version 6.0 (McCune & Mefford 2011) software for multivariate analysis of ecological data. Raw data for the ordination was in the format of a basal area per species per quadrat matrix (similar to Appendix 1). Prior to running the ordination, species that occurred in <5% of the quadrats were omitted following the recommendations of McCune & Grace (2002), and the remaining data was modified with a general relativisation by quadrat. Using the NMS 'slow and thorough' auto-pilot mode ordination with Sorenson (Bray-Curtis) distances and a random starting configuration, PC-ORD determined that the quadrat data could be adequately summarised with two ordination axes. The two-dimensional solution resulted in a mean stress in real data (250 runs) of 20.588 and in randomised data (250 permutations for Monte Carlo test) of 23.247 (p = 0.004). The final (minimum) stress of the best solution was 18.715, with an instability value of 0.00000 over 61 iterations. The Monte Carlo test result confirms that a similar final stress could not have been obtained by chance. The number of dimensions used to summarise the data (two) was confirmed by analysing a scree plot of final stress versus the number of dimensions. Although PC-ORD is capable of producing an ordination with up to six axes, the scree plot revealed that there was no significant reduction in stress between the second and third axes, which suggested a two-dimensional solution could adequately summarise this data set. Stress is a measure of dissimilarity between ecological relationships and graphed relationships, so solutions with low stress are better graphical representations of the points in ecological space than solutions with higher stress (McCune & Grace 2002).

In the final ordination (Figure 2.8), quadrats were coded with one of four symbols to depict which quadrat grouping they were previously assigned to (severe, minor, outside, Pouakai Range), and convex hulls were overlaid to show the extent of each group in ordination space. A secondary matrix of data specific to each quadrat was used to add two known vectors to the ordination, Burrell Lapilli thickness and elevation. The ordination was then rotated to obtain maximum correlation between axis one and the thickness of Burrell Lapilli (r = 0.573). There was also moderate negative correlation between axis two and elevation (r = -0.316). Correlation coefficients between each axes and a selection of species and vectors used in the ordination are presented in Table 2.12.

The four quadrat groups separated out in ordination space with minimal overlap. *Weinmannia*, *Myrsine salicina* and *Libocedrus* displayed the strongest negative correlations with axis one (r = -0.79, -0.60, -0.30 respectively), which, given the correlation between axis one and the Burrell Lapilli thickness, illustrates how these species are excluded or suppressed from the treeline where the effects of Burrell eruption were most severe. *Podocarpus, Coprosma tenuifolia* and *Myrsine divaricata* displayed the strongest positive correlations with axis one (r = 0.59, 0.46, 0.33 respectively), indicating these species are more abundant where the Burrell eruption was most severe.

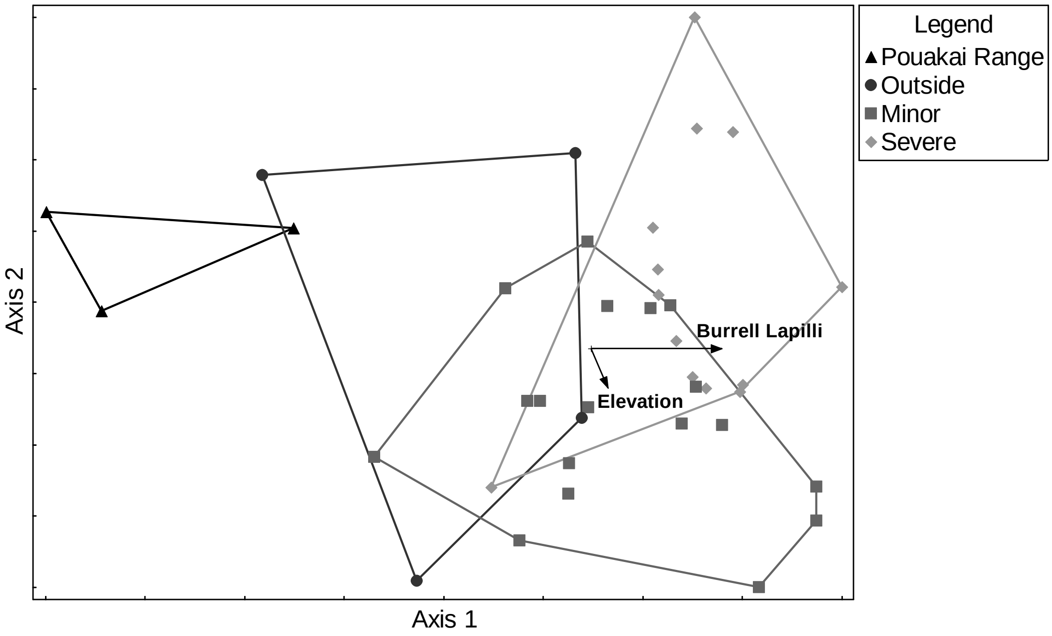

Figure 2.8: NMS ordination of Mt Taranaki treeline vegetation quadrats. The plot was constructed using relativised basal areas of 27 species found in 38 quadrats. The ordination has been rotated to obtain maximum correlation between the axis 1 and Burrell Lapilli thickness (r = 0.573). Moderate negative correlation also exists between elevation and axis 2 (r = -0.316). The final solution had two-dimensions (stress = 18.715, p = 0.004).

Table 2.12: Correlation coefficients (r) between selected variables and the NMS ordination axes; n = 38. Correlation coefficients of r <0.1 are not presented; moderate (r = 0.3–0.49) and significant (r >0.5) correlations are displayed in Bold Type.

	Axis 1	Axis 2
Burrell Lapilli	**0.58**	
Elevation	0.21	**-0.34**
Weinmannia racemosa	**-0.79**	**0.31**
Myrsine salicina	**-0.60**	**0.38**
Podocarpus hallii	**0.59**	**-0.44**
Libocedrus bidwillii	**-0.30**	**-0.54**
Myrsine divaricata	**0.33**	**-0.37**
Podocarpus hallii Dead	0.21	**0.55**
Raukaua simplex	0.26	**-0.54**
Aristotelia serrata	0.16	**0.55**
Libocedrus bidwillii Dead	**-0.54**	
Coprosma tenuifolia	**0.46**	0.16
Schefflera digitata	0.12	**0.40**
Coprosma grandifolia	**0.31**	0.14
Melicytus lanceolatus	0.15	**0.32**
Griselinia littoralis	0.28	0.24
Coprosma dumosa	0.27	-0.27
Pseudowintera colorata	0.26	-0.20
Fuchsia excorticata	0.22	0.27
Coprosma pseudocuneata		-0.27
Rubus cissoides	0.29	-0.14
Pseudopanax colensoi	0.28	
Carpodetus serratus		0.22
Cyathea smithii		0.21

2.5 Discussion

This investigation has revealed that the composition and structure of treeline vegetation on Mt Taranaki displays notable differences across the AD 1655 Burrell Lapilli deposit. The total density of trees was found to be higher within the area where the effects of the Burrell Lapilli were minor (1–20 cm lapilli), compared with where the effects were more severe (20–40 cm); while total densities outside the Burrell Lapilli distribution, and on the adjoining Pouakai Range were lower in comparison. In contrast, the total basal area of stems displayed the inverse trend, with lower basal areas found within the distribution of Burrell Lapilli compared with outside. The composition of treeline vegetation across the lapilli deposit also displayed notable differences, with results suggesting that *Podocarpus* and *Griselinia* have been the most successful treeline species where the effects of the Burrell Lapilli were most severe, while *Libocedrus* was more abundant where the deposition of lapilli was thinner and in areas unaffected by the eruption. Outside the eruption zone, undisturbed forest was characterised by a mix of all three of these species, along with the addition of *Weinmannia*. On the adjoining Pouakai Range, *Weinmannia* was the most important component of treeline vegetation, with Clarkson (1990) having noted that its upper limit there is several hundred metres higher than on Mt Taranaki. A number of large emergent snags were also present around the treeline of Mt Taranaki and Pouakai, though it is difficult to differentiate with certainty which individuals have been killed by the Burrell eruption and which have died as a result of other causes such as natural senescence or possum browse. The composition patterns observed across the Burrell Lapilli distribution are probably the result of a combination of interspecific differences in variables such as resilience, morphology, light and substrate and nutrient requirements, climatic tolerance, regeneration strategy, lifespan etc., some of which are discussed in further detail in Chapter 4. The impact that browsing mammals may have had is also considered in Chapter 3.

Following the 1980 eruption of Mt St. Helens, Antos & Zobel (1986) reported that the density of tree seedlings in the understory greatly increased within the tephra fall zone where canopy vegetation was damaged (tephra thickness 5–15 cm). The new tephra supported twice the density of tree seedlings than the original forest floor there, with greater seedling establishment and survival. The fact that the density of trees was found to be highest in areas where effects of the Burrell eruption were minor on Mt Taranaki, suggests that the thin dusting of tephra stimulated greater regeneration than in the severely affected areas, or that more individuals survived there (a combination of both would also be plausible). Although several hundred years have passed since the Burrell eruption, total stem density still remains higher within the distribution of Burrell Lapilli than outside, and total basal area is yet to equilibrate with the pre-eruption levels indicated outside the eruption zone (suggesting that self-thinning is not yet complete).

The species composition of seedlings on the forest floor also changed following the addition of tephra on Mt. St. Helens. The successional patterns there were unlike that of other disturbances, because of the combination of a mostly intact tree canopy with a drastically altered substrate. Often following a disturbance, species not previously present in the vegetation will invade, but on Mt St. Helens, despite nearly 100% plant death in some locations, few species absent from the forest invaded. Instead, there was a compositional divergence of existing species, with some recovering rapidly while others failed to increase. This resulted in a complex mosaic of survival over the landscape (Dale et al. 2005). In the decades after the event, this compositional shift has not been towards pre-disturbance conditions, because the successional trajectory of the vegetation has been altered (Antos & Zobel 1986, 2005). Likewise on Mt Taranaki, forests within the Burrell Lapilli distribution are considerably different to areas which were not affected. The treeline vegetation on Mt St. Helens is now an unusual mix of conifers and hardwoods, which differs considerably from adjoining ranges which were not affected by such recent volcanic disturbance (Swanson et al. 2005). For example, some species which were rare in the understory prior to the eruption (e.g., conifer *Tsuga*) have become much more common than they were previously, which is equivalent to the *Libocedrus* pattern observed on Mt Taranaki.

In New Zealand, the Taupo tephra eruption c. 1781 BP caused widespread disturbance with complete and partial burial by tephra up to 170 km from the source. Analysis of pollen and macrofossils indicated significant damage was associated with tephra deposits of <10 cm, but patterns of damage and vegetation response were highly variable and not always related to tephra thickness. Vegetation was damaged via mechanical stripping of branches and foliage, with the crowns of canopy and emergent trees being most affected. Mechanical damage was exacerbated further with chemical damage by the acidic tephra. Within 200 years of the eruption, revegetation of areas totally overwhelmed was completed, and post eruption forests were similar to pre-eruption forests (Wilmshurst & McGlone 1996). In a different pollen study, Horrocks & Ogden (1998) noted vegetation changes that occurred on Mt Hauhungatahi, following the deposition of the Taupo tephra. *Libocedrus* increased rapidly after the eruption in areas where tephra was <9 cm thick, which is similar to the pattern on Mt Taranaki. At Mt Hauhungatahi, this was attributed to an increase in canopy gaps (created by the eruption), which permitted the light demanding *Libocedrus* to proliferate. Violent rainstorms which cause land slips can also be associated with large volcanic eruptions, and slips too provide ideal sites for *Libocedrus* colonisation (Boase 1988).

In another parallel with Mt Taranaki, *Libocedrus* was able to dominate upper montane forest at the expense of *Weinmannia* following the Taupo tephra eruption, probably because *Libocedrus* was more tolerant of cooler conditions associated with exposure (Horrocks & Ogden 1998). As a result of volcanic disturbance, the majority of the treeline around Mt Taranaki occurs at a lower elevation than on the adjoining Pouakai Range, with upper limits of species (including *Weinmannia*) often being higher on Pouakai (Clarkson 1990). Such suppression of the treeline elevation by volcanic disturbance has also been reported on Mt St. Helens. Prior to the 1980 eruption there, the treeline was still advancing up the mountain in response to an eruption in AD 1800, but it was again suppressed considerably by the 1980 eruption, and now is advancing upwards again (Swanson 2005). Some species were quite capable of resprouting following burial by mud or tephra following the AD 1886 eruption of Mt Tarawera (c. 1000 m asl), New Zealand, particularly *Weinmannia* and *Griselinia*, while *Coriaria* and *Pteridium* were more prevalent primary colonisers and acted as facilitating species in completely devastated areas (Nicholls 1963). As with Mt Taranaki, emergent species (including *Podocarpus*) suffered the most deleterious effects during the eruption of Mt Tarawera, while vegetation of lower stratums was more protected. The succession and suite of species resulting after the eruption of Mt Tarawera were similar to those on Mt Taranaki (Clarkson & Clarkson 1983, 1995). In particular, *Coriaria* and *Pteridium* became common on Mt Taranaki after the Burrell eruption (McGlone et al. 1988), and furthermore, *Griselinia* and *Weinmannia* became abundant in eruption affected areas at both sites; with Clarkson & Clarkson (1983) noting that the greater palatability of *Weinmannia* (in comparison to *Griselinia*) has inhibited its success on Mt Tarawera in the presence of browsing mammals.

Vegetation would have responded variably across the Burrell Lapilli distribution on Mt Taranaki, with a mosaic of the survival of some species, deaths of some, and arrival of others. Considering the critical tephra thicknesses reported by Vucetich & Pullar (1963), Tsuyuzaki (1989) and Dale et al. (2005), it is likely that where the effects of the Burrell Lapilli were most severe, the large majority of trees and shrubs were killed, and a succession close to primary was initiated. Pollen studies by McGlone et al. (1988) and Lees & Neall (1993) confirm a succession from *Coriaria* and *Pteridium* followed by *Kunzea* and *Fuchsia* occurred in montane forest after the eruption, though at the treeline elevation specifically, the climatic conditions may have favoured more cold tolerant seral taxa such as *Griselinia*, *Brachyglottis*, *Hebe*, *Fuchsia* and *Aristotelia serrata* (all of which were still present in the vegetation).

One may predict that where the effects of the eruption were most severe, *Libocedrus* would be most prevalent, given its status as a highly light demanding species (Boase 1988), though it was found to be more abundant where the eruption disturbance was less significant. In a South Island study, Veblen & Stewart (1982) suggested that *Libocedrus* appears to only benefit from an opening of the canopy when drainage is so poor that other species are excluded, thus perhaps the loose lapilli substrate was unsuitable for the establishment of *Libocedrus*. Instead, it is *Podocarpus* which has been the most successful in the severely affected areas, along with *Griselinia*. The size and form of most *Podocarpus* suggests they have colonised since the eruption, as with *Griselinia* which has grown both epiphytically on snags, as well as terrestrially. Where disturbance was less severe, *Libocedrus* has either been able to persist though the eruption, or alternatively, the opening of the canopy has favoured its establishment and success. On unaffected sections of the treeline, *Weinmannia* is much more abundant, suggesting that although it was known to coppice and proliferate after the eruption in lower elevation forests on the mountain (Clarkson 1990), it has not tolerated or recovered from such a disturbance at the treeline position within the distribution of Burrell Lapilli.

Controlled greenhouse experiments with the key canopy species (*Podocarpus*, *Griselinia*, *Libocedrus*, *Weinmannia*) and tephra would be a valuable aid to explaining the treeline vegetation patterns observed. The experiments could measure both the ability of species to tolerate burial by different thicknesses of tephra, and their potential to colonise onto tephra. At least one such experiment has been conducted elsewhere (Gomez-Romero et al. 2006), and similar experiments have been conducted for burial by sand (e.g., Zhang & Maun 1990; Martinez & Maun 1999). Differing light requirements of species are also thought to have contributed to shaping the treeline vegetation patterns observed; Chapter 4 presents a survey conducted to determine the light requirements of (juvenile) key treeline species.

Chapter Three: Vegetation composition, stature and spatial configuration across the treeline ecotone

3.1 Introduction

Plant ecologists regularly examine vegetation changes along environmental gradients (Austin 1987), with altitudinal gradients being a regular focus (Whittaker 1967). Altitude represents a complex gradient along which many environmental variables change simultaneously; on Mt Taranaki for example, temperature, precipitation, and wind velocity are all known to vary with altitude (see Chapter 1). Clarkson (1977) conducted a direct gradient analysis on Mt Taranaki, in order to "examine quantitatively the changes in composition, physiognomy and structure of the vegetation between 792–1869 m asl". With increasing elevation, the composition, growth form and stature of vegetation displayed prominent changes referred to as altitudinal zonation (see Section 1.2.4). Although Clarkson's (1977) study included an inspection of the tree-shrub interface (i.e., treeline ecotone) at several locations on the mountain, it was not comprehensive and did not take account of the spatial configuration of species.

Here, I present and discuss changes observed in the vegetation composition, structure, and spatial configuration along six belt transects through the treeline ecotone, positioned both within and outside of the Burrell Lapilli distribution. This supplements the main thesis component, a quadrat survey across the Burrell Lapilli distribution (Chapter 2), because in that survey, quadrats were dispersed laterally around the mountain and thus could not capture fine-scale altitudinal variations. Mueller-Dombois & Ellenberg (1974) regard the belt transect (essentially an elongated quadrat) as a useful method for examining vegetation change along gradients, and thus belt transects were utilised here. Belt transects have an advantage over discrete quadrats in that they survey vegetation continuously along a gradient.

3.2 Sampling methods

3.2.1 Belt transect size and positioning

A fixed width of 5 m was utilised for all transects, but transect lengths were variable. The resulting length of each belt transect was a trade-off between the time available to complete the survey, and the need for adequate information. The location of each belt transect on the mountain was tentatively determined based on the availability of treeline access tracks, and the necessity to capture several positions within and outside the Burrell Lapilli distribution. Transects were oriented with their longer axis parallel to the primary altitudinal gradient of the mountain. For each transect, the lower elevation starting position was selected first, based on the criterion that vegetation was predominantly montane forest type with a canopy height of ≥6 m. From this lower position, it was necessary for the belt transect to be surveyed continuously to higher mountain elevations without topographical obstructions, until the vegetation was predominantly shrubland type with a canopy height of ≤3 m.

3.2.2 Belt transect survey method

All trees (≥2 cm dgh) inside the belt transect were recorded by species and measured for dgh. Heights of trees were estimated to the nearest half metre, and the spatial position of each tree within the transect was recorded using an x:y co-ordinate system, with distances measured to a resolution of 10 cm. This enabled the production of spatial configuration maps, and detection of fine-scale patterns occurring across the transition. The belt transect was further divided along its length into 5 × 5 m quadrants for surveying the abundance of saplings and seedlings. In each 5 × 5 m division along the transect, all saplings (<2 cm dgh but >50 cm high) were identified and tallied, and all seedlings (5–50 cm high) were identified and approximately tallied. At 10 m intervals along the belt transect, site attributes including elevation, slope, aspect and GPS position were recorded.

3.2.3 Data collection

Fieldwork was conducted intermittently from March–October 2011. Six belt transects were positioned at treeline locations within and outside the Burrell Lapilli distribution: located near Brames Falls, Dawson Falls, The Plateau, Curtis Falls, North Egmont, and the Kokowai Track.

3.2.4 Data analysis

Because of the narrow (5 m) width of the belt transects, and the large number of quadrats already analysed in Chapter 2, the decision was made not to present densities and basal areas for tree species recorded in the belt transects. As an alternative, tree diameters, tree heights, sapling density and spatial configuration of trees along the length of each transect were examined. Spatial configuration of the species within the transects were described only qualitatively, not analysed statistically (e.g., Moeur's 1993 recommended nearest neighbour analysis and Ripley's *K*-function) as is regularly done with stem mapped data (e.g., Skarpe 1991; Szwagrzyk & Czerwezak 1993; Gibson & Menges 1994) because altitudinal gradients are usually avoided when examining spatial configuration because they mask underlying patterns resulting from biotic interactions (Haase 1995). Furthermore, spatial configuration studies regularly examine patterns over much larger tracts of forest than was permitted by the belt transect size used here.

3.3 Results

3.3.1 Site attributes

A summary of site attributes for the six belt transects is given in Table 3.1, and the position of each transect on the mountain is mapped in Figure 3.1 Transect lengths ranged from 35–120 m, and aspect and slope values were variable between transects. Altitude increased c. 20–30 m along the length of each transect. The thickness of Burrell Lapilli at the sites ranged from 0–30.5 cm. All but one of the belt transects were successful in capturing the vegetation transition through treeline. Bad weather prevented the Dawson Falls transect from being completed;

it was abandoned before the treeline position had been reached, though the incomplete data is still presented here.

3.3.2 Flora

No vascular taxa additional to the quadrat survey (Section 2.4.2) were encountered in the belt transects.

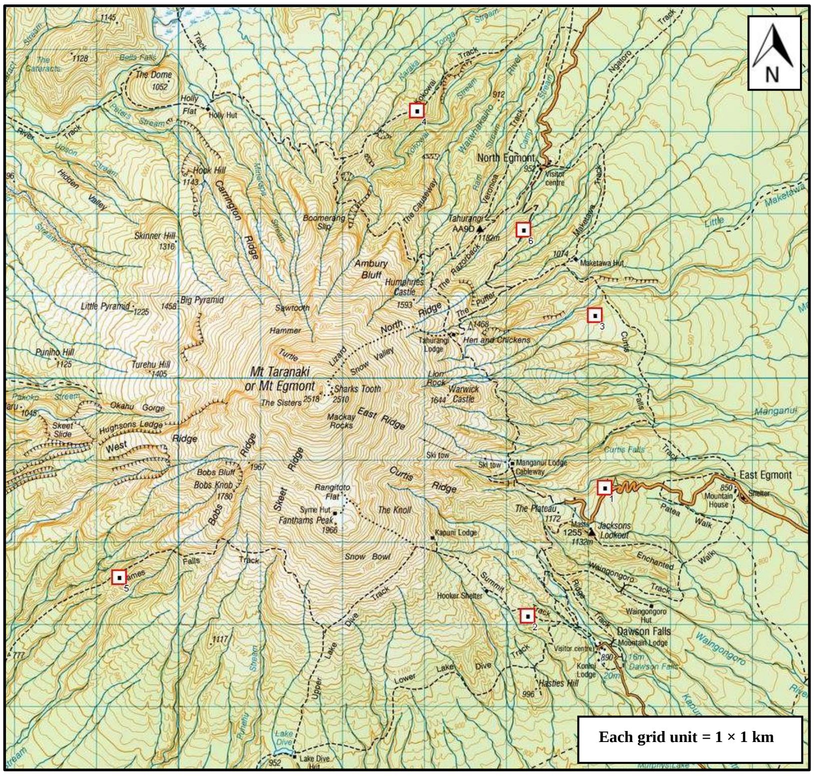

Figure 3.1: Location of the six belt transects through the treeline ecotone on Mt Taranaki.

Table 3.1: Summary of site attributes for six belt transects through the treeline ecotone on Mt Taranaki.

Transect #	Proximate geographic reference	Lower GPS reference (NZTM)	Upper GPS reference (NZTM)	Transect length (m)	Slope range (°)	Aspect (°)	Elevation range (m asl)	Treeline elevation (m asl)	Burrell Lapilli thickness from Druce (1966) (cm)	Burrell Lapilli thickness from Topping (1972) (cm)
		Easting Northing	Easting Northing							
5	Brames Falls	1689269 5647577	1689245 5647567	35	5–30	241	1080–1100	1095	0	0
2	Dawson Falls	1694266 5647056	1694247 5647108	60	4–25	128	1030–1060	-	15	30
1	The Plateau	1695206 5648765	1695192 5648667	120	5–27	60	1040–1095	1080	30.5	30
3	Curtis Falls	1695096 5650830	1695065 5650772	90	5–10	38	1045–1065	1065	15	10
6	North Egmont	1694218 5651840	1694202 5651808	50	3–5	10	1075–1105	1100	7.5	10
4	Kokowai Track	1692924 5653314	1692901 5653256	80	0–10	40	1010–1035	1025	2.5	0

3.3.3 Tree diameters

To examine how tree diameters varied across the treeline ecotone, transects were first divided into 10 × 5 m (50 m^2) divisions/intervals, and then the average and maximum stem diameters in each division were calculated (Table 3.2). Generally, the maximum stem diameter in each division displayed a reduction with increased elevation, despite the transects being <120 m long. Maximum diameters in each division reduced markedly from c. 100 cm dgh to 30 cm dgh. There were no obvious patterns in maximum stem diameters between the sites. The average stem diameters also tended to decrease with increased elevation, though these changes fluctuated more and were not as pronounced as the trend observed with maximum diameters. Differences were probably not as pronounced because the minimum stem size measured was 2 cm dgh; stems c. 2–5 cm were abundant throughout the lengths of the transects, and they thus acted as a buffer on the calculation of mean stem size in each division. Tree diameters were also visually mapped in Section 3.3.5.

Table 3.2: Maximum and mean stem diameter at ground height (cm) in 50 m^2 divisions along belt transects through the treeline ecotone on Mt Taranaki. Belt transect lengths were variable.

	Belt transect length	Stem dgh (cm) in 50 m^2 divisions along belt transects											
		Brames Falls		Dawson Falls		The Plateau		Curtis Falls		North Egmont		Kokowai Track	
		Max	Ave	Max	Ave	Max	Ave	Max	Ave	Max	Ave	Max	Ave
	120	-	-	-	-	144	14	-	-	-	-	-	-
	110	-	-	-	-	104	14	-	-	-	-	-	-
Increasing elevation ↓	100	-	-	-	-	53	12	-	-	-	-	-	-
	90	-	-	-	-	93	23	74	18	-	-	-	-
	80	-	-	-	-	68	27	131	21	-	-	78	9
	70	-	-	-	-	73	25	42	11	-	-	66	9
	60	-	-	107	12	53	18	36	11	-	-	14	7
	50	-	-	119	16	55	14	94	16	55	14	19	8
	40	104	15	75	12	50	21	31	10	43	12	22	8
	30	153	22	39	11	49	26	93	12	44	12	29	8
	20	89	8	46	11	40	15	28	10	88	13	53	9
	10	27	8	49	11	38	15	30	11	39	10	62	8

3.3.4 Treeline stature and profile

To summarise the changes in stature (height) of vegetation through the treeline ecotone, two stylised treeline vegetation profiles (Figure 3.2 a,b) were produced from tree height differences observed along the length of each transect (Figure 3.3–Figure 3.8). For all transects, the maximum height of trees decreased progressively with increased altitude from around c. 8–15 m high down to c. 2–3 m. Along this transition from montane forest to shrubland, the position of the treeline can be approximately indicated as the point where maximum tree heights reduce such that the canopy becomes uniformly 2–3 m high, with only a minimal number of emergent trees above this height (indicated by an arrow on each figure). Although all belt transects displayed a decrease in maximum tree height with increased elevation, subtle differences were apparent between the transects, of which two main trends are identified here.

Transects positioned where the effects of the Burrell eruption were moderate to severe (i.e., Burrell Lapilli is >15 cm thick) displayed a reduction in maximum tree height towards the treeline that could be described as gradual (Figure 3.2 a). For example, for the transect located at The Plateau (Burrell Lapilli 30.5 cm thick), over a distance of 30 m back from the treeline position (i.e., into montane forest), maximum tree heights decreased progressively towards the treeline from 6–3 m high; therefore the decrease in maximum tree height towards treeline occurred at a rate of 0.10 m/m. For Curtis Falls (Burrell Lapilli 15 cm thick), over the same distance this rate was also gradual at 0.08 m/m. Although the rate could not be calculated exactly for Dawson Falls (Burrell Lapilli 15 cm thick) due to an insufficient transect length, the rate was also projected to be gradual at around 0.13 m/m.

In contrast, transects positioned outside the Burrell Lapilli distribution, or where the effects of the Burrell Lapilli were only minor (Burrell Lapilli <15 cm thick), displayed a more rapid or abrupt reduction in maximum tree heights towards the treeline (Figure 3.2 b), and with the exception of the Kokowai Track transect, the elevation of the treeline was also higher. For example, maximum tree heights decreased at rates of 0.43 m/m over 30 m at Brames Falls (outside Burrell Lapilli distribution), 0.3 m/m at North Egmont (Burrell Lapilli 7.5 cm thick) and 0.17

m/m at Kokowai Track (Burrell Lapilli 2.5 cm). Field observations suggest that the maximum heights of trees (regardless of species) decrease at a faster rate with increased altitude across the treeline ecotone on steeper slopes. However, when the average slope of the terrain in each transect was compared against the tree height decrease rates, no such pattern was detected. This was probably because the average terrain slopes in each transect were c. <15°; not a steep enough slope to exhibit the trend.

The major differences in maximum tree heights are attributed to the presence or absence of *Libocedrus* in the treeline vegetation. Chapter 2 has demonstrated that *Libocedrus* was most common outside of the Burrell Lapilli distribution, or where Burrell Lapilli is <20 cm thick; while little or no *Libocedrus* was present in areas where the lapilli is >20 cm thick. Because of these compositional differences, the profile of the treeline ecotone also exhibited differences, in a trend which is closely allied with the differing height reduction rates of the trees. In transects at Brames Falls and North Egmont, where *Libocedrus* was most common, *Libocedrus* grew as a tall emergent (c. 13 m high), well above the main canopy which was c. 5 m high. This creates a notable step in the profile of the vegetation, with two distinct tiers (emergent and canopy) represented (Figure 3.2 b). As a contrast, in transects where *Libocedrus* was absent, the emergent species *Podocarpus* did not grow as tall (8 m cf. 13 m high), and only just protruded above the main canopy, creating a profile that was without distinct separation of the emergent and canopy tiers (Figure 3.2 a).

Although not directly obvious from Figure 3.3–Figure 3.8, (or the later figures in this chapter), the treeline vegetation stature profile also appeared to be heavily influenced by the browsing of feral goats (*Capra hircus*). Whilst conducting the surveys, it was noted that the abundance of goats at the treeline was variable around the mountain, with (for example) goats being more common near The Plateau than at North Egmont. Where goats congregated, the understory vegetation tier was more sparse with fewer seedlings, saplings and shrubs, compared with areas where there was little goat sign present (pers. obs.). Goats were also thought to have an effect on vegetation composition, which is discussed at the end of this chapter.

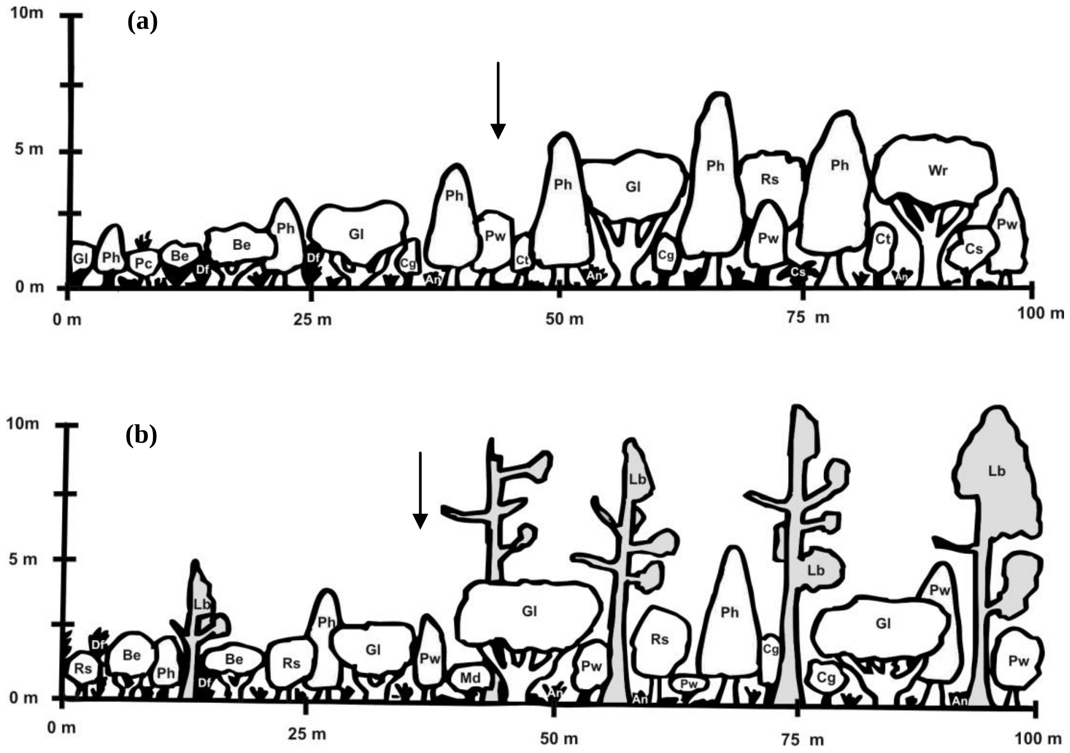

Figure 3.2: Stylised vegetation profiles through the treeline ecotone on Mt Taranaki showing contrasting transitions where (a) *Libocedrus* is absent (i.e., areas severely affected by the Burrell Lapilli), and (b) where *Libocedrus* is present (i.e., areas not heavily affected by the Burrell Lapilli). Approximate treeline position in each profile is indicated by an arrow. Lb *Libocedrus bidwillii*, Ph *Podocarpus hallii*, Wr *Weinmannia racemosa*, Gl *Griselinia littoralis*, Be *Brachyglottis elaeagnifolia*, Pw *Pseudowintera colorata*, Rs *Raukaua simplex*, Pc *Pseudopanax colensoi*, Cg *Coprosma grandifolia*, Ct *Coprosma tenuifolia*, Md *Myrsine divaricata*, Df *Dracophyllum filifolium*, An *Astelia nervosa*. Cs *Cyathea smithii*.

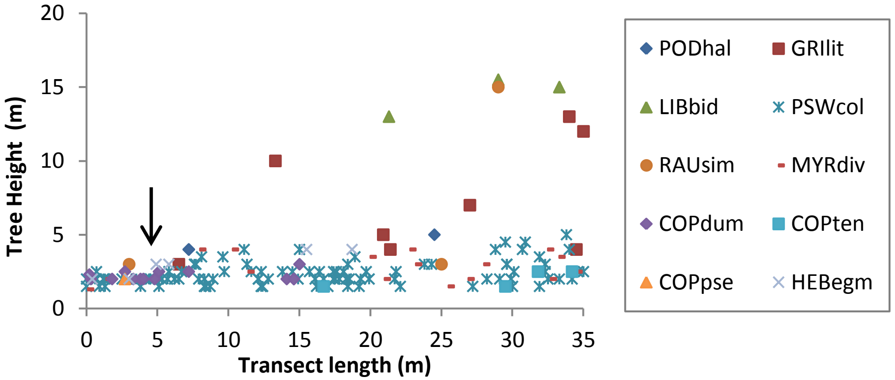

Figure 3.3: Heights of species ≥2 cm dgh along the belt transect through treeline vegetation near Brames Falls on Mt Taranaki. Elevation increases towards the left. Black arrow indicates approximate position of the treeline (1095 m asl).

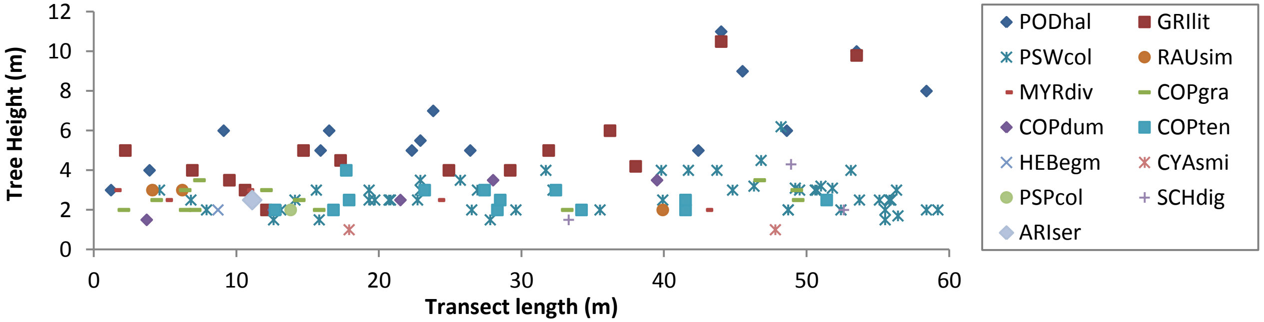

Figure 3.4: Heights of species ≥2 cm dgh along the belt transect through treeline vegetation near Dawson Falls on Mt Taranaki. Elevation increases towards the left. Transect approaches but does not extend through the treeline position.

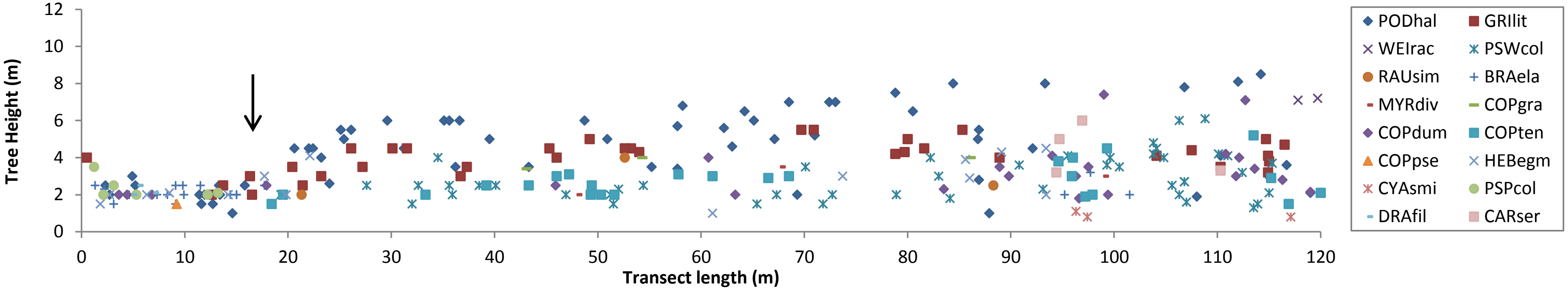

Figure 3.5: Heights of species ≥2 cm dgh along the belt transect through treeline vegetation near The Plateau on Mt Taranaki. Elevation increases towards the left. Black arrow indicates approximate position of the treeline (1080 m asl).

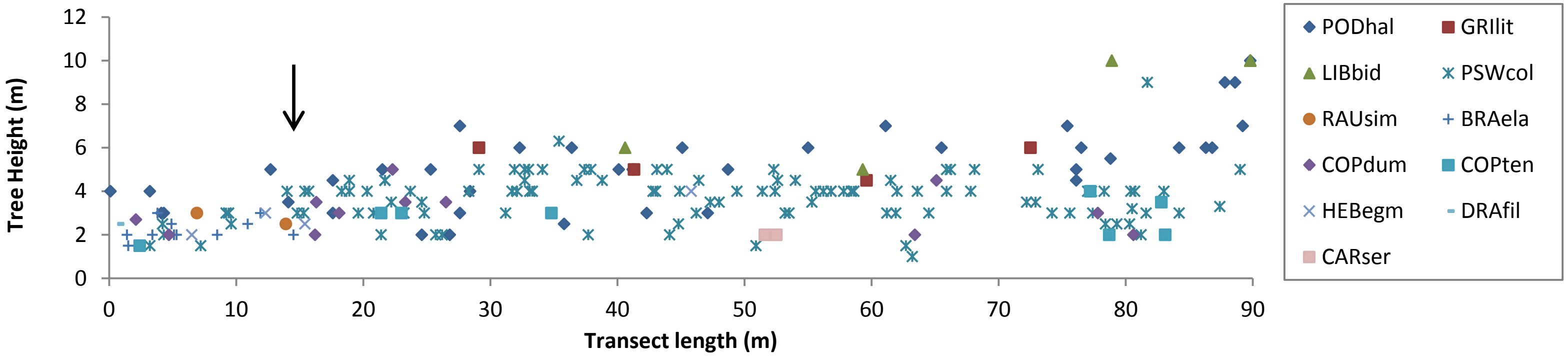

Figure 3.6: Heights of species ≥2 cm dgh along the belt transect through treeline vegetation near Curtis Falls on Mt Taranaki. Elevation increases towards the left. Black arrow indicates approximate position of the treeline (1065 m asl).

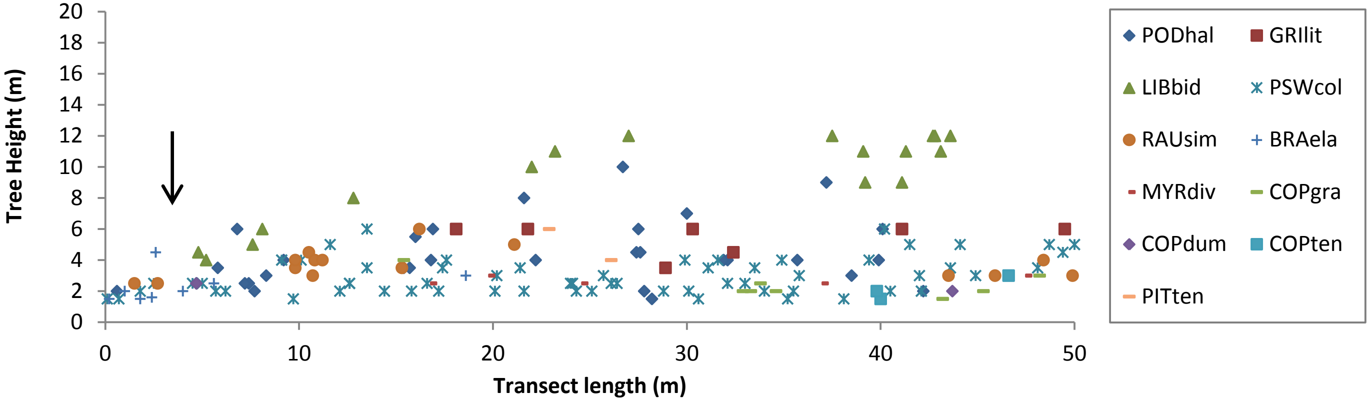

Figure 3.7: Heights of species ≥2 cm dgh along the belt transect through treeline vegetation near North Egmont on Mt Taranaki. Elevation increases towards the left. Black arrow indicates approximate position of the treeline (1105 m asl).

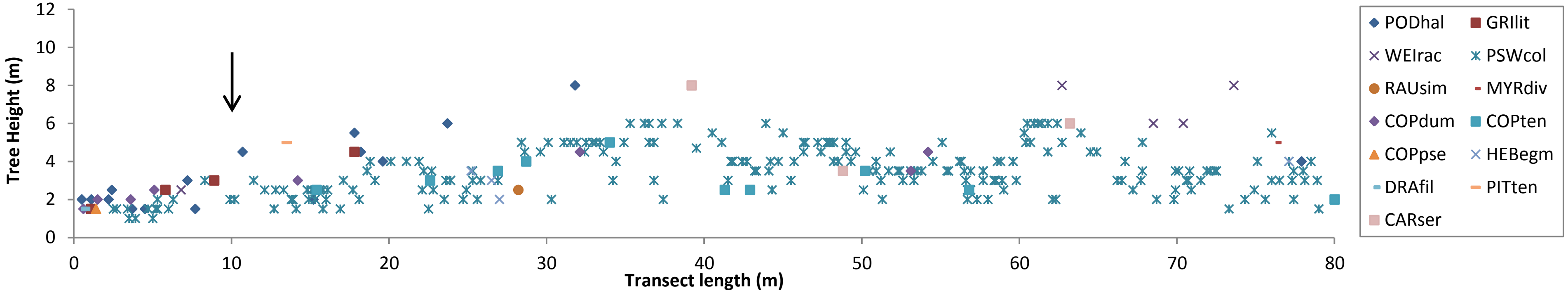

Figure 3.8: Heights of species ≥2 cm dgh along the belt transect through treeline vegetation near Kokowai Track on Mt Taranaki. Elevation increases towards the left. Black arrow indicates approximate position of the treeline (1025 m asl).

3.3.5 Composition and spatial configuration

Because of the narrow (5 m) width of the belt transects, and the large number of quadrats already analysed in Chapter 2, densities and basal areas for species recorded in the belt transects were not calculated. However, all stems ≥2 cm dgh in each transect were able to be mapped; with each species coded by colour and each stem presented at a size proportionally scaled to its actual diameter. These types of figures visually summarise the majority of the data collected in the belt transect survey, and when considered in combination with the tree height figures in Section 3.3.4, a three-dimensional (tree height, tree diameter, tree position) summary of the vegetation transition through treeline is provided. To enable a further layer of detail, changes in the densities of saplings in 10 m divisions along each transect have also been graphed. Using this combined information, a description is given for the vegetation observed in each of the six belt transects.

Brames Falls

The treeline vegetation transition near Brames Falls, outside the Burrell Lapilli distribution, is summarised in Figure 3.3, Figure 3.9 and Figure 3.10. The lower elevations of this transect were characterised by several large, evenly dispersed *Libocedrus* and *Griselinia*, emergent over an understory of mostly *Pseudowintera*, *Myrsine divaricata* and *Coprosma tenuifolia*. The stem map suggests that some of the larger individuals, particularly those of *Libocedrus* and *Griselinia*, have had the effect of suppressing (or excluding) both the number and the size of stems immediately around them. Consequently, areas further away from these larger individuals appear to display higher densities (clusters) of smaller sized stems. In particular, clustering of *Pseudowintera* was apparent in multiple locations across the length of the transect, while the larger (canopy) trees were dispersed more evenly. With increasing elevation along the transect, these large emergent species disappeared, *Pseudowintera* remained common in the understory, and *Myrsine divaricata* was progressively replaced by *Coprosma dumosa*. Above the treeline position, vegetation was dominated by mostly *Pseudowintera*, *Coprosma dumosa* and *Hebe “egmontiana”*. A cluster of *Coprosma dumosa* was also apparent, and *Hebe “egmontiana”* appeared to be excluding stems from close proximity, probably a result of its sprawling branches and canopy. Other less common tree species present in this transect included *Podocarpus*, *Coprosma pseudocuneata* and *Raukaua*. Individuals of *Raukaua* were found in very close proximity to another stem, which is attributed to this species having either established epiphytically, or utilising support from another tree to gain access to the canopy (pers. obs.). Several large patches of ground were found to be void of trees and not associated with a large canopy tree (according to the stem map), but examination of sapling densities shows that despite an absence of larger stems, saplings were in fact regenerating abundantly in some of these spaces. The most abundant sapling was *Pseudowintera*, which although present throughout the length of the transect, decreased markedly in number towards the treeline position. Other saplings were sporadic in distribution along the transect, with *Coprosma tenuifolia*, *Coprosma dumosa*, and *Raukaua* being the most common species. In the seedling/groundcover class, the most common species were *Pseudowintera*, *Blechnum montanum*, *Brachyglottis*, *Raukaua* and *Astelia nervosa*.

Dawson Falls

The treeline vegetation transition near Dawson Falls, where Burrell Lapilli was 15 cm thick, is summarised in Figure 3.4, Figure 3.11 and Figure 3.12. This transect did not extend fully through to the treeline position. The vegetation transition observed was different to that at Brames Falls, and was characterised by large, evenly dispersed *Podocarpus* and *Griselinia*, over an understory of mostly *Pseudowintera* and *Coprosma tenuifolia*. Overall, all stems in the Dawson Falls transect were more dispersed and not spaced as closely (i.e., were at lower densities) compared with the Brames Falls transect (potentially as a result of goat browsing), and the maximum stem size was also smaller in comparison (107 cf. 153 cm dgh) which could be related to the suppression of the largest tree species (*Libocedrus*) by the Burrell eruption. As observed in the Brames Falls transect, the larger trees here appeared to partially suppress the number of other stems in immediate proximity, and small clusters of *Pseudowintera* were present in locations away from larger canopy trees. Other less common species included *Aristotelia serrata*, *Myrsine divaricata*, *Coprosma dumosa*, *Hebe "egmontiana"*, *Pseudopanax colensoi*, *Raukaua*, *Cyathea smithii*, and *Schefflera digitata*. The few *Raukaua* individuals in this transect were solitary, and not directly associated with another supporting tree as noted at the Brames Falls transect. Several large areas void of trees and not associated with a large canopy species were again found to have a number of saplings present. With regards to saplings, *Pseudowintera*, *Coprosma grandifolia*, and *Coprosma tenuifolia* were distributed almost continuously along the length of the transect, though *Pseudowintera* saplings reduced in abundance at the upper limits of the transect in a similar way to the Brames Falls transect, indicating the treeline position was close by. No strong trends were apparent with the other saplings species. The most abundant seedlings/ground cover species were *Pseudowintera*, *Blechnum fluviatile, Polystichum vestitum, Astelia nervosa* and *Asplenium bulbiferum*.

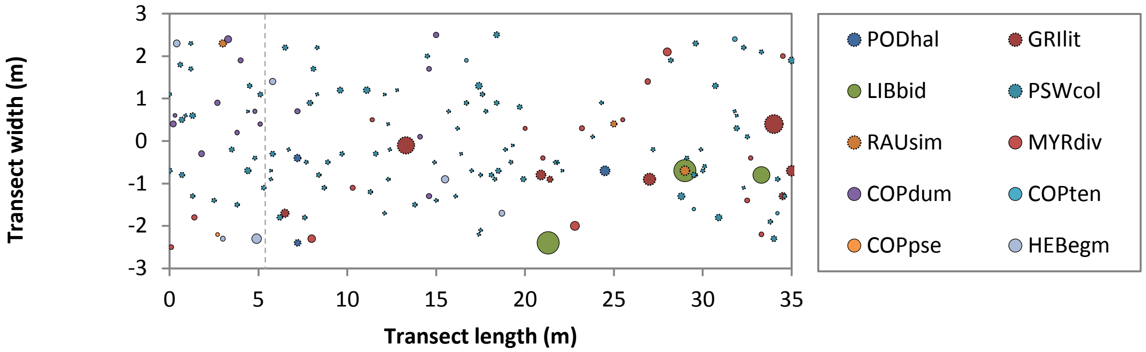

Figure 3.9: Stem map of species ≥2 cm dgh in the belt transect through treeline vegetation near Brames Falls on Mt Taranaki. Stem sizes are proportionally scaled, with the largest stem 153 cm dgh. Elevation increases towards the left. The dashed line indicates the approximate position of the treeline.

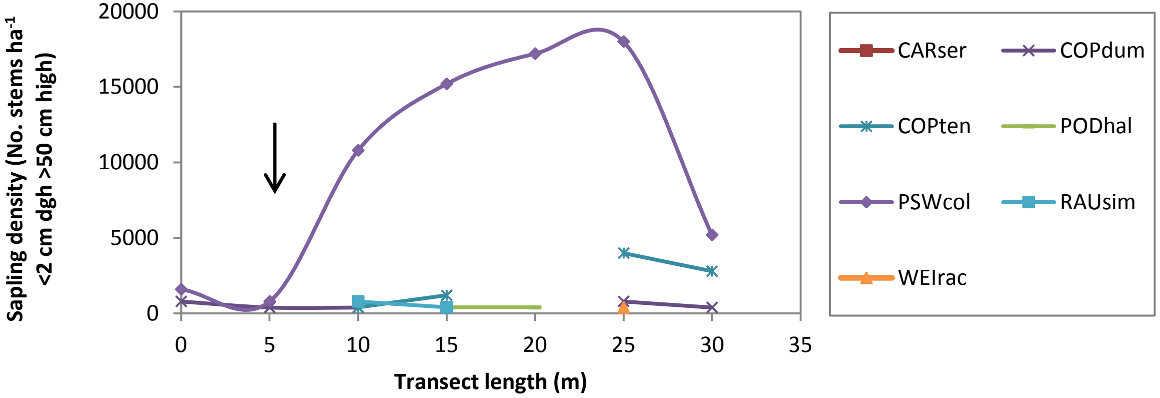

Figure 3.10: Sapling density (No. stems ha^{-1} <2 cm dgh >50 cm high) change along the belt transect through treeline vegetation near Brames Falls on Mt Taranaki. Black arrow indicates approximate position of the treeline.

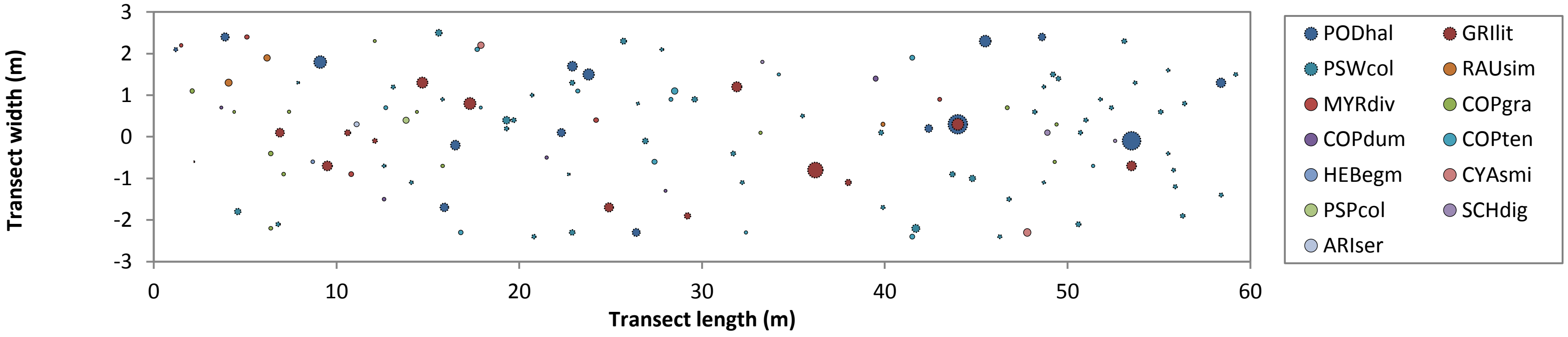

Figure 3.11: Stem map of species ≥2 cm dgh in the belt transect through treeline vegetation near Dawson Falls on Mt Taranaki. Stem sizes are proportionally scaled, with the largest stem 107 cm dgh. Elevation increases towards the left. The transect did not extend all the way to the treeline position.

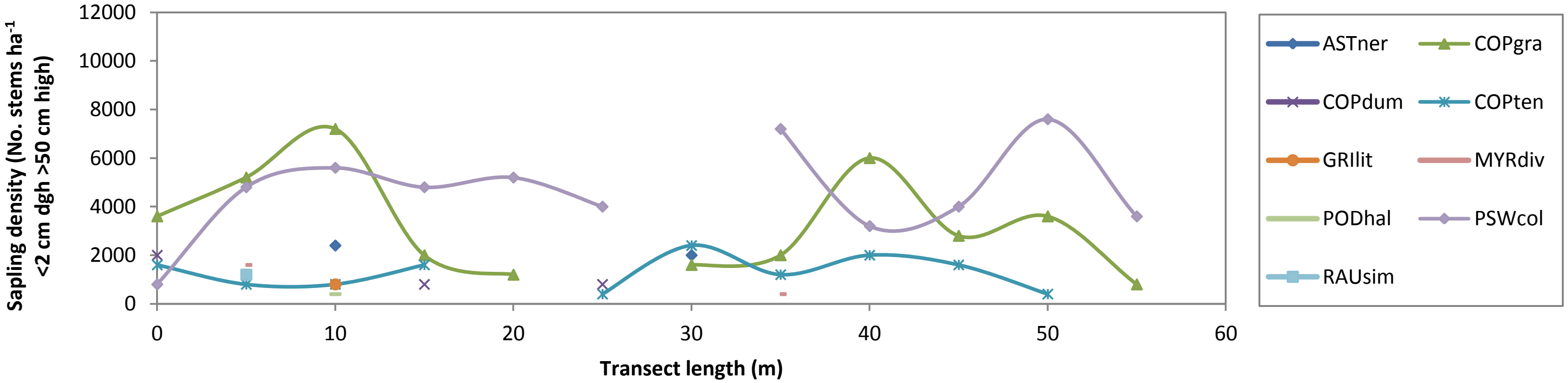

Figure 3.12: Sapling density (No. stems ha^{-1} <2 cm dgh >50 cm high) change along the belt transect through treeline vegetation near Dawson Falls on Mt Taranaki. The transect did not extend all the way to the treeline position.

The Plateau

The treeline vegetation transition near The Plateau, where Burrell Lapilli was 30.5 cm thick, is summarised in Figure 3.5, Figure 3.13 and Figure 3.14. This transect was almost identical in composition to the Dawson Falls transect, with mixed *Podocarpus* and *Griselinia* emergent over *Pseudowintera* and *Coprosma tenuifolia*. Both *Carpodetus serratus* and *Weinmannia* were only present at the lower elevations of this transect, while *Griselinia*, *Pseudopanax colensoi*, *Hebe "egmontiana"* and *Brachyglottis* were common above the treeline position. Other tree species present here were *Raukaua*, *Myrsine divaricata*, *Coprosma dumosa*, *Coprosma pseudocuneata*, *Coprosma grandifolia*, *Cyathea smithii* and *Dracophyllum filifolium*. The highest densities of smaller stems in this transect were found in clusters with multiple species, and positioned away from larger trees; the larger trees (mostly *Griselinia* and *Podocarpus*) appeared to be less evenly dispersed than in the other transects, and grouped together with their own kind in several places; in doing so, they excluded small stems immediately around them altogether. Several patches void of any trees were in fact found to have a number of saplings present, particularly *Coprosma tenuifolia* and *Pseudowintera*. Most of the *Raukaua* here were again directly associated with another structurally supporting species. Densities of sapling *Coprosma tenuifolia* and *Pseudowintera* decreased in number towards the treeline, and *Griselinia littoralis* saplings increased above the treeline. As with the Dawson Falls transect, stem densities at The Plateau were also lower than the Brames Falls transect. There were also fewer small sized (2–5 cm dgh) stems measured, with most stems being of a larger size, probably as a result of selective removal of smaller stems by goats. The most abundant species in the seedling/ground cover class were *Pseudowintera*, *Polystichum vestitum, Coprosma tenuifolia, Blechnum fluviatile, Astelia nervosa* and *Microlaena avenacea*.

Curtis Falls

The treeline vegetation transition near Curtis Falls, where Burrell Lapilli was 15 cm thick, is summarised in Figure 3.6, Figure 3.15 and Figure 3.16. The vegetation composition in this transect was intermediate to that observed in Brames Falls and The Plateau transects. Evenly dispersed *Podocarpus, Griselinia,* and *Libocedrus* were emergent above clusters of *Pseudowintera* and *Coprosma tenuifolia*. Above the treeline, *Brachyglottis*, *Hebe "egmontiana"* and *Coprosma dumosa* became more common. Other tree species included *Raukaua*, *Dracophyllum filifolium*, and *Carpodetus serratus*. As in the other groups, the large *Griselinia* and *Libocedrus* appeared to exclude other stems around them, although there was a greater number of smaller sized stems present than at The Plateau, some of which formed very tight clusters of mixed *Coprosma tenuifolia* and *Pseudowintera*. Saplings of *Pseudowintera* were common throughout, with saplings of *Griselinia, Raukaua, Myrsine divaricata* and *Podocarpus* increasing above the treeline position. Common seedling/groundcover species included *Pseudowintera*, *Polystichum vestitum*, *Blechnum fluviatile*, *Microlaena avenacea* and *Coprosma tenuifolia*.

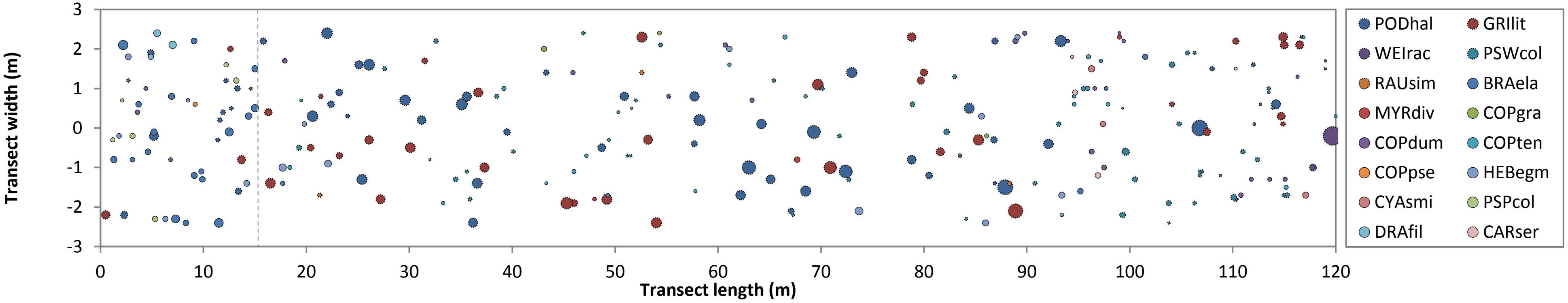

Figure 3.13: Stem map of species ≥2 cm dgh in the belt transect through treeline vegetation near The Plateau on Mt Taranaki. Stem sizes are proportionally scaled, with the largest stem 144 cm dgh. Elevation increases towards the left. The dashed line indicates the approximate position of the treeline.

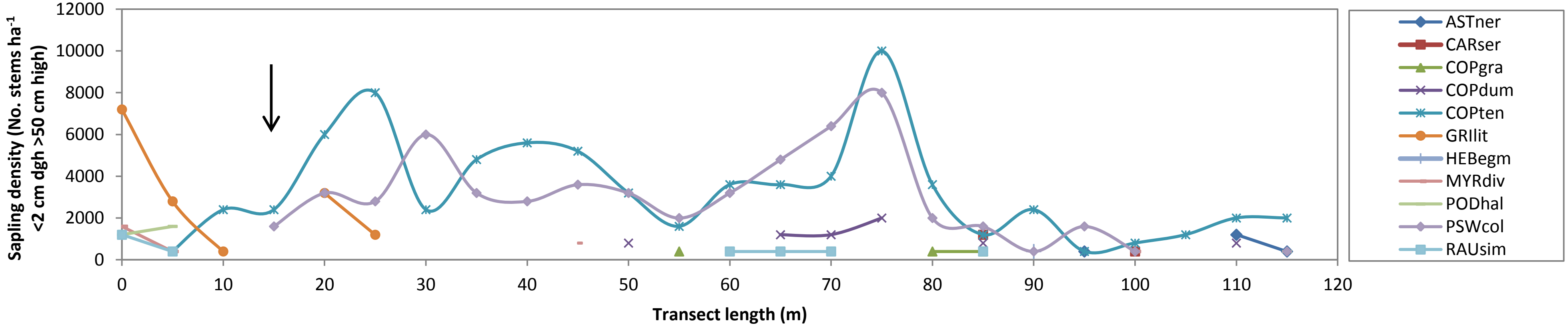

Figure 3.14: Sapling density (No. stems ha^{-1} <2 cm dgh >50 cm high) change along the belt transect through treeline vegetation near The Plateau on Mt Taranaki. Black arrow indicates approximate position of the treeline.

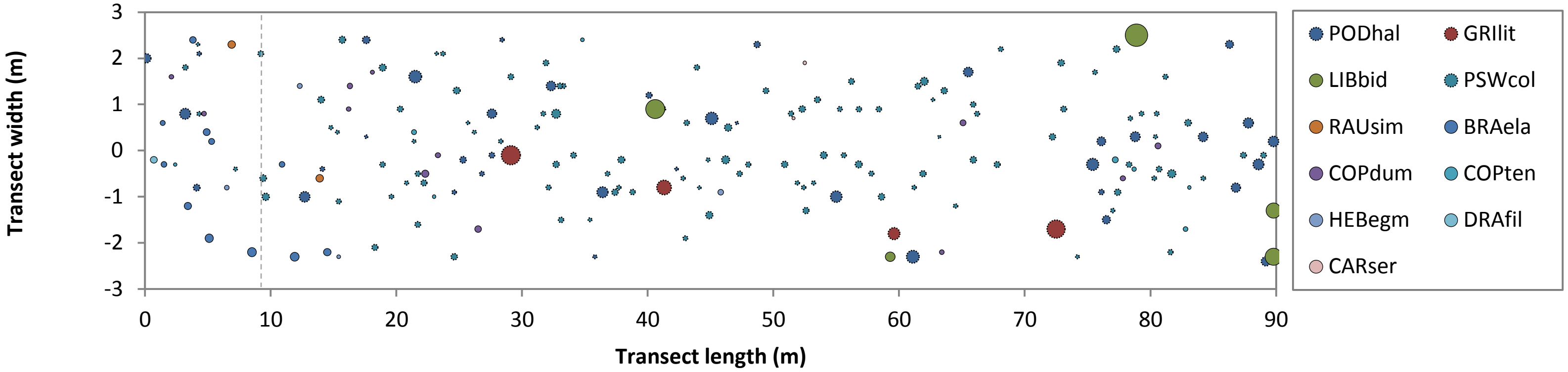

Figure 3.15: Stem map of species ≥2 cm dgh in the belt transect through treeline vegetation near Curtis Falls on Mt Taranaki. Stem sizes are proportionally scaled, with the largest stem 132 cm dgh. Elevation increases towards the left. The dashed line indicates the approximate position of the treeline.

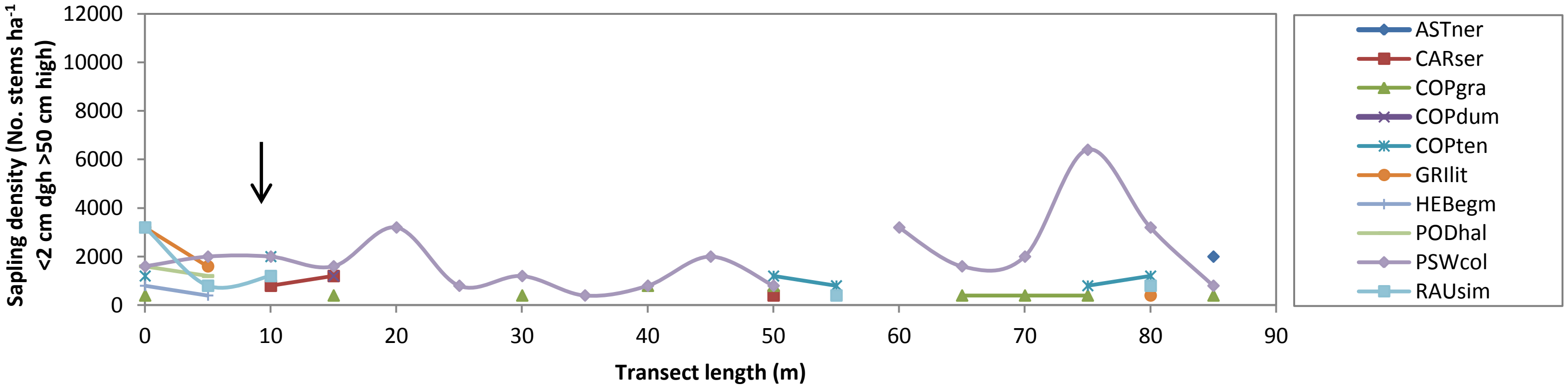

Figure 3.16: Sapling density (No. stems ha^{-1} <2 cm dgh >50 cm high) change along the belt transect through treeline vegetation near Curtis Falls on Mt Taranaki. Black arrow indicates approximate position of the treeline.

North Egmont

The treeline vegetation transition near North Egmont, where Burrell Lapilli was 7.5 cm thick, is summarised in Figure 3.7, Figure 3.17 and Figure 3.18. In this transect, *Libocedrus* was the dominant species, emergent over a canopy of mostly *Griselinia* and *Podocarpus*. Three clusters of *Libocedrus* with near-identical diameters were present along the transect, while *Griselinia* and *Podocarpus* were distributed more evenly. This transect also displayed some evidence for exclusion of species around the larger trees, but clusters of smaller stems (away from large trees) were less pronounced than in the other transects. The understory was dominated by *Pseudowintera*, with lesser amounts of *Raukaua*, *Coprosma grandifolia* and *Coprosma tenuifolia*. Above the treeline position, *Brachyglottis* became more common. Other tree species included *Myrsine divaricata*, *Pittosporum tenuifolium* and *Coprosma dumosa*. Saplings of *Pseudowintera*, *Coprosma grandifolia* and *Coprosma tenuifolia* were abundant throughout the transect, and unlike the other transects, the number of *Pseudowintera* saplings did not decrease significantly above the treeline. The majority of *Podocarpus* saplings were found above the treeline position. The seedling/ground cover class was dominated by *Pseudowintera*, *Polystichum vestitum*, *Griselinia* and *Astelia nervosa*.

Kokowai Track

The treeline vegetation transition near the Kokowai Track is summarised in Figure 3.8, Figure 3.19 and Figure 3.20. In contrast to the adjacent North Egmont transect, no *Libocedrus* was present at this site, despite Burrell Lapilli being only 2.5 cm thick. *Libocedrus* was perhaps suppressed here by another earlier eruption/debris flow, or by the weather patterns at this site which are concentrated between Mt Taranaki and the Pouakai Range. At the lower elevations of this transect, large and evenly dispersed *Weinmannia* were emergent along with several large *Carpodetus serratus*, over an almost pure stand of small sized *Pseudowintera*. The maximum stem size (78 cm dgh) in this transect was smaller than in the other transects, and there were also fewer empty areas void of trees. *Weinmannia* appeared to suppress the number of *Pseudowintera* in close proximity, and although *Pseudowintera* was abundant along the length of the transect, several particularly dense clusters were apparent. Higher in elevation, *Podocarpus* became more common in the canopy, and a single large *Pittosporum tenuifolium* was found. Above the treeline, *Coprosma dumosa* increased in number. Other species present included *Coprosma tenuifolia*, *Coprosma pseudocuneata*, *Raukaua*, *Dracophyllum filifolium*, and *Myrsine divaricata*. Along the transect, saplings of *Pseudowintera*, *Coprosma tenuifolia* and *Hebe "egmontiana"* were common, with *Coprosma dumosa*, *Podocarpus*, and *Pseudowintera* saplings increasing above the treeline position. In the seedling/ground cover class, *Pseudowintera*, *Microlaena avenacea*, *Blechnum fluviatile* and *Astelia nervosa* were abundant.

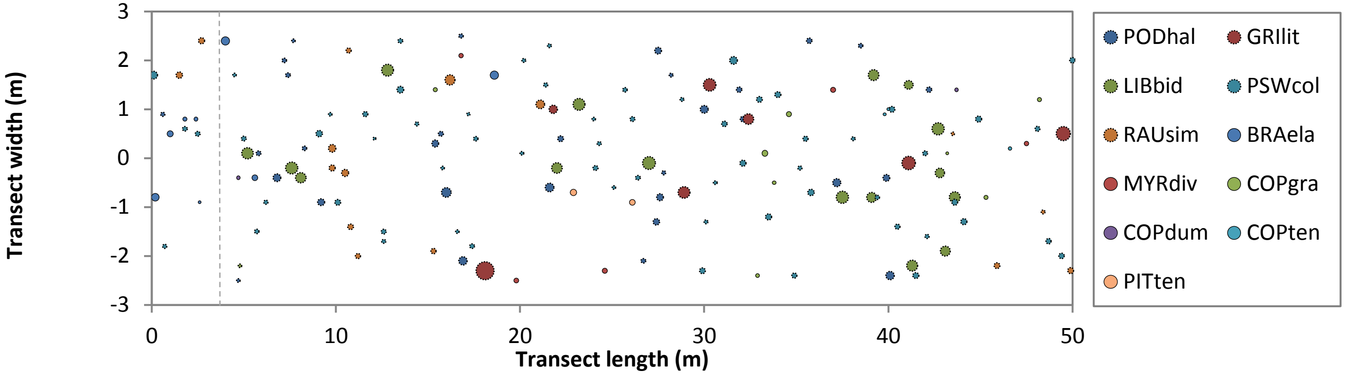

Figure 3.17: Stem map of species ≥2 cm dgh in the belt transect through treeline vegetation near North Egmont on Mt Taranaki. Stem sizes are proportionally scaled, with the largest stem 88 cm dgh. Elevation increases towards the left. The dashed line indicates the approximate position of the treeline.

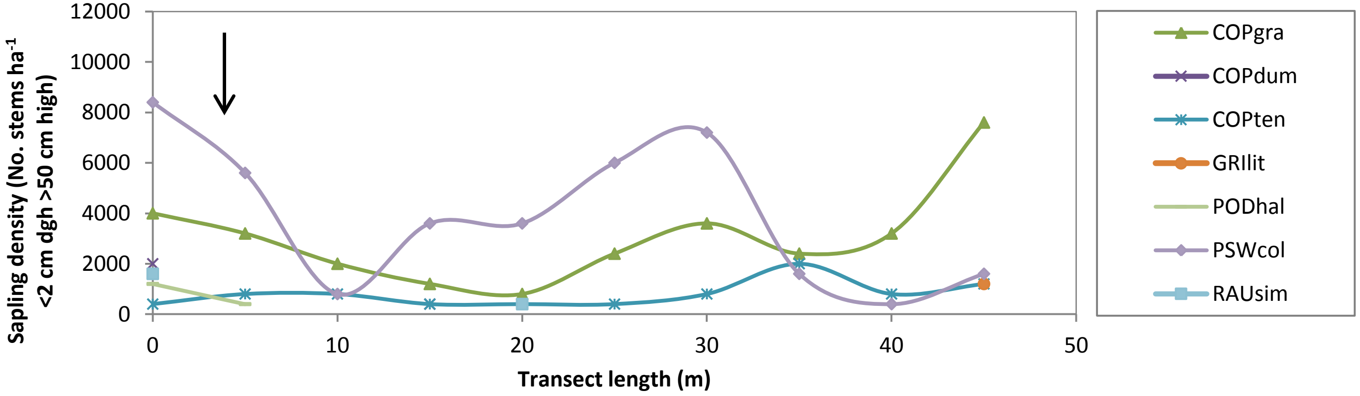

Figure 3.18: Sapling density (No. stems ha^{-1} <2 cm dgh >50 cm high) change along the belt transect through treeline vegetation near North Egmont on Mt Taranaki. Black arrow indicates approximate position of the treeline.

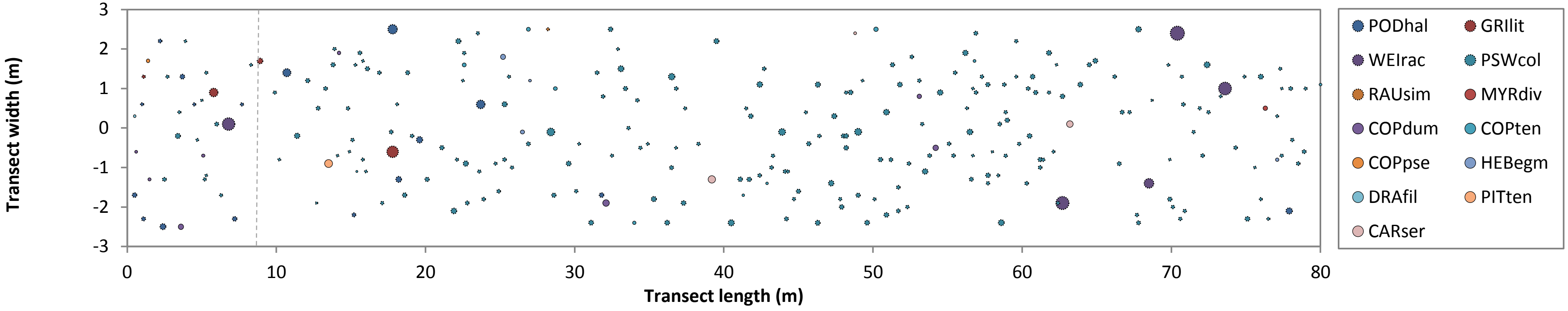

Figure 3.19: Stem map of species ≥2 cm dgh in the belt transect through treeline vegetation near Kokowai Track on Mt Taranaki. Stem sizes are proportionally scaled, with the largest stem 78 cm dgh. Elevation increases towards the left. The dashed line indicates the approximate position of the treeline.

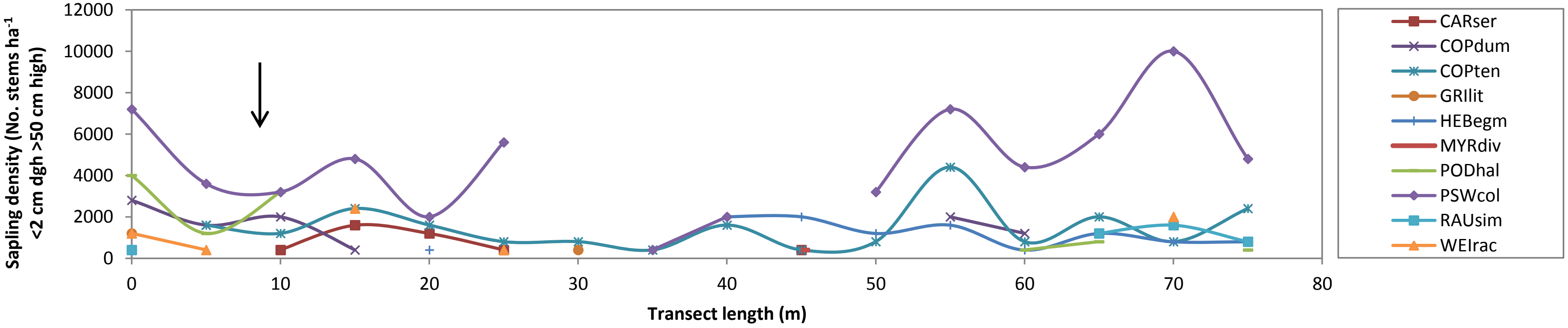

Figure 3.20: Sapling density (No. stems ha^{-1} <2 cm dgh >50 cm high) change along the belt transect through treeline vegetation near Kokowai Track on Mt Taranaki. Black arrow indicates approximate position of the treeline.

3.4 Discussion

As well as illustrating the change in composition, stature and spatial configuration that occurs across the treeline ecotone, this belt transect survey has indicated that the treeline ecotone is itself variable across the Burrell Lapilli distribution around Mt Taranaki. The changes in species composition that occur with increased elevation on Mt Taranaki are already well documented, and have been discussed comprehensively by Clarkson (1977, 1981, 1986) in previous studies, and are thus not repeated in this discussion. The present study (Chapter 2) has demonstrated that treeline composition varies significantly across the Burrell Lapilli distribution. It is these differences in composition which subsequently determine the two contrasting stature transitions found to occur across the treeline ecotone.

At the treeline elevation, *Libocedrus*, growing most abundantly in areas where the effects of the Burrell Lapilli were minor, appears to be capable of growing much taller than *Podocarpus*, a species which was more common where the effects of the eruption were severe. These differences in height could potentially relate to a difference in the upper altitudinal limit of the two species, with *Libocedrus* being more resilient than *Podocarpus*. If the upper altitudinal limits of these species are the same, then physiological differences could explain why *Libocedrus* is more capable of attaining a taller stature than *Podocarpus* around the treeline position. Clarkson’s (1977) data shows that little difference is likely to exist between the upper altitudinal limits of these species, and thus a physiological explanation may be most appropriate. Furthermore, On Mt Hauhungatahi, central North Island, the upper altitudinal limit of these two species is also very similar, though *Libocedrus* becomes dominant over *Podocarpus* as the upper altitudinal limit is approached (Druitt et al. 1990), which may suggest it is more competitive at this position.

Across the treeline ecotone, practically all the species present displayed a reduction in height, which, with the possible exception of *Nothofagus* spp., is the typical response expected for most indigenous trees approaching their upper altitudinal limits (Wardle 1973). Vegetation along altitudinal gradients worldwide exhibits this same trend (Körner 2003). As well as height, the maximum tree diameter also reduced with increased elevation, which would probably relate to physiological restrictions to plant growth at this altitude (Wardle 1971). This could be expected to be reflected in total basal area; with Druitt et al. (1990) also recognising a reduction in total basal area with altitude on Mt Hauhungatahi, central North Island. The pattern observed in the spatial configuration of stems on Mt Taranaki, whereby large trees suppressed/excluded the number and size of those immediately around them, is a phenomenon which is also often reported; and could relate to any number of factors, including reduced light levels, different soil properties (e.g., pH, nutrients), litter thickness, or allelopathic effects differing below a large tree (Beatty 1984). The observed clustering of (mostly) *Pseudowintera* and *Coprosma tenuifolia* is potentially their preference for a microsite of some sort (e.g., a canopy opening), or their seed dispersal and regeneration occurring directly around a parent plant. A statistical analysis of spatial configuration in combination with the field-measurement of microsite variables was beyond the scope of this study, but would be a valuable aid to understanding the patterns observed in the stem maps produced here.

Feral goats have been present on Mt Taranaki for a century, despite extensive culling efforts by the Government (Husheer 2006). Browsing by goats not only affects the stature of the vegetation (by browsing out seedlings, shrubs and other vegetation within their reach), but also the composition of the vegetation. Goats are known to preferentially browse on palatable species, and avoid unpalatable ones, which can have a considerable impact on species composition and the successional trajectory of the vegetation (Smale & Smale 2003). The most palatable species to goats at the treeline ecotone (and thus most heavily browsed) include *Griselinia*, *Coprosma* spp., *Raukaua*, *Pseudopanax colensoi*, *Schefflera digitata*, *Weinmannia*, *Astelia nervosa*, and *Fuchsia*; while unpalatable species include *Pseudowintera*, *Podocarpus*, *Libocedrus*, *Myrsine salicina* and *Microlaena avenacea* (pers. obs.; Husheer 2006). The unpalatably of these species gives potential for them to become more prolific, and certainly *Pseudowintera* is overwhelmingly abundant on the mountain. Although this is in part attributed to goats, Clarkson (1977) notes that early botanists listed this species as being very common too, well before goats became prevalent on the mountain. Smale & Smale (2003) suggest that *Pseudowintera* may alter soils in ways inimical to some potential successors, which could potentially explain both its abundance prior to goat introduction, as well as its clustering tendency. *Pseudowintera* and

Microlaena were among the most common seedling/ground cover species recorded in the survey, for which goats must be responsible to a degree.

On Mt Taranaki, *Griselinia* and *Weinmannia* are capable of epiphytic regeneration (pers. obs.), so can partially avoid browsing by goats, though this in itself has the potential to change the vegetation profile, as in the past (prior to the introduction of goats) these species may have had much higher success establishing on the forest floor. Most other palatable species are not capable of epiphytic growth, so their regeneration has more than likely been affected by goats. Atkinson (1964) blamed goats for the progressive replacement of palatable *Weinmannia* by unpalatable *Myrsine salicina* and *Pseudowintera* on Mt Taranaki, and believed they were preventing further *Weinmannia* regeneration. Introduced brush-tailed possums (*Trichosurus vulpecula*), also common on the mountain, have different browsing preferences to goats, preferring to feed there on *Podocarpus*, *Libocedrus*, *Weinmannia* and *Metrosideros robusta*. It is thought that *Libocedrus* is browsed by possums in proportionally smaller amounts than *Podocarpus*, but *Podocarpus* is capable of more rapid foliar recovery than *Libocedrus*, which has poorer resprouting capabilities (Rogers 1997; Husheer 2006). It could be possible that following mechanical damage by tephra fall, the same interspecific differences in resprouting capabilities could be true, and thus this provides another explanation for why *Libocedrus* has been suppressed from the areas worst affected by the Burrell eruption. The effect that possums have had on composition and/or stature was not directly obvious from this study, and no possum browse was specifically noted (Mt Taranaki is subject to periodic aerial poison drops targeting possums). But, as suggested by Smale & Smale (2003) for Waihaha forest, “the greatest contemporary influence on successional pathways is introduced herbivores”; the same would undoubtedly be true for Mt Taranaki, particularly considering the abundance of goats there.

Because of the non-*Nothofagus* treeline and the history of volcanic disturbance on the western slopes of Mt Hauhungatahi, central North Island, it represents a good site with which to compare Mt Taranaki’s treeline floristics. There is a greater number of woody species at the treeline ecotone on Mt Hauhungatahi compared with Mt Taranaki (c. 50 cf. c. 30 spp.). Taxa shared between the sites include *Alseuosmia*, *Aristotelia*, *Carpodetus*, *Coprosma*, *Cyathea*, *Dracophyllum*, *Fuchsia*, *Gaultheria*, *Griselinia*, *Hebe*, *Libocedrus*, *Myrsine*, *Pseudopanax*, *Podocarpus*, *Pseudowintera*, *Raukaua*, and *Weinmannia*. However, in comparison with Mt Hauhungatahi, Mt Taranaki treeline lacks *Cyathodes*, *Halocarpus*, *Neomyrtus*, *Phyllocladus*, *Nothofagus* (though *Nothofagus* does not form a treeline at Mt Hauhungatahi) and the diversity seen with *Coprosma* and *Hebe* genera. Exotic treeline species *Pinus contorta* (North American) and *Eucalyptus pauciflora* (Australian) found on Mt Hauhungatahi are also fortunately absent from Mt Taranaki (Druitt et al. 1990). Clarkson (1986) has attributed the absence of many species on Mt Taranaki to its isolation from other mountains combined with an ongoing history of volcanic disturbance.

Chapter Four: Demography and light requirements of key treeline species

4.1 Introduction

A forests disturbance regime is an important determinant of its composition and structure (Ogden et al. 1991). Chapters 2 and 3 have demonstrated how the composition and structure of treeline vegetation on Mt Taranaki is variable across the AD 1655 Burrell Lapilli distribution. To further understand and explain the reasons for these differences, this chapter examines the demography and light requirements of key species found at the treeline. Demographic studies on population structure (e.g., diameter or age frequency distributions) are a useful way of elucidating past and present regeneration (Lusk & Ogden 1992). It is common to differentiate three main types of regeneration patterns in forest trees, each of which is related to both the individual light requirements (i.e., shade tolerance) of the species, and the scale of the disturbance (Veblen & Stewart 1982; Ogden 1985; Lusk & Ogden 1992).

1. ‘Catastrophic regeneration’, refers to a population which all establishes at the same time as a result of infrequent massive large-scale disturbances such as a fire, landslide or windthrow. Population structures are characterised by a cohort of stems of a similar size (i.e., even-aged), and will often display discontinuities as a result of the infrequency of regeneration events. Species that exhibit catastrophic regeneration are usually highly light demanding (i.e., shade-intolerant).
2. ‘Gap-phase’ regeneration refers to regeneration in smaller, more frequently occurring gaps, caused by things such as tree falls; consequently, population structures display fewer discontinuities. Although species exhibiting gap-phase regeneration can be light demanding, they are probably less-so than species exhibiting catastrophic regeneration.
3. ‘Continuous regeneration’ refers to the growth of shade-tolerant seedlings and saplings beneath canopies lacking obvious gaps, so that there is a continuous replacement of the older dying trees. This results in population structures which are continuous, with all sizes/ages represented.

Given that the differences between these regeneration strategies are strongly related to light requirements, it is necessary to quantify species shade-tolerance differences. Lusk et al. (2009) notes that ecologists have often debated the most meaningful way to quantify shade-tolerance; and in the past, assessments of New Zealand tree species' relative shade tolerance have depended on indirect evidence from population structures, and on subjective or semi-quantitative assessments alone. Although many measures of shade-tolerance exist, comparing the range of light environments naturally occupied by juveniles of a species is a technique which has been successfully utilised in other studies (e.g., Davies 1998; Lusk & Reich 2000; Lusk et al. 2008, 2009), and is therefore used in the present study to elucidate light requirement differences between key species at the treeline.

It is known that the Burrell eruption would have, in places, inflicted considerable damage to the treeline vegetation on Mt Taranaki, consequently opening up the canopy by mechanical and chemical striping of vegetation (see Section 1.2.5). As a result, the light environment on the forest floor would have been increased in places. The amount of canopy damage sustained could be assumed to be related to the thickness of the Burrell Lapilli on the ground. For example, it is likely that in areas where the Burrell Lapilli approaches its maximum thickness of 40 cm, vegetation damage would have been extensive, and large light gaps would have been created as trees succumbed to the eruption. With higher light environments, more light demanding species which may otherwise have been suppressed under closed-canopy vegetation, could potentially colonise and/or become more dominant, thus altering the composition and successional trajectory of the vegetation. Such species may have been locked in a state of stasis/inactivity in either the seed bank or juvenile stage prior to the eruption, with light levels being insufficient for them to regenerate and grow to their maximum potential; or alternatively, they may not have been present in the vegetation at all, and thus opportunistically colonised into the new light environments created on the forest floor by the eruption, perhaps with the aid of other facilitating species. Already, it is known that light demanding *Kunzea* and *Fuchsia* presently grow in montane forest affected by the Burrell eruption, indicating that well-lit sites have been available for their establishment and continued growth (Druce 1966); while the abundance of *Coriaria* pollen in the sediment record suggests it may have been an important facilitating species soon after the eruption (McGlone et al. 1988).

However, there remains potential for better understanding what role the light requirements of key treeline species have played in shaping the current vegetation pattern at the treeline of Mt Taranaki. Here, I examine population structures (diameter frequency distributions) of key species at the treeline, and quantify light environments presently occupied by their juveniles. The objective is to understand how species may have responded to higher light levels following Burrell Lapilli canopy disturbance. This information will then be used to aid with the explanation of the treeline vegetation pattern.

4.2 Sampling methods

4.2.1 Diameter frequency distributions and estimates of age

Diameter frequency distributions (population structures) for key canopy species *Podocarpus*, *Griselinia*, *Libocedrus* and *Weinmannia* were derived from the quadrat survey data (Chapter 2), and are presented individually for each of the four quadrat groups (i.e., severe, minor, outside, Pouakai Range) as described and justified in Section 2.3.6. All diameter frequency distribution data were scaled to units of stems ha^{-1}, with sapling counts used for the smallest size class, followed by a 2–10 cm dgh class, and then progressive 10 cm dgh increments. Such size classes have been used in other demographic studies of New Zealand trees (e.g., Lusk & Ogden 1992).

In an attempt to relate the population structures of species back to the AD 1655 Burrell eruption, estimated ages were added to some of the size classes. These were based on agreeable diameter:age regressions published for *Podocarpus*, *Griselinia*, and *Weinmannia* from montane forest on both Mt Pureora (Smale & Kimberley 1993) and at Waihaha (Smale & Smale 2003); for *Libocedrus*, data from montane forest on Mt Taranaki was available (Boase 1988). The Mt Pureora and Waihaha sites where diameter:age regressions were determined were slightly below the elevation of the Mt Taranaki treeline, and thus if tree growth is assumed to slow with elevation, as Körner (2003) suggests, regressions may lead to underestimates of tree ages on Mt Taranaki. Furthermore, Smale & Smale (2003) note that diameter:age regressions for *Griselinia* and *Weinmannia* may also underestimate the age of individuals because both these species often have trunks formed by the fusion of descending roots and are capable of prolonging their lifespan by vegetative re-growth. The *Libocedrus* aged at Mt Taranaki by Boase (1988) exhibited a strong diameter:age regression ($r^2 = 0.97$) and thus estimates are probably quite accurate. On Mt Hauhungatahi, Ogden et al. (2005) also reported a strong diameter:age regression ($r^2 = 0.84$) for *Libocedrus* growing at the treeline elevation; with the regression equations being very similar to that from Mt Taranaki. It must be noted however, that overall, these are purely estimates of age only; Ogden (1985) has gone as far as to say "It is wholly unrealistic and very dangerous to assume any relationship between the size of trees and their age, other than the vague principle that the largest trees in a canopy are likely to be old".

4.2.2 Quantifying light requirements (shade tolerance)

Canopy analysers (e.g., Licor Inc.) and hemispherical photography are the two techniques most regularly used for indirectly quantifying light environments and canopy openness in forests, with each having a number of benefits and disadvantages (see Thimonier et al. 2010). Hemispherical photography has been selected in this instance because of the availability of the equipment and its ease of use. A hemispherical photograph maps the size, magnitude and distribution of gaps in the forest canopy in relation to the position at which the photograph was taken (Jarcuska 2008). Distributions of seedlings and saplings at the treeline on Mt Taranaki were quantified in relation to canopy openness measurements using a Nikon Coolpix 995 digital camera with a hemispherical lens adapter (FC-E8 0.21×, Nikon), mounted on a tripod equipped with a levelling bubble. Following the recommendations of Zhang et al. (2005), the built-in light meter of the camera was first used to obtain a reference exposure for open sky conditions at the time of sampling, and photographs were then taken under the canopy with two stops of more exposure than the reference exposure. For example, if the open sky reference was F5.3 (aperture) and shutter speed was 1/1000 s, the correct exposure to use under the canopy was F5.3 and shutter speed 1/250 s. This has the effect of making the sky appear white, and maximises the contrast between the sky and foliage. Photographs were only taken during overcast sky conditions, or near to dawn and dusk when the sun was close to the horizon and not within the camera's field of view.

Canopy openness quantified at random intervals along transects were compared with the presence/absence of common saplings. Sampling was carried out with transects at three main locations in the treeline vegetation near North Egmont, East Egmont and Dawson Falls. Starting from a random position within the treeline vegetation, the direction of the transect was selected with a random bearing, and sample points were located at random intervals 2–10 m apart along the transect. At each sample point, presence/absence data for juveniles of tree and shrub species were recorded in two height classes in a circular plot of 1 m diameter (centred on the sample point). The height classes used were 5–50 cm and 50–150 cm, and only individuals of seedling origin (not basal shoots) were recorded. Although multiple individuals of some species were found within the plots, only presence/absence data was recorded. Both height classes were considered to be associated with the canopy openness measured (photographed) at a height of 1.5 m above the centre of the sampling point. The camera was levelled and aligned with the tripod, in such a way that the direction of north could be determined from the photographs (a requirement for some photo analyses). Photographs were taken even if no juveniles were present within the plot. When transects were obstructed by terrain, either a new random bearing was selected and the transect continued, or else a new starting point was randomly chosen. An effort was made to keep transects within the belt of the treeline ecotone (see Figure 1.1 for definition); when they strayed too far into montane forest or shrubland vegetation, the bearing was altered. Sampling was conducted at the three treeline sites (North Egmont, East Egmont, Dawson Falls), collectively obtaining a total of 360 sample points (i.e., photographs).

Data analysis

The hemispherical photographs were analysed with Gap Light Analyser (GLA) software, Version 2.0 (Frazer et al. 1999). Thresholding of photographs was conducted manually within the GLA software; the threshold determines which pixels in the photograph represent sky and which represent vegetation, and is thus necessary to calculate percentage of canopy openness for each sample site. Percentage canopy openness is simply the percentage of open sky seen from beneath a forest canopy. Percentage canopy openness data were presented on log scale, as used by other authors in similar studies (Kobe et al. 1995; Porter 1999; Lusk et al. 2008, 2009). Log scales, rather than arithmetic scales are used because the difference between (for example) 1% and 2% canopy openness has more physiological significance for plants than the difference between 21% and 22%. The geometric mean was used as the main measure of central tendency, because light environment (percentage canopy openness) distributions were approximately log-normally distributed. The 10th percentile of the distribution of light environments occupied by each species was used as an approximation of the minimum light levels tolerated (referred to as the minimum light requirement), as has been used previously by Lusk et al. (2008, 2009). The inter-quartile ranges of the distributions were used as a measure of niche breadth for each species, with species occupying a wider range of light environments consequently having a wider inter-quartile range. The forest understory light environment is used as a baseline to compare species' distributions against, and was determined by pooling the data from all sample points (regardless of whether a species was present or not). ANOVA and *a posteriori* Fisher LSD tests were used to detect significant differences between the light environments occupied by each species (and the forest understory); as well as light requirement differences between juvenile height classes.

4.3 Results

4.3.1 Population structures (diameter frequency distributions)

Podocarpus hallii

Diameter frequency distributions of *Podocarpus* (Figure 4.1) in the two groups affected by the Burrell eruption (severe and minor) were similar to one another, though subtle differences exist. In the severe group, the almost equal number of stems across the sapling–30 cm size classes suggests that regeneration is ongoing, which is indicative of either a gap-phase or continuous regeneration strategy. The minor group approached more of a cohort distribution, suggesting gap-phase or catastrophic regeneration is possible here. No living *Podocarpus* stems identified within the severe or minor groups were thought to pre-date the Burrell eruption, with the older individuals present appearing to have arisen around 150 years after the eruption. This could possibly indicate that facilitation by a shorter lived species was involved here. In the severe group, several dead snags >140 cm dgh

> (not illustrated in Figure 4.1) were predicted to be around 500 years old; with their state of decay suggesting they may well have died as a result of the eruption, and at the very least, indicates that this species is capable of living for several hundred years longer than the ages of the current populations would suggest.

The diameter frequency distribution of *Podocarpus* in the outside group was different to the other groups, with the number of saplings being much greater than the number of stems in the succeeding size classes. It is possible that either sapling mortality was previously high here, or alternatively, a gap-phase event has recently stimulated a wave of regeneration. Stems >2.0 cm dgh persist in all size classes in the outside group, and the slightly higher number of stems in the 20–30 dgh cm class could also be indicative of a gap-phase regeneration event, and interestingly, almost coincides with the modal age of the cohort identified in the minor group. The Pouakai Range group exhibited a contrasting diameter frequency distribution to the other groups. It can be referred to as a reverse "J" distribution, typical of either balanced, self-replicating climax populations, or even-aged thinning hierarchies. Given that Pouakai is not known to have suffered any landscape-scale disturbances in recent times, a stable self-replicating climax population is the most likely explanation here. The abundance of saplings found across all the groups suggests a pattern of more or less continuous regeneration is possible for *Podocarpus*, with saplings at least being shade-tolerant, but benefiting from some gap-phase disturbance (indicated by the distributions approaching that of a cohort).

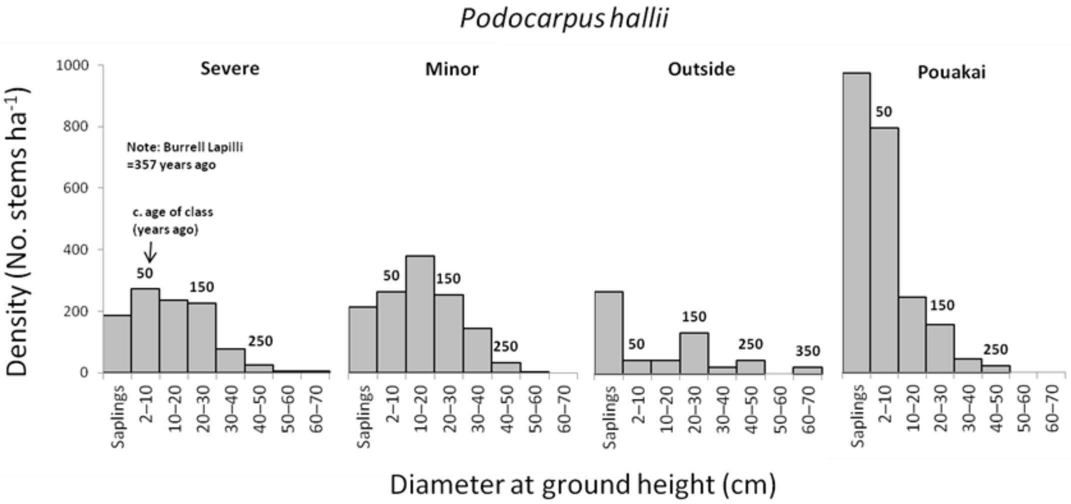

Figure 4.1: Diameter frequency distributions of *Podocarpus hallii* in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range. Numbers given above bars represent the approximate age (years ago) of the size class.

Griselinia littoralis

Griselinia displayed several different population structure trends across the groups (Figure 4.2). The diameter frequency distribution in the severe group was approaching that of a cohort distribution, with a modal size class of 10–20 cm estimated to be around 50 years old. The minor group displayed a clear reverse “J” distribution, with a far greater number of saplings present here than in the other groups. In the outside group, the population structure was discontinuous, with a young cohort present. There was a total absence of saplings in this group, but a cohort of stems in the 10–20 cm size class. The modal size of this cohort coincided with that of the cohort in the severe group, suggesting they could have potentially been initiated by the same regeneration event c. 50 years ago, (perhaps a heavy snowfall on the mountain). *Griselinia* was uncommon in the Pouakai Range group, with only saplings and one larger size class represented. *Griselinia* was similar to *Podocarpus* in that both reverse “J” and cohort distributions were present across the groups. Overall, *Griselinia* appeared to be capable of growing to slightly larger diameters than *Podocarpus*, though the maximum ages predicted for the populations were very similar (<300 years).

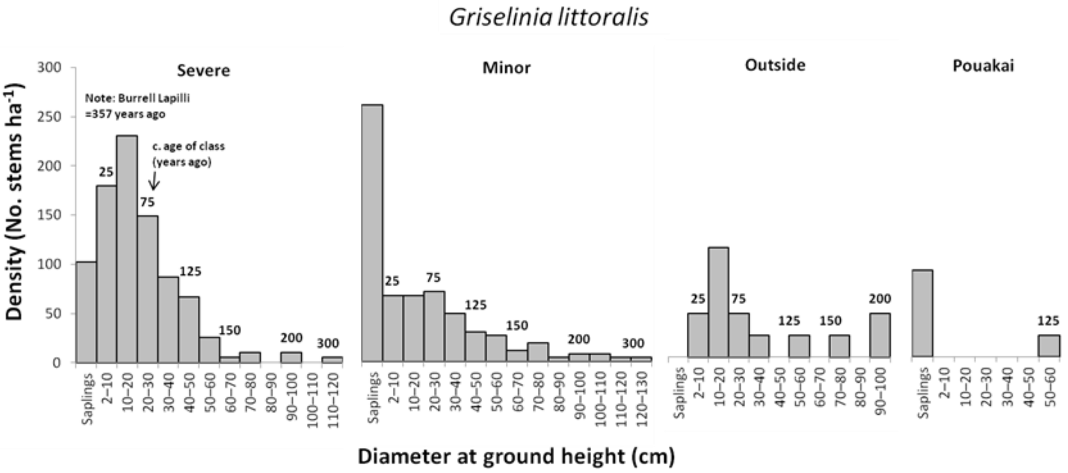

Figure 4.2: Population structure of *Griselinia littoralis* in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range. Numbers given above bars represent the approximate age (years ago) of the size class.

Libocedrus bidwillii

The population structure of *Libocedrus* (Figure 4.3) across the groups was more erratic than *Podocarpus* and *Griselinia*. In the severe group, where *Libocedrus* was uncommon, there were large discontinuities, with only three size classes represented, one of which included large stems 140–150 cm dgh estimated to be >1000 years old. These discontinuities and absence of regeneration (i.e., no juveniles) suggests that the trees present are relicts of older populations, with others individuals perhaps having been destroyed by the Burrell Lapilli. All stems >50 cm dgh here have probably survived the eruption disturbance, and were estimated to have been around 2–20 cm dgh at the time of the eruption; at this size, they may have survived the eruption because they were not emergent, and thus would have had some protection from the lapilli fall. The minor group was markedly different, displaying a pronounced cohort of stems about the 30–40 cm dgh size class, estimated to be around 350 years old; a discontinuity at 60–70 cm; and then another smaller cohort of stems 70–100 cm dgh estimated to be >600 years old. This bimodal cohort distribution, may be indicative of two separate waves of regeneration having occurred in the past. It is highly likely that the c. 350 year old cohort was initiated by the Burrell Lapilli disturbance 357 years ago, and reflects the light demanding nature and catastrophic regeneration strategy of this species. The age of the older cohort suggests it has survived through the Burrell eruption, and was likely initiated by a previous wide-scale disturbance.

The minor group was the only group where any *Libocedrus* saplings were recorded, and if these stems survive, they will represent a small but significant wave of regeneration in this area. In the outside group, there were no stems represented in any classes <100 cm dgh, which suggests that no regeneration has occurred for several hundred years; only the remnants of one or two relict cohorts exists. The Pouakai Range group also exhibited the remnants of one or two cohorts, though they were of a smaller, younger size than the outside group and thus the disturbances initiating these two cohorts are probably unrelated.

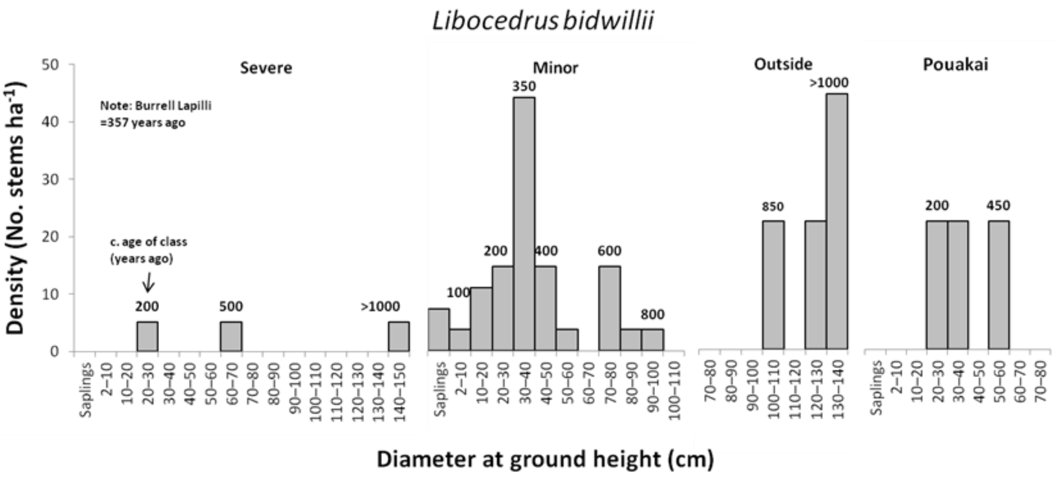

Figure 4.3: Population structure of *Libocedrus bidwillii* in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range. Numbers given above bars represent the approximate age (years ago) of the size class. Note that the x-axis of the outside group graph is abridged due to an absence of stems in the smaller classes.

Weinmannia racemosa

Weinmannia (Figure 4.4) was virtually absent from the severe group, with only a few saplings present. In the minor group, the species was only slightly more common and exhibited a reverse "J" distribution. Most of the stems in this group were thought to be <100 years in age, and thus have either colonised quite recently, or are struggling to compete. In the outside group, *Weinmannia* was much more abundant and displayed a strong cohort distribution with a modal size class of 10–20 cm and an absence of any saplings; though stems were still relatively young. In the Pouakai Range group, it could be possible that either two overlapping cohorts are present (perhaps relating to gap-phase regeneration), or alternatively, there is a continually recruiting all-aged population with only a low level of sapling mortality. Given that a strong cohort was present in the outside group, perhaps two overlapping cohorts is the most likely explanation. A few larger stems present in the 90–100 cm and 150–160 cm classes suggest that at least some *Weinmannia* individuals are capable of obtaining a large size and age (>300 years) at the treeline.

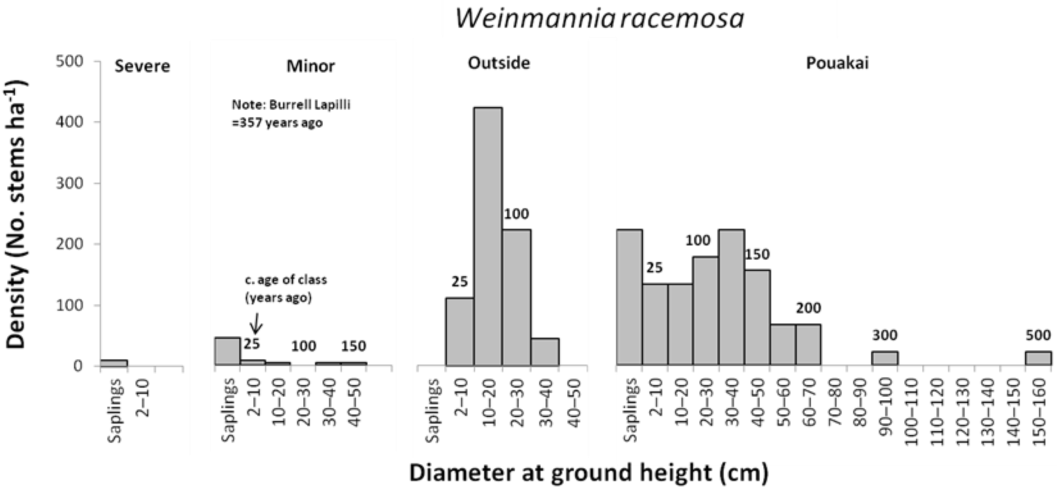

Figure 4.4 Population structure of *Weinmannia racemosa* in the four quadrat groups at the treeline position on Mt Taranaki and the Pouakai Range. Numbers given above bars represent the approximate age (years ago) of the size class.

4.3.2 Light requirements

Across the 360 sample points, a combined total of 844 occurrences of 15 species were recorded in the two juvenile height classes. Only the seven most common species are reported here, with a focus on the canopy dominants. The results are presented first as the distribution of light environments (percentage canopy openness) occupied by each species without differentiating between size classes, and second, the intraspecific variations between size classes are examined. The forest understory light environments were log-normally distributed in the canopy openness range of 1%–64%; and each of the seven species also occupied an approximately log-normal distribution of light environments (Figure 4.5). Highly significant interspecific differences were detected (F = 26.3; d.f. = 7, 1252; P < 0.001).

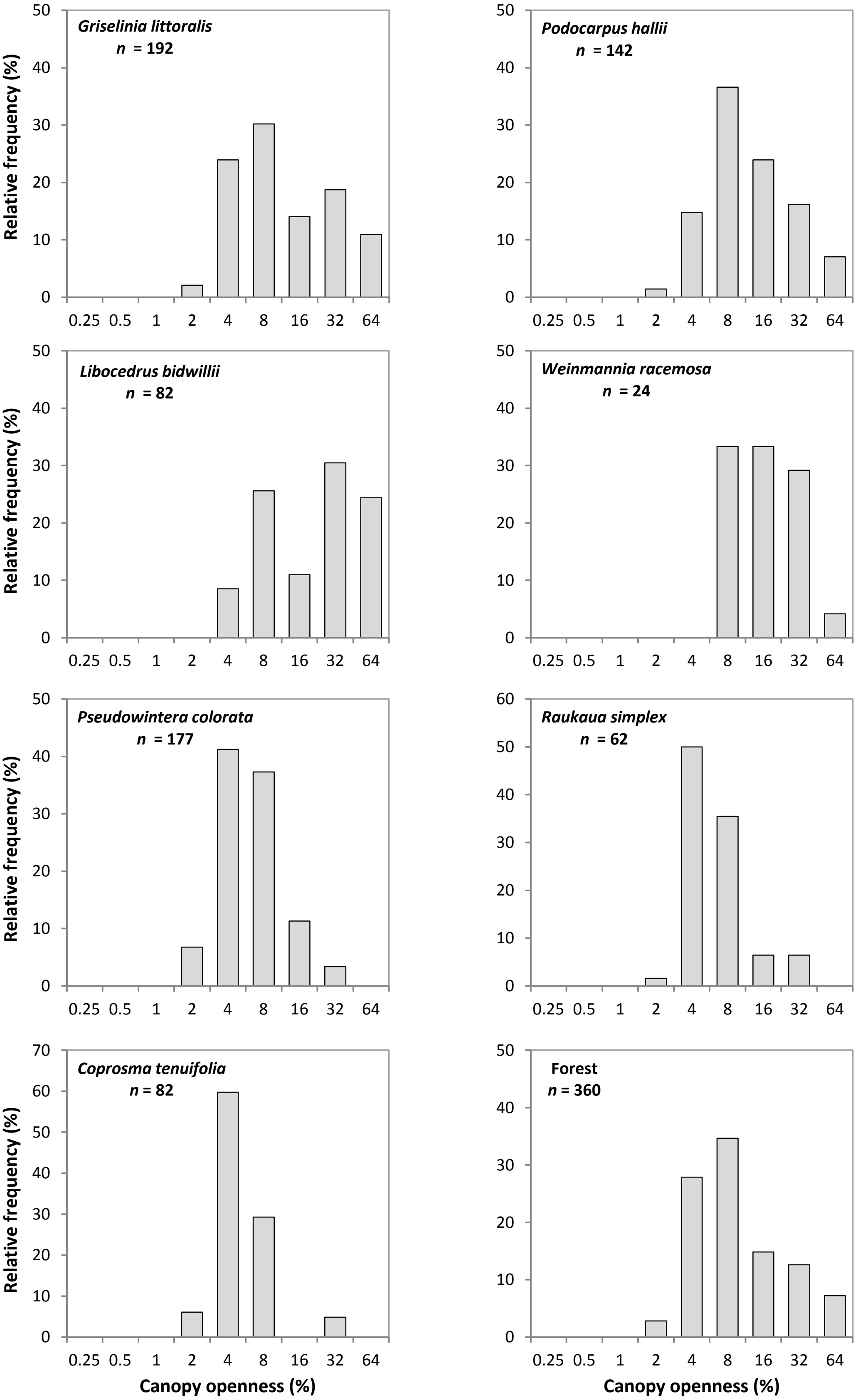

Figure 4.5: Relative frequency distributions of light environments (percentage canopy openness) occupied by juveniles of seven species at the treeline of Mt Taranaki. 'Forest' shows the distribution of a random sample of light environments in the forest understory.

Of the species reported here, the most shade-tolerant (i.e., lowest minimum light requirement) was *Coprosma tenuifolia*, closely followed by *Pseudowintera* and *Raukaua*, with minimum light requirements of around 2.5% canopy openness (Figure 4.6). These species' distributions showed little interspecific variation (P = NS); but were distributed in light levels significantly lower than that of the average forest understory ($P < 0.001$), and displayed the narrowest inter-quartile ranges. This suggests that these three shade-tolerant species were constrained to occupying the same, narrow, low-light niche (c. 4% canopy openness), which was too dark to be tolerated by the other species. The average (geometric mean) forest understory light environment was c. 7% canopy openness. Light environments occupied by *Podocarpus* and *Weinmannia* did not differ significantly from the average forest understory light ($P = 0.10$; 0.57 respectively), or from each other ($P = 0.48$), despite their slight bias towards higher than average light levels.

Both *Griselinia* and *Libocedrus* were found in significantly higher light environments than the average forest understory ($P < 0.01$; 0.001 respectively), and were also significantly different from each other ($P < 0.001$). *Griselinia* exploited the widest niche breadth, distributed evenly about the average forest understory light level. *Libocedrus* displayed the highest geometric mean of all species surveyed (10.5% canopy openness), implying it was probably the most light demanding (i.e., shade-intolerant); although the 10th percentile values would suggest it was slightly more shade-tolerant than *Weinmannia*, the species displaying the highest minimum light requirement value (5.5% canopy openness).

Considering both the geometric mean and 10th percentile values of the distributions of light environments occupied, species can be ranked in order from most shade-tolerant to least shade-tolerant (i.e., light demanding) as follows: *Coprosma tenuifolia* > *Pseudowintera* > *Raukaua* > *Griselinia* > *Podocarpus* > *Weinmannia* > *Libocedrus*. Forest light levels have been presented here as percentage canopy openness values, though this parameter does not take the polar orientation of canopy gaps (i.e., solar tracks) into consideration. It is expected that a north facing gap in the canopy would supply a higher level of direct irradiance to the forest floor than a gap of the same size facing towards the south; though the amount of diffuse light availability would probably remain the same (Poulson & Platt 1989; Lusk et al. 2009). Because all hemispherical photographs were oriented to the north, the GLA software has the ability to place a higher weighting on north facing gaps by using solar tracts to calculate the percent total light transmitted to each site (includes both direct and diffuse irradiance). When these calculations were undertaken, although subtle differences occurred in the results compared with the percentage canopy openness data, the ranking of species from most shade-tolerant to most light demanding remained largely unchanged.

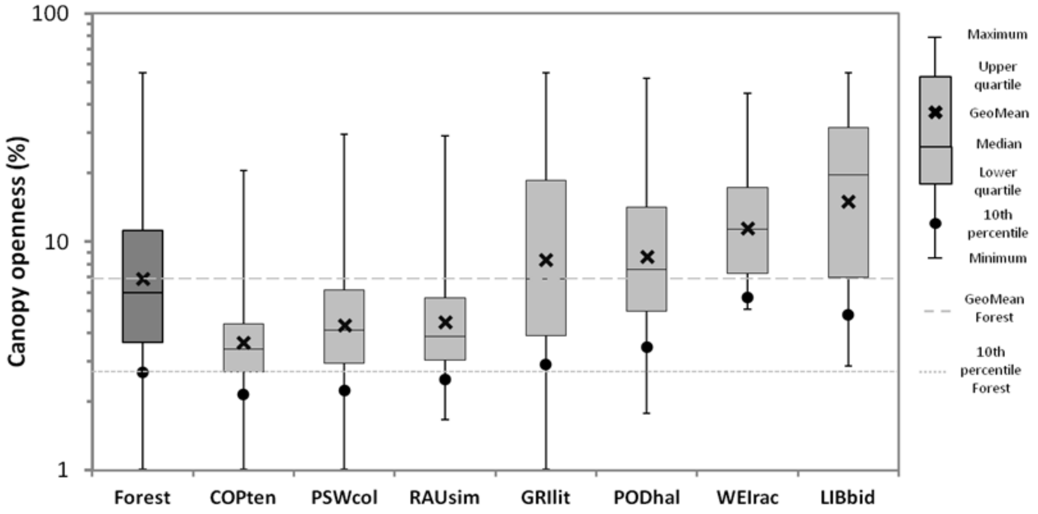

Figure 4.6: The distribution of forest light environments (percentage canopy openness) occupied by juveniles of seven species at the treeline of Mt Taranaki. 'Forest' shows the distribution of a random sample of light environments in the forest understory. The 10th percentile of the distribution of canopy openness occupied by each species (circles) was used as an approximation of the minimum light levels tolerated. 'GeoMean' (crosses) show the geometric mean, a suitable measure of central tendency given all data were approximately log-normally distributed.

The final analysis of this data involved using the seedling height classes to determine whether or not any intraspecific ontogenetic changes in light requirements were occurring. The minimum light requirement for small (5–50 cm high) and large (50–150 cm high) seedlings of each species were compared, but no significant differences were detected between height classes in any of the species (Figure 4.7); suggesting that these species' light requirements probably do not differ with ontogeny.

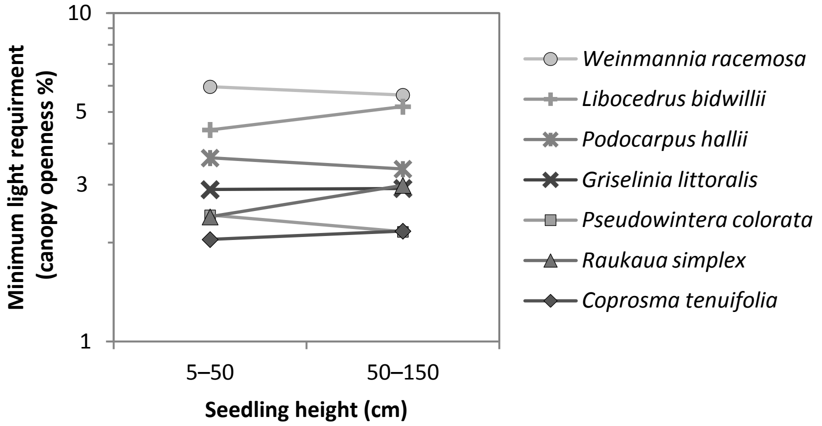

Figure 4.7: Minimum light requirements of two juvenile size classes of seven species from the treeline of Mt Taranaki. None of the species exhibited a significant change in light requirements across size classes: *Weinmannia* (F = 0.03; d.f. 1, 22; P = 0.85), *Libocedrus* (F = 0.01; d.f. 1, 80; P = 0.90), *Podocarpus* (F = 0.52; d.f. 1, 140; P = 0.47), *Griselinia* (F = 0.64; d.f. 1, 190; P = 0.42), *Pseudowintera* (F = 2.0; d.f. 1, 175; P = 0.15), *Raukaua* (F = 0.06; d.f. 1, 60; P = 0.80), *Coprosma tenuifolia* (F = 1.6; d.f. = 1, 80; P = 0.20).

4.4 Discussion

The population structures observed for canopy species *Podocarpus*, *Griselinia*, *Libocedrus* and *Weinmannia* at the treeline of Mt Taranaki can be largely explained by the results of the investigation into the light requirements of each species. *Libocedrus* was found to be the most shade-intolerant species, and consequently displayed a strong cohort population structure indicative of its requirement for a catastrophic canopy-opening disturbance to regenerate. As a result of their inability to tolerate shaded sites, population structures showed that virtually no juvenile *Libocedrus* were found within the closed canopy of treeline vegetation. The estimated age of the main *Libocedrus* cohort found in the area which received minor damage from the Burrell Lapilli (1–20 cm lapilli) strongly suggests that it arose as a result of increased light levels shortly after the Burrell eruption. However, in areas severely affected by the Burrell Lapilli (20–40 cm lapilli) no such *Libocedrus* cohort was initiated, despite light levels probably being more than sufficient for regeneration. This was possibly because of the significant change in substrate which *Libocedrus* could not tolerate, or competitive exclusion by other more light demanding pioneer species. It is also possible that the prevailing southerly winds on this side of the mountain may have greatly inhibited the dispersal of *Libocedrus* seed onto the devastated areas, and/or the timing of the eruption may not have coincided with seed release. Outside the

Burrell Lapilli distribution, it would appear that older cohorts of *Libocedrus* are in the process of senescing, with a major disturbance to initiate mass regeneration not having occurred at all in the last 800–1000 years.

The stand dynamics of *Libocedrus* have possibly been more studied than any other conifer species in New Zealand, with a myriad of papers from across the country supporting the notion that (1) *Libocedrus* regenerates in dense even-aged stands following massive disturbance, (2) its juveniles are unable to mature under a closed canopy, and (3) long-lived cohorts eventually succumb to synchronous senescence after around 600–1000 years (Clayton-Greene 1977; Wardle 1978; Stewart & Veblen 1981; Veblen & Stewart 1982; Norton 1983; Haase 1986; Boase 1988; Stewart & Rose 1989; Rogers 1989; Palmer & Xiong 2004; Ogden et al. 2005). Much of this research was stimulated in response to a now largely rejected theory proposed by several authors (e.g., Holloway 1954; Wardle 1963) who attributed the ‘regeneration gap’ observed in New Zealand conifers to a period of lacking or insufficient regeneration caused by climatic deterioration with a shift to cooler dryer climates.

Results of the light requirement investigation suggest that *Weinmannia*, like *Libocedrus*, is very light demanding, though the sample size for this species was small in comparison with the other species surveyed, and thus results are interpreted with caution (n = 24 cf. n = >62 for all other species). The population structure for *Weinmannia* outside of the Burrell Lapilli distribution on Mt Taranaki reveals a cohort of even-aged stems and absence of regeneration, which agrees with the shade-intolerant finding. On the Pouakai Range however, more of an all-aged *Weinmannia* population was present; possibly interpreted as either two regeneration events (overlapping bimodal distribution of stems), or alternatively that the species is reasonably shade-tolerant with continual regeneration occurring. A review of other studies presenting *Weinmannia* population dynamics gives somewhat conflicting views on its light requirement status. All-sized or all-aged population structures have been reported for *Weinmannia* by Stewart & Veblen (1981), Lusk & Ogden (1992) and Lusk & Smith (1998), which suggests that perhaps this species is more shade-tolerant than the present study’s findings would imply. In contrast, Ogden et al. (2005) refer to *Weinmannia* as “quite light demanding” and Smale & Kimberley (1993) reported strong cohort distributions and suggested it had intermediate shade tolerance with seedlings being suppressed and incapable of regenerating effectively beneath their own canopy. Smale & Smale (2003) have suggested that *Weinmannia* is solely a coloniser of forest gaps, and use it as a marker (indicator) species along with *Griselinia* to signify the position of previous openings in a forests canopy. Lusk & Smith (1998) note that the establishment of *Weinmannia* is dependent on the availability of suitably elevated substrates (e.g., fallen logs, tip-up mounds, tree ferns) as much as the occurrence of canopy gaps. Such elevated sites were overlooked by the method in the present study. However, given the short stature and patchy cover of treeline forest on Mt Taranaki, such elevated sites may not be as vital for *Weinmannia* regeneration at this location, with terrestrial regeneration being equally possible (pers. obs.).

At the treeline elevation, the response of *Weinmannia* to the Burrell Lapilli disturbance was not that expected for a light demanding species; where vegetation was damaged by the eruption, this species was virtually absent. This probably relates to its inability to compete with other more cold-tolerant light demanding species in an exposed setting so close to its upper altitudinal limit. There would have surely been an abundance of elevated sites (e.g., snags) for it to epiphytically establish on after the eruption, but it appears to have not been capable of taking advantage of these. In lower altitudinal forest however, *Weinmannia* is known to have proliferated after the eruption, a result of both its ability to resprout epicormically, and the copious amount of light wind dispersed seed it produces (Clarkson 1995). Veblen & Stewart (1982) also note its ability to regenerate abundantly on recently devastated sites elsewhere. As with *Libocedrus*, this illustrates the importance of variables other than shade tolerance in determining how vegetation responded after the eruption. At the treeline elevation, competitive interactions also involve the hardiness and resilience of species to the sub-alpine climate (i.e., interspecific differences in upper altitudinal limits), as well as their ability to tolerate drastically altered substrates.

There was little difference in light requirements detected between *Podocarpus* and *Griselinia*, although both were somewhat more shade-tolerant than *Libocedrus* and *Weinmannia*. Despite this, *Podocarpus* and *Griselinia* were most abundant at treeline areas where the Burrell Lapilli damaged vegetation, perhaps an indication of their tolerance to variables other than shade (e.g., substrate, exposure). Interestingly, seed of both these species are bird (as opposed to wind) dispersed, which could indicate that prevailing winds may have made it difficult for some species to colonise up the mountain from intact forest at lower elevations. The population structure of *Podocarpus* partially agreed with the intermediate shade-tolerance finding from the survey. *Podocarpus* juveniles were common, but distributions did approach that of a cohort; indicating both the shade-tolerance of the juveniles and their positive response to increased light levels. The *Podocarpus* cohort apparent on Mt Taranaki was weak in comparison with that of *Libocedrus*, and modal stem age suggests it may relate to a gap-phase event more recent than the Burrell Lapilli, perhaps something occurring around 100–150 years ago. Major storm and snowfall events on the mountain cause significant damage to vegetation (pers. obs.), and such events increase light levels on the forest floor perhaps releasing seedlings and saplings. On the Pouakai Range, lacking any recent volcanic disturbance, the population structure of *Podocarpus* was of the reverse "J' type, typical of a stable self-replicating climax population as would be expected. Rogers (1989) and Veblen & Stewart (1982) also noted the shade-tolerating ability of *Podocarpus,* reporting steady-state reverse "J" distributions analogous with the pattern observed on the undisturbed Pouakai Range. Smale & Kimberley (1993) reported erratic population structures in *Podocarpus*, and Smale & Smale (2003) ranked the species as having intermediate shade-tolerance, suggesting that juveniles can persist under a closed canopy, but remain suppressed until a suitable canopy thinning allows them to mature. According to Enright & Ogden (1995) *Podocarpus* may have a lifespan over 600 years, with some individuals reaching over 1000 years, though Smale & Kimberley (1993) predict a maximum age of 750 is most likely. On Mt Taranaki, all *Podocarpus* stems were thought to be younger than the Burrell eruption (with the majority having arisen around 150 years after the eruption), thus perhaps this species has only become more abundant in the years following the eruption, or its lifecycle-turnover is much shorter than reported at other locations. In a close parallel with this finding, Clarkson & Clarkson (1995) noted that at c. 1000 m elevation on Mt Tarawera, in areas devastated by the AD 1886 eruption, *Podocarpus* was only just beginning to colonise c. 110 years after the eruption; with facilitation by *Coriaria* (and to a lesser extent *Griselinia*) thought to be important factors for its arrival. Ogden (1985) suggests that dense stands of podocarps can become common after fire, and certainly *Podocarpus* is abundant in areas damaged by the Burrell Lapilli.

Griselinia was found to be marginally more shade-tolerant than *Podocarpus*, but of all species, it occupied the widest range of light regimes, coinciding with the distribution of random forest understory light. The population structure of *Griselinia* was cohort like in the area severely affected by the eruption, but reverse “J” shaped in character where effects were minor. A cohort of stems was also present outside the eruption zone, but saplings were virtually the only size class present in the Pouakai Range group. *Griselinia* is predicted to live for c. 450 years (Smale & Kimberley 1993), and no stems older than c. 300 years were identified on Mt Taranaki. In areas affected by the Burrell Lapilli (where *Griselinia* was most common), stems were thought to mostly be <150 years old; although this could imply that this species has not colonised till several hundred years after the volcanic disturbance, other studies have reported phenomena for *Griselinia* that seem applicable to Mt Taranaki, and could provide an explanation for its distribution and abundance. Smale & Smale (2003) treat *Griselinia* as a sole coloniser of forest gaps, and indicate the species’ preference to colonise epiphytically at montane sites. At the treeline elevation, *Griselinia* is thought to be more resilient to climate extremes than the other epiphytic establisher *Weinmannia*, because it displays a higher altitudinal limit (Clarkson 1977); and thus following the Burrell Lapilli deposition, it is probable that *Griselinia* would have readily colonised onto brightly lit snags present in areas damaged by the eruption. Assuming that this occurred, then why are the *Griselinia* found in the eruption zone mostly <150 years old? Smale & Kimberley (1993) provide the likely explanation. Senescent *Griselinia* commonly replaces itself *in situ*; site occupation and canopy residence is thus prolonged indefinitely. This occurs because *Griselinia* continues to establish epiphytically in the crowns of senescing parent trees, thus maintaining its dominance. Smale & Kimberley (1993) and Lusk & Smith (1998) have reported reciprocal regeneration cycles that occur between *Weinmannia* or *Griselinia* and *Podocarpus,* the broadleaved species capturing gaps formed by *Podocarpus* wind falls, the later, in turn, regenerating beneath the thinning crowns of older *Weinmannia* and *Griselinia*. This process could also be occurring on Mt Taranaki, given the number of years since the last major volcanic disturbance; the majority of *Podocarpus* are probably several hundred years older than *Griselinia*.

The three other species included in the light requirement survey, *Coprosma tenuifolia*, *Pseudowintera* and *Raukaua*, were found to be equally shade-tolerant, with their minimum light requirements suggesting they are capable of surviving in quite deep shade. Population structures for these species (not presented here) were all of the reverse “J” type, confirming their ability to regenerate continuously below a closed canopy. This may be the main reason why these species were among the most common understory and seedling constituents at the treeline position.

The average (geometric mean) light environments occupied by species in this study were generally found to be higher than those reported for other New Zealand species by Lusk et al. (2009) in a lowland podocarp-broadleaved forest (600 m asl). Treeline species’ distributions on Mt Taranaki averaged around 5%–15% diffuse light availability, while all species reported by Lusk et al. (2009) averaged around 1.5%–3%. Furthermore, they reported the average forest light level at their site was 1.5% diffuse light availability, compared with 10% at the treeline of Mt Taranaki. This difference probably results from the low canopy stature (<10 m) of montane vegetation on Mt Taranaki compared with their taller (20 m) lowland forest site. Taller forest generally has a greater number of vegetation tiers, and thus more light is probably intercepted before reaching the forest floor. The harsher climatic conditions on Mt Taranaki could also prevent species from surviving in as lower light regimes at the more hospitable lowland site. With regards to intraspecific ontogenetic variation in light requirements, Lusk et al. (2008) has found that shade-tolerance differences between Chilean evergreens become increasingly apparent with increasing size, (particularly between the size classes of 50 cm and 120 cm high), but no such ontogenetic variation was detected for any species at the treeline of Mt Taranaki. It is possible that light levels at the Mt Taranaki survey site were not dark enough for species to exhibit such ontogenetic variations.

This study has shown that the light requirements of species can largely explain the population structures exhibited, but these interspecific differences in light requirement alone cannot fully explain the vegetation patterns observed across the Burrell Lapilli distribution at the Mt Taranaki treeline. The Burrell Lapilli disturbance was much more complex than a typical canopy opening disturbance (e.g., windthrow), because of the extreme alteration/addition of substrate involved and the widespread physical damage that would have been inflicted. Other competitive interactions involving interspecific physiological differences in climate tolerance, response to physical damage, dispersal/establishment mechanisms and substrate requirements could have played equally important roles in shaping the vegetation.

Chapter Five: Synthesis

5.1 Discussion

This research has examined treeline vegetation composition, structure and dynamics across the AD 1655 Burrell eruption lapilli deposit on Mt Taranaki. Winter temperature measurements across the study site suggested that no major temperature anomalies occur around the mountain, and thus any differences detected in the vegetation are more likely to be related to some other variable. The major differences detected in treeline vegetation are attributed to both the presence and thickness of the Burrell Lapilli deposit. The current thickness of lapilli in the soil profile is considered as a proxy for the degree of vegetation damage that would have been inflicted at the time of the eruption. Lapilli deposits with a thickness of 20–40 cm were deemed to have had a severe effect on the vegetation, while deposits of 1–20 cm would have had a minor effect. It is likely that in locations severely affected by the Burrell Lapilli, large openings in the canopy would have been created as vegetation was mechanically and chemically stripped off by falling lapilli, resulting in the widespread death of many trees and drastically altering the substrate. This stimulated widespread regeneration, indicated by the higher density of trees supported within the Burrell Lapilli distribution than outside; while basal area displays the inverse trend, suggesting that self-thinning is yet to complete.

Current treeline vegetation in areas severely affected by the Burrell Lapilli was characterised by *Podocarpus* and snags emergent over a canopy of *Griselinia*. Results suggest *Griselinia* is less common outside of the distribution of Burrell Lapilli. *Griselinia* has probably increased in importance after the eruption due to its ability to colonise epiphytically on brightly lit snags, and once established, has remained dominant there due to its *in situ* mode of regeneration whereby seedlings establish epiphytically in parent trees. *Weinmannia*, another species with potential to epiphytically regenerate, was probably not capable of exploiting this opportunity because its upper altitudinal limit is lower than that of *Griselinia*, and thus it could not tolerate the climatic conditions of exposed sites at this elevation. *Podocarpus* appears to be maintaining its dominance by regenerating below the *Griselinia* canopy, perhaps with the aid of small openings in the canopy caused by mechanisms such as snowfall damage and windthrow. Estimated ages for *Podocarpus* here suggest it is likely that it did not colonise immediately after the eruption, instead requiring a period of c. 150 years to establish; probably time for suitable substrate to form as lapilli was removed by erosion and soil developed. The state of decay of many of the snags present in treeline vegetation suggest they probably died as a result of the Burrell eruption, and certainly emergent trees at the time would have suffered the most direct impact from the lapilli. However, natural senescence or possum damage can not be fully ruled out as possible explanations for the deaths.

Where the effects of the Burrell Lapilli were minor, a different vegetation type characterised by *Podocarpus*, *Libocedrus* and snags emergent over *Griselinia* was present. *Libocedrus* is highly light demanding, and canopy damage inflicted by the lapilli is thought to have initiated widespread regeneration of *Libocedrus* in this area, creating an even-aged cohort population coinciding with the eruption event. Where the effects of the eruption were more severe, although light levels would have been suitable for *Libocedrus*, it did not succeed due to either (1) intolerance of the substrate, (2) competition with other species, or (3) absence of seed bank or seed dispersal. Prevailing southerly winds on this side of the mountain may have greatly inhibited the dispersal of *Libocedrus* seed onto the devastated areas, and/or the timing of the eruption may not have coincided with seed release.

Outside of the Burrell Lapilli distribution on Mt Taranaki, *Weinmannia* was a common canopy constituent in treeline vegetation, along with *Libocedrus*, *Podocarpus*, and *Griselinia*. Consequently, it is likely that *Weinmannia* has been suppressed from the treeline area affected by the Burrell eruption, and has yet to regain lost ground. Given the time that has elapsed since the eruption, the successional trajectory of the vegetation has probably been altered such that it may never regain its previous dominance there, perhaps because of suppression by more competitive species or due to the effects of introduced browsing mammals (goats, possums) which preferentially feed on this species. *Weinmannia* has a higher upper altitudinal limit outside the Burrell lapilli distribution on Mt Taranaki, and higher again on the undisturbed Pouakai Range. This may imply that areas damaged by the eruption were too exposed for *Weinmannia* to re-establish, whereas outside the eruption zone, other species have provided shelter, permitting it to advance higher up the mountain (perhaps in a time before the introduction of browsing mammals). The *Libocedrus* present outside the Burrell Lapilli distribution were thought to be much older than those found within the eruption zone, and were displaying a degree of cohort senescence. Because the Burrell Lapilli did not damage any vegetation here, no *Libocedrus* regeneration was initiated, with the population probably relating to a different widespread disturbance event occurring around 1000 years ago.

On the Pouakai Range, treeline vegetation was largely dominated by *Weinmannia*, with lesser amounts of emergent *Podocarpus*. The *Podocarpus* population here was in a state of equilibrium, probably regenerating more or less continuously with thinning in the *Weinmannia* canopy. The *Weinmannia* also displayed ongoing regeneration, but being more light demanding than *Podocarpus*, was perhaps capitalising on bigger canopy openings associated with disturbances such as windthrow. Some relicts of >1000 year old *Libocedrus* cohorts were also present on the Pouakai Range, but *Libocedrus* was more common above the treeline position (i.e., in shrubland) than on Mt Taranaki. Understory species *Myrsine salicina* was also abundant at the treeline on Pouakai Range, but was largely absent from areas affected by the Burrell eruption, and only occurred rarely outside the eruption zone on Mt Taranaki.

The current stature of the treeline ecotone vegetation suggests that *Podocarpus* is not capable of attaining as taller emergent heights as *Libocedrus*, despite the two species having similar upper altitudinal limits. Consequently, maximum heights of *Libocedrus* decrease at a faster rate with increased elevation across the treeline ecotone, compared with a more gradual rate with *Podocarpus*. The fact that *Libocedrus* is capable of attaining such emergent heights at the treeline partially explains its suppression from areas severely affected by the Burrell Lapilli; its exposed foliage above the surrounding canopy would have suffered a very direct impact from the lapilli shower, as there was no trees above it to offer any protection. Another possible reason why *Libocedrus* was suppressed relates to its resprouting capabilities, with are thought to be much poorer than *Podocarpus* following browse by possums; perhaps the same is true following lapilli shower damage. With increasing elevation across the treeline ecotone, the maximum diameter of trees has also been shown to reduce, probably as a result of physiological growth limitations common at this altitude. Spatial configuration of stems across the treeline ecotone indicates that larger canopy trees are mostly dispersed evenly, but around these trees, other smaller stems appear to be suppressed to a degree. Clusters of smaller stems (mostly *Pseudowintera* and *Coprosma tenuifolia*) were found to occur in gaps away from the larger canopy trees. Also, *Raukaua* stems were often found in close proximity to a structurally supporting stem. An examination of seedling and sapling composition across the treeline areas described here suggests that in the near future at least, the canopy compositional differences will remain; that is until another large scale disturbance such as a volcanic eruption alters the successional trajectory of the vegetation once more.

This study has contributed to the understanding of vegetation patterns that ensue on areas affected by tephra eruptions, and several of the findings may have relevance in locations elsewhere in New Zealand and the world. When tephra falls occur, emergent species suffer a much more direct impact than those species with shelter (i.e., having foliage beneath the canopy), and thus emergent species are the most likely to be deleteriously affected. Consequently, understory species would probably suffer less damage, as tephra is intercepted by higher vegetation stratums and its momentum is reduced. The ability of species to recover (resprout) following mechanical striping of foliage by tephra (for which few examples exist), could perhaps be considered analogous with recovery following severe mammalian browse (for which more information probably exists); and species capable of coppicing probably have a better chance of recovering from tephra damage than those which are not. The light requirements of species are also an important consideration, given that tephra showers act to open forest canopies, in turn increasing the amount of light reaching the forest floor and potentially permitting light demanding species to proliferate. Tephra falls can be considered as less devastating events in comparison with some other volcanic disturbances (e.g., pyroclastic flows, blow downs, lava flows), in that they can potentially kill large areas of vegetation in such a way that most dead trees would remain standing and largely intact. If substrates are drastically altered with the addition of tephra to the extent that plants cannot immediately colonise, such snags could still provide brightly lit sites for the regeneration of epiphytically establishing species (of particular relevance to high humidity environments where epiphytes thrive). Perhaps most importantly, this study has demonstrated that even after a considerable lapse of time following a tephra eruption, the successional trajectory of vegetation in affected areas can be markedly different to unaffected locations in close proximity, and it is likely that in the absence of further disturbance, such anomalies will persist.

5.2 Recommendations for future research

In order to gain a greater understanding of the determinants of compositional differences in vegetation across the Burrell Lapilli deposit, it would be beneficial to conduct experiments with the key canopy species to determine (1) relative growth rates of juveniles, (2) how they respond to mechanical and chemical damage, (3) their potential to survive and grow up (or germinate) through different thicknesses of tephra, and (4) their potential to establish on top of different thicknesses of tephra. Dendrochronological studies of trees on Mt Taranaki would also allow more accurate age estimates of individuals and populations in relation to eruption events. A more extensive study, examining vegetation differences across the Burrell Lapilli deposit at a range of elevations other than the treeline (e.g., herbfield, shrubland, montane forest, lowland forest) could further explain other vegetation patterns across Mt Taranaki. In approximately 10 years time, it would be appropriate to re-measure some of the quadrats and belt transects from this study to verify the predictions on lack of convergence made by the present study.

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Appendices

Appendix 1: Basal area (m^2 ha^{-1}) of species >2 cm dgh in the thirty-eight 10 × 15 m quadrats at the treeline position of Mt Taranaki and Pouakai Range. Site attributes of quadrats are summarised in Table 2.5.

Plot #	PODhall	PODhall Dead	GRIlit	LIBbid	LIBbiddead	PSWcol	RAUsim	BRAele	MYRdiv	COPten	COPdum	COPgra	COPpse	HEBegm	HEBegm DEAD	PSPcol	CARser	FUCexc	ARIser	MELlan	SCHdig	CYAsmi	CARcun	PITten	ALSmac	OLEarb	RUBcis	DRAfil	WEIrac	MYRsal
1	22.2	102.6	40.3	-	-	3.3	-	-	-	1.5	-	6.1	-	0.7	-	1.5	3.9	-	3.6	2.1	3.5	1.3	-	-	0.0	-	-	-	-	-
2	53.4	-	32.2	-	-	3.8	0.7	-	2.2	0.9	-	6.6	-	-	1.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	40.6	-	43.4	-	-	0.3	9.6	7.5	0.8	0.3	0.2	0.4	0.2	0.1	-	2.2	-	-	-	-	-	-	0.7	-	-	-	-	-	-	-
4	76.4	-	9.1	-	-	11.6	1.2	-	0.8	7.2	0.1	5.8	-	2.5	-	-	-	-	-	-	-	6.5	-	-	-	-	-	-	-	-
5	30.4	-	34.2	-	-	8.3	19.1	-	2.1	0.3	0.8	4.0	-	3.0	-	9.2	-	-	-	-	-	11.9	-	-	0.2	-	-	-	-	-
6	7.8	-	50.5	45.6	108.1	7.8	7.2	22.4	-	0.8	2.1	0.3	1.0	15.4	-	-	-	-	-	-	-	-	-	-	-	3.5	-	-	-	-
7	48.8	-	45.7	-	-	2.1	8.5	24.3	0.9	3.3	6.0	0.2	-	2.3	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-
8	74.2	-	41.5	-	-	3.2	0.1	4.7	0.9	2.3	4.1	1.3	-	1.4	-	0.2	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-
9	6.3	77.5	12.8	-	-	12.5	0.1	-	0.6	6.7	2.3	-	-	4.3	-	-	-	-	8.2	-	-	-	-	-	-	-	0.0	-	-	-
10	41.1	4.0	124.5	-	-	16.4	4.6	-	0.7	1.1	0.7	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	68.9	-	33.3	-	-	13.0	12.2	1.9	1.6	0.6	1.1	-	-	-	-	1.3	-	-	-	-	-	-	-	-	-	-	0.3	-	-	-
12	21.3	6.0	31.9	-	-	15.1	17.5	-	3.5	0.8	6.6	-	-	0.9	-	4.4	-	-	-	-	-	-	-	-	-	-	0.6	-	-	-
13	45.4	-	39.9	64.7	10.0	10.2	7.8	2.8	0.2	1.2	0.5	-	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	60.4	52.2	27.1	45.6	37.1	9.1	11.6	2.4	0.4	0.8	0.2	0.0	-	1.1	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	28.9	-	18.7	75.4	5.8	8.1	22.4	0.0	0.9	0.1	0.4	-	5.0	-	-	0.0	0.0	-	-	-	-	-	0.7	-	-	1.1	0.0	1.1	-	-
16	93.9	-	6.4	-	-	9.3	6.9	-	-	0.6	0.5	0.1	-	-	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	0.1	-
17	13.9	5.1	68.6	-	-	1.1	2.1	0.5	0.2	1.8	1.1	2.4	-	23.7	-	-	-	-	-	0.8	-	-	-	-	-	1.1	0.2	-	-	-
18	21.4	142.5	148.1	-	-	8.4	-	-	-	3.9	-	2.0	-	-	-	-	3.2	140.1	11.3	-	1.5	7.0	-	-	-	-	1.7	-	-	-
19	36.1	-	102.9	-	-	1.4	2.4	0.8	0.8	1.4	0.6	1.2	-	0.7	-	0.3	-	-	-	0.3	-	-	-	-	-	-	-	-	-	-
20	14.3	-	19.0	-	-	3.5	6.9	7.8	1.1	2.9	0.4	0.8	-	-	-	28.8	-	22.8	-	-	-	-	-	-	-	3.0	0.1	-	-	-
21	26.2	-	43.3	36.5	-	16.4	5.4	5.5	1.0	0.9	2.2	0.1	-	1.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
22	73.3	-	56.4	-	0.7	13.9	10.6	-	0.9	2.1	2.4	-	0.7	3.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23	61.8	37.6	115.0	-	29.3	18.6	0.6	-	0.3	0.7	0.7	-	-	5.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24	11.1	-	58.6	46.0	-	17.7	15.6	-	1.6	0.6	2.0	-	0.3	7.3	-	-	-	-	-	-	-	-	-	3.2	-	-	0.1	-	-	-
25	72.8	-	88.9	84.5	12.2	10.4	4.2	-	1.0	0.8	1.0	-	-	1.4	-	-	1.1	-	-	-	-	-	-	-	-	-	-	-	-	-
26	32.6	-	60.8	-	-	2.1	8.4	6.4	0.8	2.8	0.3	1.6	-	-	-	-	-	-	-	-	-	2.6	-	-	-	-	-	-	-	-
27	16.1	-	64.9	131.7	-	1.5	11.0	12.9	-	2.2	0.9	-	-	0.6	-	5.5	-	-	-	-	-	0.1	-	-	-	-	-	-	-	-
28	10.4	-	60.3	48.6	-	2.6	18.6	0.3	-	0.4	0.6	0.1	-	2.5	-	1.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	1.2	-	150.4	26.1	21.0	22.6	0.9	-	-	1.2	0.2	0.3	-	4.4	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-
30	0.3	-	19.2	-	-	2.5	-	-	0.6	0.4	-	0.0	-	-	-	-	3.4	-	-	-	0.1	1.9	-	-	-	-	-	-	72.0	9.1
31	1.0	6.5	36.8	-	-	10.0	1.2	-	-	0.2	-	6.1	-	0.9	-	-	0.7	-	-	-	0.9	31.2	-	-	-	-	0.0	-	-	8.2
32	44.5	-	17.9	-	-	3.6	3.2	-	0.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	131.3	23.2
33	10.2	-	-	22.4	10.9	1.0	0.7	-	0.5	0.1	0.6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	162.4	14.0
34	5.9	-	-	-	137.0	6.9	0.1	0.5	0.0	0.6	0.3	-	-	0.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	189.5	9.1
35	38.0	9.2	85.6	-	-	33.0	1.8	-	2.5	1.2	4.9	-	-	-	-	-	11.6	-	-	-	-	-	-	-	-	-	-	-	-	-
36	22.3	22.3	103.6	-	-	26.9	1.4	-	-	1.3	-	-	-	1.1	-	-	0.1	-	-	-	-	-	-	-	-	-	-	-	18.8	-
37	16.9	4.6	66.7	-	-	1.9	5.2	0.7	-	1.7	3.3	1.7	-	0.9	-	-	-	-	-	-	-	-	0.1	-	-	-	-	-	-	-
38	4.0	-	47.1	195.7	-	25.9	1.4	-	2.1	0.3	3.4	-	-	-	-	-	3.2	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 2: Density (stems ha^{-1}) of species >2 cm dgh in the thirty-eight 10 × 15 m quadrats at the treeline position of Mt Taranaki and Pouakai Range. Site attributes of quadrats are summarised in Table 2.5.

Plot #	PODhall	PODhall Dead	GRIlit	LIBbid	LIBbiddead	PSWcol	RAUsim	BRAele	MYRdiv	COPten	COPdum	COPgra	COPpse	HEBegm	HEBegm DEAD	PSPcol	CARser	FUCexc	ARIser	MELlan	SCHdig	CYAsmi	CARcun	PITten	ALSmac	OLEarb	RUBcis	DRAfil	WEIrac	MYRsal
1	533	67	600	-	-	1267	-	-	-	1200	-	1867	-	67	-	133	733	-	400	133	667	67	-	-	67	-	-	-	-	-
2	600	-	933	-	-	1600	67	-	200	533	-	4600	-	-	67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	1133	-	1933	-	-	267	800	600	133	533	200	400	267	67	-	400	-	-	-	-	-	-	200	-	-	-	-	-	-	-
4	800	-	467	-	-	3733	67	-	200	2600	67	1600	-	200	-	-	-	-	-	-	-	333	-	-	-	-	-	-	-	-
5	733	-	333	-	-	1400	400	-	200	333	200	2600	-	267	-	333	-	-	-	-	-	200	-	-	200	-	-	-	-	-
6	1200	-	800	667	267	3867	1600	2533	-	533	800	400	533	1467	-	-	-	-	-	-	-	-	-	-	-	533	-	-	-	-
7	1933	-	1067	-	-	1133	400	1467	67	1533	1067	267	-	200	-	-	-	-	-	-	-	-	-	-	-	-	133	-	-	-
8	1600	-	800	-	-	2867	133	200	333	1200	400	1067	-	67	-	67	-	-	-	-	-	-	-	-	-	-	267	-	-	-
9	133	333	133	-	-	2600	67	-	200	867	200	-	-	133	-	-	-	-	333	-	-	-	-	-	-	-	67	-	-	-
10	1200	67	400	-	-	2667	267	-	333	1200	133	67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
11	1533	-	67	-	-	4000	267	200	333	467	133	-	-	-	-	67	-	-	-	-	-	-	-	-	-	-	200	-	-	-
12	933	67	67	-	-	5333	800	-	600	333	933	-	-	67	-	67	-	-	-	-	-	-	-	-	-	-	467	-	-	-
13	2133	-	1267	133	67	4067	733	67	67	867	133	-	-	67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
14	1333	200	533	267	267	3533	867	200	267	467	67	67	-	67	-	133	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15	1533	-	467	267	67	3067	1800	67	133	133	333	-	133	-	-	67	67	-	-	-	-	-	200	-	-	133	67	67	-	-
16	2067	-	67	-	-	3533	333	-	-	200	200	67	-	-	-	-	67	-	-	-	-	-	-	-	-	-	-	-	67	-
17	933	67	867	-	-	533	133	67	133	933	200	1200	-	1067	-	-	-	-	-	67	-	-	-	-	-	133	200	-	-	-
18	333	67	400	-	-	2400	-	-	-	933	-	400	-	-	-	-	67	667	267	-	667	133	-	-	-	-	267	-	-	-
19	533	-	800	-	-	467	133	67	400	867	333	867	-	133	-	133	-	-	-	67	-	-	-	-	-	-	-	-	-	-
20	467	-	267	-	-	1533	333	133	267	933	67	267	-	-	-	400	-	333	-	-	-	-	-	-	-	67	67	-	-	-
21	533	-	400	333	-	4267	333	67	133	400	467	67	-	67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
22	2133	-	200	-	67	4333	400	-	200	267	333	-	67	200	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23	1600	267	200	-	67	6133	67	-	67	333	67	-	-	200	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24	933	-	533	333	-	5533	400	-	133	667	600	-	200	400	-	-	-	-	-	-	-	-	-	67	-	-	67	-	-	-
25	667	-	133	67	67	2267	200	-	67	467	200	-	-	67	-	-	67	-	-	-	-	-	-	-	-	-	-	-	-	-
26	933	-	667	-	-	1200	400	400	200	1800	133	200	-	-	-	-	-	-	-	-	-	67	-	-	-	-	-	-	-	-
27	1067	-	533	200	-	267	533	933	-	1000	333	-	-	67	-	133	-	-	-	-	-	67	-	-	-	-	-	-	-	-
28	467	-	400	200	-	1067	1533	200	-	333	400	67	-	267	-	467	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	67	-	333	200	133	3467	67	-	-	467	67	200	-	133	-	-	200	-	-	-	-	-	-	-	-	-	-	-	-	-
30	133	-	600	-	-	533	-	-	133	267	-	67	-	-	-	-	133	-	-	-	67	67	-	-	-	-	-	-	2400	333
31	67	67	333	-	-	1133	133	-	-	200	-	800	-	67	-	-	67	-	-	-	67	867	-	-	-	-	67	-	-	533
32	1867	-	67	-	-	1533	400	-	67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1133	1867
33	1133	-	-	200	67	667	67	-	267	133	200	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1000	733
34	800	-	-	-	333	2800	67	67	67	67	133	-	-	200	-	-	-	-	-	-	-	-	-	-	-	-	-	-	867	667
35	600	133	267	-	-	5200	67	-	333	267	467	-	-	-	-	-	133	-	-	-	-	-	-	-	-	-	-	-	-	-
36	133	67	133	-	-	7800	67	-	-	600	-	-	-	400	-	-	67	-	-	-	-	-	-	-	-	-	-	-	267	-
37	800	67	1000	-	-	1000	333	133	-	667	600	333	-	133	-	-	-	-	-	-	-	-	67	-	-	-	-	-	-	-
38	133	-	200	200	-	5867	67	-	133	67	467	-	-	-	-	-	133	-	-	-	-	-	-	-	-	-	-	-	-	-